

POLYZOA FROM WEST AFRICA
THE CUPULADRIIDAE
(CHEILOSTOMATA, ANASCA)



BY

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I INTRODUCTION

THE Collections from which the specimens originate have been described by Cook (1964 : 44) ; they comprise the " Calypso " Collections (Collection I from Senegal to the Bay of Biafra, Collection II from the Cape Verde Islands) ; the Marche-Marchad Collections (from Senegal) ; and the Achimota Collections (from Ghana). The Collections are rich in lunulitiform colonies belonging to the family Cupuladriidae ; 8 species occur round the west African coast, and it is estimated that approximately 2,000 colonies have been available for examination.

The lunulitiform and selenariiform types of zoarium are found among several unrelated genera of Polyzoa (see Harmer, 1926 and 1957, and Cook, 1965) ; they are both associated with sandy or muddy substrates, upon which other Polyzoa are usually unable to grow directly. Harmer (1957 : 649, 726, 885, 891 and 1009) discussed the correlation between substrate and selenariiform habit. A large number of the specimens in these Collections are known to be from a sandy or muddy bottom ; for example, those from the Achimota Collection are nearly all from stations close to, or included in, the " silty sand community " of Buchanan (1958 : 16, 26) and Bassindale (1961 : 492). Stations where the bottom is known to be of this type are marked with an asterisk in the lists of material examined. The lunulitiform zoarium

has been discussed by Waters (1921), Harmer (1926: 261 and 1957) and Lagaaij (1952: 31, 43; 1953; and 1963). Briefly it may be described as free, discoidal or subconical, with zooecia arranged in radial rows. In the Cupuladriidae each zooecium is associated with a distal vibraculum, which has a long seta.

METHODS. Colonies were treated with eau de javelle and fragments mounted dry. Others were decalcified in dilute acid, sometimes only partially, and stained to show the relationship of muscles to the calcareous parts, etc. Dry specimens were treated with trisodium phosphate solution to restore shape to shrunken chitinous parts before preparations were made.

The length of the zooecia were measured from the distal edge of the aperture to the distal edge of the next succeeding radial zooecial aperture, thus including the vibraculum.

The dimensions quoted give the range of variation of 50 measurements (where possible). Generally, measurements of the central area or of very young colonies have not been included. It is hoped to make a survey of measurements useful for specific determination, with a morphometric analysis of at least one population complex, in the near future.

The measurements made are :

Length of zooecium	Lz	Length of vibracula seta	Ls
Width of zooecium	lz	Length of vicarious seta	Lvs
Length of ancestrula		Length of operculum	Lo
(including vibraculum)	La	Width of operculum	lo
Length of vibracular opesia	Lvo	Length of opesia	Lop
Length of vicarious vibraculum	Lv	Width of opesia	lop

Definition of terms and symbols. The registration numbers of specimens in the British Museum (Zoology Department) are given thus: 1899. 7. 1 . . . ; (Palaeontological Department) thus: D 6764 . . .

Horizontal cryptocyst lamina. A porous lamina, formed from fused cryptocystal denticles, extending from the descending cryptocyst across the opesia, parallel to, and below, the frontal membrane.

Vestibular arch. The distal, raised portion of the aperture. Usually accompanied in the Cupuladriidae by a pair of distal cryptocystal denticles.

Vicarious vibraculum. A large vibracular individual, taking the place of a zooecium, and itself having a distal vibraculum.

In the lists of material examined, the presence of vicarious vibracula is indicated thus: (V); of Acrothoracid Cirripedes thus: (C), see p. 194; and of a sandy or muddy substrate thus: *.

2 CUPULADRIIDAE Lagaaij

Cupuladriidae Lagaaij, 1952: 31. Cook, 1965: 154.

The series of species described below links the membraniporan forms assigned to *Cupuladria* with the microporan forms represented by *Discoporella*, and both genera have therefore been placed in the family Cupuladriidae.

Diagnosis. Lunulitiform *Anasca* with vibracula alternating with zooecia in the same radial series. Ancestrula surrounded by seven zooecia and a distal vibraculum. Cryptocyst variously developed. Ovicells absent.

The systematic position of the two genera here included in the Cupuladriidae has been discussed by Canu & Bassler (1923 : 75), Harmer (1926 : 266), Hastings (1930 : 714, 717), Lagaaij (1952 : 32, and 1953), Marcus & Marcus (1962), and Cook (1965 : 154). Bassler (1953) placed *Cupuladria* in the Membraniporidae (p. G 156) and *Discoporella* in the Calpensiidae (p. G 171), but the small distinction between the membraniporan and microporan forms had already been indicated by Canu & Bassler (1923 : 75) who remarked "The union of spines is not a generic character. In fact it may be accidental (*Cupuladria denticulata*), partial (*Cupuladria reussiana*), almost complete (*Cupuladria umbellata*)". *D. ocellata* n. sp. links the irregular opesiular indentations and fused cryptocystal denticles typical of *D. reussiana* with the microporan *D. umbellata* (see p. 221).

3 GENERAL NOTES ON LUNULITIFORM COLONIES

a. *Budding*. The method of budding and development of lunulitiform colonies has been discussed by Silén (1942 : 7-13), Lagaaij (1963) and Cook (1965 : 155), and the regeneration of broken colonies by Darteville (1935 : 559-561). A large number of the colonies in these collections are regenerated from broken fragments; approximately 80% of *D. umbellata* in the "Calypso" Collection are of this type, as are many specimens of the other species. It is interesting that the drawings of *C. owenii* by Gray (1828, pl. 3, figs. 15a) and of *D. umbellata* by d'Orbigny (1853, pl. 717, figs. 3, 4) are of regenerated colonies.

b. *Sexual reproduction*. Ovicells are absent; large eggs ("about 0.5 mm. long"), were seen in *C. canariensis* and *C. doma* (as *C. johnsoni*) by Waters (1921 : 404 and 414), and smaller eggs, which may not have been fully developed, by Hastings (1930 : 726) in *D. umbellata depressa* (as *D. umbellata*). These eggs (Gorgona, 1929. 4. 26. 103 pt.), have an average diameter of 0.05 mm. (9% of Lz); those found in zooecia of *C. multispinata* (Stn. 299, Cape Verde Is., Discovery Coll.), have an average diameter of 0.30 mm. (45% of Lz). Eggs in *C. owenii disciformis* ("Calypso" Coll., C47A) average 0.20 mm. (60% of Lz), and one egg in *C. biporosa* ("Calypso" Coll., C49G) has a diameter of 0.20 mm. (50% of Lz). The date of breeding shows great variation and is probably dependent upon several unknown factors. Marcus & Marcus (1962 : 297) found no evidence of germ cells in material from the Brazilian coast collected in December, January, March, April, June and August. The "Calypso" specimen of *C. biporosa* was breeding on 26th May and that of *C. owenii disciformis* on 26th July, 1956. The Madeiran *C. doma* described by Waters was received from Norman, who collected in March and May (see Norman, 1909 : 275). The fertile *C. multispinata* from the Cape Verde Islands was collected on 4th September, 1927, and Hastings's *D. umbellata depressa* from Gorgona, was breeding in July, 1924. Specimens of *D. umbellata* collected in March, 1963, from Funchal, Madeira, were not breeding,

but one very young, recently settled, colony was found. This suggests that perhaps the breeding season here was in early spring.

Generally, the present evidence is that the eggs of the membraniporan and denticulate species are larger than those of the microporan species. This may be connected with the development of the cryptocyst and the size of the opesia, but until observations are made upon living, breeding colonies, the importance of these differences cannot be assessed. The relatively large size of some of the eggs may indicate that the larvae have a yolk and therefore a short free-living existence; but Lagaaij (1963 : 178) considered that the larval life may persist for some time. Settlement is upon a sand grain, small stone, or Foraminiferan shell, and the ancestrula buds one proximal, a pair of proximal-lateral zooecia, and a distal vibraculum. A pair of lateral zooecia follows, and the ancestrular area is later completed by a pair of distal-lateral zooecia (see Lagaaij, 1963, text-fig. 10; and Cook, 1965, text-fig. 1B).

c. *Mode of life.* The mode of life of lunulitiform colonies was virtually unknown, but living specimens have now been observed (Marcus & Marcus, 1962; and Cook, 1963). Their orientation is normally with the zooecial face upward. All the evidence at present available indicates that colonies belonging to the Cupuladriidae, at least, are not capable of free-swimming movement through the water, but are maintained by their peripheral vibracular setae in a position just above the surface of the substrate. The zooecia of the central area do not appear to have either a "hydrostatic" or "radicular" function (cf. Canu & Bassler, 1920 : 75, 1923 : 238, and 1929 : 144). The single instance of 9 colonies being taken at the surface was recorded by Silén (1942 : 13, in the Atlantic, 1881, 27° 16' N., 23° 21' W.), who commented on the lack of any similar occurrence. These specimens have been re-examined (see p. 207). All have vibracular setae and intact frontal membranes; the zooecia have polypides. They were therefore presumably alive when collected, but I agree with Silén, who later remarked (1947 : 10), "the free, swimming life of *C. canariensis* is not at present to be accepted as proved fact".

d. *Associated Cirripede.* West African Cupuladriidae are often hosts to individuals of an Acrothoracid Cirripede, the presence of which is indicated on the basal side of the colony by slightly thicker calcification, which in *C. canariensis* obscures the basal kenozoocial pores. On the frontal side a slit, surrounded by a calcified border, marks the opening through which the cirri of the Acrothoracid protrude for feeding (see Pl. 3, fig. 3). Members of this group of Cirripedes have been reported from localities including Cadiz and South Africa (see Utinomi, 1950 : 5), inhabiting barnacle plates and corals, and producing similar slit openings in these hosts. Most of the slits are found near the central area of the colony. The majority of Acrothoracid specimens have been found in large colonies of *C. canariensis* and *D. umbellata*, but they also occur in *C. multispinata*, *C. doma* and *D. reussiana*. Other conical zoaria with slits evidently made by similar Acrothoracids are those of *Selenaria maculata* Busk (Bass's Straits, 1854. 11. 15. 52, incinerated specimen) and *Stylopoma duboisii* (Audouin) (Holothuria Bank, 1892. 1. 28. 43, see Cook, 1965a, in press).

The majority of other Polyzoa of the silty sand community encrust the large Foraminiferan, *Jullienella foetida*, which has an argillaceous test. Neither these nor

the associated large, erect branching Polyzoan colonies of *Metrarabdotos unguiculatum* Canu & Bassler and *Cleidochasma oranense* (Waters), show any evidence of being inhabited by the Acrothoracid Cirripede.

Without observation of living specimens it is difficult to establish whether the association described above is one of symbiosis, commensalism or parasitism, but it should be noted that many of the zooecia surrounding the slit and thus directly overlying the cavity containing the Acrothoracid appear to be unaffected, and have well-developed polypides. The successful functioning of the Cirripede suggests that the Polyzoan zoarium has a degree of stability surprising in an unattached organism. Inhabited specimens are marked in the lists of material examined thus, (C).

e. *Epifauna*. The colony may provide a substrate for the settlement of larvae of species of Polyzoa which would otherwise not be able to establish themselves successfully in a sandy or muddy habitat. Osburn (1914 : 190) described *Beania cupulariensis* and (1950 : 176) *Membraniporella pulchra*, growing on the basal side of colonies of *Cupuladria*, and Soule (1959 : 22) reported *Chaperiella condylata* on *C. canariensis* and *D. umbellata*. *Smittipora levinseni* (Canu & Bassler) has been found on *C. canariensis* from the "Calypso" Coll. (C 72B), and a specimen of *Onychocella angulosa* (Reuss) budded from a central ancestrula completely covers the frontal surface of a colony of *C. biporosa* from the Canaries (1962. 10. 8. 7), the peripheral zooecia of which can be seen beneath the growing edge of the *Onychocella*.

The colonies are frequently the substrate for other groups, notably small barnacles, tube-worms, hydroids and sponges. The barnacles and worms are found on the basal side of zoaria with a well domed cavity, where there is presumably sufficient room for their cirri and branchiae to be protruded. Hydroid stolons are found on the frontal surface, running between the zooecia, and sponges on the basal side. Apparently these last may cause deformation of the zoaria, by the suppression of growth of one or more radial rows of zooecia. *C. multispinata* (see p. 210) was referred to by Waters (1921 : 413) under Busk's MS. name, *Cupularia deformis*, and specimens labelled "*C. deformis*" by Busk nearly all show fragments of sponges covering the area where the zooecia have failed to develop. Deformed colonies of *D. umbellata* were described as *C. lowei* by Waters, and his type-material and other specimens in the British Museum Coll. have sponge colonies on the basal side. Zoaria of *D. umbellata* ("Calypso" Coll. C56G and Marche-Marchad Coll. I 39D) are also covered basally with a sponge belonging to the Plocamiidae. Here the sponge appears to prevent the connection of the intercalary rows of zooecia produced on either side of the abortive row; the sponge eventually lines the radial slit thus produced. This may, of course, be a secondary effect, but the correlation of the occurrence of deformity and sponges is significant (see Cook, 1965 : 158).

The geographical, bathymetrical and palaeontological distribution of the Cupuladriidae is very wide. Recent specimens of *C. canariensis* have been found from the S.W. Mediterranean to the Gulf of Mexico; "*D. umbellata*" has been reported from a depth of 2,723 fathoms (Canu & Bassler, 1929 : 144); and the majority of the species have also been recorded from the Tertiary, *D. reussiana* and *D. umbellata* having originally been described as fossils.

4 KEY TO THE SPECIES OF CUPULADRIIDAE DESCRIBED BELOW

Note on the identification of worn specimens. Lunulitiform colonies are frequently found to be worn and identification under these conditions is extremely difficult. Lagaij (1952 : 34 and 1953 : 13) stressed the importance of the character of the basal surface, which is less susceptible to wear, and this is emphasized in the following key. Characters not found in fossil or worn specimens are placed in parentheses. All other features have been found to be present in a few zoecia at least of moderately worn Recent and fossil specimens examined.

- | | | |
|----|---|--------------------------------------|
| 1 | Basal surface divided by radial and tangential boundaries into sectors | 2 |
| - | Basal surface not divided into sectors | 4 |
| 2 | Basal sectors nearly always (95%) small, square, with 1-6 pores, vicarious vibracula frequently present (Operculum longer than wide). | 3 |
| - | Basal sectors irregular, majority (75%) long with 6-20 pores. Vicarious vibracula infrequent, zoecial vibracula of two kinds. (Operculum wider than long) | |
| | <i>C. canariensis</i> (p. 197) | |
| 3 | Basal sectors with 1-3 pores per sector, one layer only of basal kenozoecia, vicarious vibracula present throughout colony. (Operculum within a thickened area of the frontal membrane) | <i>C. monotrema</i> (p. 209) |
| - | Basal sectors with 1-6 pores per sector, basal surface frequently filled in by many layers of kenozoecia, vicarious vibracula near central area. (Operculum longer than wide) | <i>C. biporosa</i> (p. 203) |
| 4 | Colonies small (3-7 mm. diameter), steep-sided, solid basally, or with a small concavity lined with spinous tubercles. Peripheral zoecia closed, several rows of enlarged peripheral vibracula present. (Operculum with incomplete proximal sclerite) | <i>C. doma</i> ¹ (p. 216) |
| - | Colonies flatter, concave basally. Cryptocyst with denticles and spinules, or with horizontal cryptocyst lamina formed of fused denticles | 5 |
| 5 | Cryptocyst denticles fused to form horizontal cryptocyst lamina, with pores | <i>(Discoporella)</i> 6 |
| - | Cryptocyst denticles not fused to form horizontal cryptocyst lamina | 8 |
| 6 | Opesia small with a pair of closed opesiules | 7 |
| - | Opesia with a pair of opesular indentations, trifoliolate. Zoarium high. Basal surface with large tubercles | <i>D. reussiana</i> (p. 219) |
| 7 | Opesia sinuate proximally, cryptocyst with a few large pores. Basal surface tuberculate with radial threads. (Operculum without a proximal sclerite) | <i>D. ocellata</i> (p. 220) |
| 8 | Opesia straight proximally with a pair of small denticles, basal surface tuberculate with pits and grooves. (Operculum with a proximal sclerite) | <i>D. umbellata</i> (p. 221) |
| 9 | Zoecia small Lz 0.37-0.47 mm., sides of vestibular arch convergent. Cryptocyst with large distal denticles. Basal surface with very small, regular tubercles, or smooth and glassy. (Operculum longer than wide) | <i>C. owenii</i> (p. 213) |
| - | Sides of vestibular arch straighter, distal denticles not well developed. (Operculum not longer than wide) | 9 |
| 10 | Zoecia large, Lz 0.55-0.76 mm., denticles spinulose. Basal surface with large, irregular tubercles and salient threads. (Operculum as long as wide) | <i>C. multispinata</i> (p. 210) |

¹ Small, *doma*-type zoaria may occur in *C. biporosa*, *C. owenii* and *D. umbellata* (see Cook, 1965 : 162). *C. biporosa* may be distinguished here by the basal surface (fork 1), *C. owenii* by the absence of closed peripheral zoecia and of a proximal sclerite in the operculum (fork 4), and *D. umbellata* by the presence of a complete horizontal cryptocyst lamina (fork 4).

- Zoarium flat, zoecia smaller, Lz 0.37–0.53 mm., denticles small, simple, few. Basal surface with small regular tubercles. (Operculum wider than long)

C. owenii subsp. *disciformis* (p. 215)

5 *CUPULADRIA* Canu & Bassler

- Cupuladria* Canu & Bassler, 1919 : 77, 1920 : 103. Hastings, 1930 : 718. Lagaaïj, 1952 : 32. Cheetham & Sandberg, 1964 : 1020.

TYPE SPECIES. *Cupularia canariensis* Busk, Madeira, Recent.

Zoarium lunulitiform. Zoecia with cryptocyst variously developed, frequently with denticles, which do not normally fuse. Vibraculum distal to each zoecium. Vicarious vibracula and basal sectors present in some species.

Vicarious vibracula have been found to occur only in the *C. canariensis* group of species (group A, Cook, 1965 : 167). They are marked in the lists of material examined thus : (V).

6 *Cupuladria canariensis* (Busk)

(Pl. 1, figs. 1A, B, Pl. 3, fig. 4, Text-figs. 1a–f)

- Cupularia canariensis* Busk (part), 1859a : 66 (not pl. 23, figs. 7, 8 = *C. biporosa* see p. 203), Madeira, Canaries.

- Cupularia canariensis* Busk : Manzoni, 1869 : 26, pl. 2, fig. 17, Pliocene, Italy. 1877 : 24, pl. 17, figs. 5a, b, c, Miocene, Austria and Hungary.

- ?*Membranipora canariensis* (Busk) Smitt (part), 1888 : 79, text-fig. 326, 120 fath. and over, Florida.

- ?*Cupularia canariensis* Busk : Angelis (part), 1899 : xxxiii, pl. B, figs. 7, 8, Pliocene, Spain (not fig. 6 = ?*C. biporosa*).

- Cupularia canariensis* Busk : Neviani 1891 : 130, Post Pliocene, Italy. 1895 : 101, Miocene, Italy.

- ?*Cupularia canariensis* Busk : Calvet (part), 1907 : 393, Canaries and Cap Blanc, 80–259 m.

- Cupularia guineensis* Busk : Norman (part), 1909 : 289, pl. 37, figs. 3 and 6, Madeira (not figs. 4, 5 = *C. biporosa*).

- ?*Cupularia guineensis* Busk : Osburn (part), 1914 : 195, Tortugas Islands, Florida, 10 fath.

- ?*Cupularia canariensis* Busk : Faura & Canu (part), 1916 : 133, Miocene, Spain (not pl. 3, fig. 8).

- Cupularia canariensis* Busk : Canu, 1917 : 137, pl. 3, figs. 4–6, Burdigalien, L. Miocene, France.

- Cupularia canariensis* Busk : Waters (part), 1921 : 410 pl. 30, figs. 11, 12 Liberia, (not pl. 29, fig. 15 = *C. biporosa*).

- Cupuladria canariensis* (Busk) : Canu & Bassler (part), 1928 : 16, pl. 1, figs. 7–9, Recent, Gulf of Mexico (not text-fig. 2 = *C. biporosa*).

- Cupuladria canariensis* (Busk) : Darteville, 1935 : 560, pl. 19, figs. 1, 2, Ràs el-Amouch, Algeria.

- Cupuladria canariensis* (Busk) : Silén (part), 1942 : 13, Pliocene, Italy ; Recent, Azores, West Indies (not text-fig. 8 = *C. biporosa* ; not text-fig. 9, pl. 4, figs. 15, 16 = *C. pyriformis*).

- Cupuladria canariensis* (Busk) : Lagaaïj, 1952 : 33, pl. 2, figs. 1a, b, Pliocene, Netherlands. 1953 : 15, pl. 1, fig. 1, Miocene, Pliocene, Netherlands.

- Cupuladria canariensis* (Busk) : Buge, 1957 : 139, pl. 9, fig. 5, Miocene, S.W. France (not pl. 10, fig. 3).

- Cupuladria canariensis* (Busk) : Gautier, 1962 : 53, Algeria, 100–300 m.

- Cupuladria canariensis* (Busk) : Lagaaïj, (part), 1963, pl. 25, figs. 1, 3–5, pl. 26, figs. 2, ?3.

- Cupuladria canariensis* (Busk) Annoscia, 1963 : 225, pl. 9, fig. 1, pl. 10, fig. 1, pl. 11, figs. 1a, 1b, pl. 12, figs. 1a, 1b, Quaternary, Italy.

- Cupuladria canariensis* (Busk) Cheetham & Sandberg, 1964 : 1021, text-figs. 11, 13, Quaternary, Louisiana.

MATERIAL. LECTOTYPE (chosen here), the top left-hand specimen on the slide B.M. 1899. 7. 1. 4697 (A), Busk Coll., M'Andrew, Canaries. Lectoparatypes, the top right-hand specimen on the same slide and 1962. 1. 24. 3, Busk Coll., M'Andrew, Canaries.

"Calypso" Coll. I. Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m., C4F. Stn. 17*, 5° N., 5° 28' 30" W., 21.v.56, 27 m., C56J (C). Stn. 29*, 4° 3' N., 6° 12' E., 26.v.56, 32 m., C49B (V). Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48B (V).

Coll. II. Stn. 24, 15° 16' 34" N., 23° 47' 44" W., 18.xi.59, 55-60 m., C86A. Stn. 26, Ile Sao Tiago, 15° 16' 30" N., 23° 47' 31" W., 18.xi.59, 50-65 m., C65G. Stn. 73, C72B (V).

Marche-Marchard Coll. I. Konakrey, Guinée Ise., 1F, 2E. Flor de la bouteille, Guinée Ise., 21.i.53, 8 m., 3B (V). Baie de Gorée, 1954, 46-48 m., 6B. Sud de Gorée, 27.x.53, 38-42 m., 7B (CV); and 24.ii.53, 40-41 m., 11H (CV). S.W. Madeleines, 15.ix.53, 48 m., 20B; 45-46 m., 26G; and 21.i.54, 46-48 m., 46E (V). Sud de presque l'île du Cap Vert, 18.ii.54, 95 m., 29A (CV), 33C (V). Baie de Seminole, Gorée, 8.xii.53, 38 m., 39C (V).

Coll. II. Baie de Gorée, 9.ix.55, 190-220 m., 3A (V); and 210-220 m., 33A (V). S.W. large du Cap Vert, 9.ix.55, 100 m., 11A (V), 14E (V). Banque de Fagaque (Joal), 15.v.53, 5 m., 15A. S.W. Madeleines, 9.i.54, 47.5 m., 31D; and 15.ix.53, 48 m., 40A (V). Devant le Cap Manuel, Oct., 1952, 35 m., 37A (CV).

Coll. III. Sud de presque l'île du Cap Vert, 18.ii.54, 46-50 m., 1C (V). Sud de Gorée, 13.xi.53, 33-35 m., 9B; and 34-37 m., 17B. Either as above, 34-37 m., or S.W. Madeleines, 15.ix.53, 48 m., 16E. Dragage 1 "Gerard Freca" 18.ii.54, 23F, dragage 4, 97 m., 28G; dragage 5, 15B. 27.xi.53, 33-34 m., 29C. No information 24G.

Achimota Coll. I, Stn. 69, Dredge haul No. 5, 22.i.51, 22 m., 90.III.C.

British Museum Coll. Madeira, 1912. 12. 21. 1002 (V), 1911. 10. 1. 647 (V) and 1962. 1. 28. 2 (V), Norman Coll. Bay of Funchal, Madeira, 1962. 1. 28. 1 (V), Norman Coll; 50 m., 1963. 2. 28. 10 Cook Coll., mud*. Tangier Bay, 35 fath., 1899. 7. 1. 1225-1229, Busk Coll. Râs el-Amouch, Algeria, 45 fath. and upward, "Porcupine", 1899. 7. 1. 84, 41 fath. 1226; 45 fath., 1222, 1264 and 1228; 4693 and 4694, Busk Coll. Mediterranean, 45 fath., 1899. 7. 1. 1223 and 1230, Busk Coll. Cape Rosa, Algeria, 95 fath., 1899. 7. 1. 1227, Busk Coll. Cape Sagraas, Portugal, 1899. 7. 1. 1221, Busk Coll. West Indies, "Blake", 1879, 1911. 10. 1. 1722, Norman Coll. Barbados, 73 fath., 9.iii.79, and 23° 13' N., 89° 10' W., 84 fath., "Blake" 1911. 10. 1. 644, Norman Coll. St. James Coast, Barbados, 1962. 1. 26. 2, Saunders Coll. Gulf of Mexico, 28° 58' N., 89° 9' W., mud lump SP 5, 1961. 11. 2. 49A, Cheetham Coll.

"Discovery" Coll., Stn. 279, off Cape Lopez, 10.vii.27, 58-67 m., mud and fine sand*, (CV).

Waters Coll. Manchester Museum. Four slides from Oran, 1 slide from "Post Pliocene", Pisa.

Naturhistoriska Riksmuseet, Stockholm Coll. (numbers in Silén, 1942: 13-14 in parentheses). St. Agata, Piemonte, Italy, Pliocene, FBD 737 (No. 2). Azores, off

Punta Delgada, FBS, 964 (No. 6). West Indies, 52 miles off Florida, 40 m., FBD 548, 1 specimen only (No. 16).

Specimens from Dr. R. Lagaaij. Beeringen, Netherlands, Miocene. Karsy, Poland, Miocene. Antwerp, Belgium, Pliocene. Gulf of Mexico "Atlantis" Stn. 161, 22 fath., Recent.

Specimens from Prof. Voigt. Rostej Banat, M. Miocene. Hamburg, Miocene. Pinneberg, nr. Hamburg. U. Miocene.

Zoarium frequently large (maximum diameter measured, 23 mm.). Cryptocyst narrow, descending steeply, finely tuberculate, not thickened in central zoecia. Operculum slightly wider than long with no proximal sclerite. Zoecial vibracula of two kinds, one with a short hooked seta. Vicarious vibracula sometimes present surrounding ancestrula, and in the central area, with a short, stout hooked seta. Basal surface divided into irregular rectangular sectors, the majority long, with from 4-20 pores (usually 6-12). Tentacles 17-19 (see p. 203).

DIMENSIONS. Lz 0.50-0.80 mm., lz 0.30-0.47 mm., La 0.45-0.60 mm., Lvo 0.12-0.19 mm., Lv 0.32-0.45 mm., Ls 0.70-1.50 mm., Lvs 0.17-0.30 mm., Lo 0.10-0.13 mm., lo 0.12-0.15 mm., Lop 0.35-0.47 mm., lop 0.21-0.32 mm.

Lagaaij (1952 : 33) first chose Busk's slide (B.M. 1899. 7. 1. 4697) as lectotype of *C. canariensis*, but did not indicate upon which of the 6 specimens present his description was based. The two specimens chosen above as lectotype and lectoparatype are definitely *C. canariensis* as described by Lagaaij, and as generally understood by European authors; although only part of Busk's description and neither of his magnified figures (1859a, pl. 23, figs. 7, 8) refer to this species. I have here followed the Recommendation 74A of the International Code of Zoological Nomenclature (1961 : 79), with regard to the "agreement with previous restriction" of the species.

Smitt² (1888 : 79, text-fig. 326) recorded *Membranipora canariensis* from 120 fathoms and over, from Florida. The figured colony is 18 mm. in diameter, and as *C. biporosa* does not appear to attain this size, is perhaps *C. canariensis*. Specimens sent to Norman by Smitt, from the "Blake" Collection from the West Indies, consist of a mixture of *C. canariensis* and *C. biporosa*, and presumably Smitt's record refers to both species, as perhaps does Osburn's from the Tortugas Islands, where some of the specimens were very large (0.75 in.). Calvet (1907 : 393) included "*C. guineensis* Kirkpatrick"³ (sic) in his synonymy; it may be presumed that part of his material, at least, was true *C. canariensis*.

Waters (1921 : 399) received material from Norman, whose figures (1909, pl. 37, figs. 3 and 6) are of *C. canariensis*. Norman's specimens from Madeira in the British Museum consist of a mixture of *C. canariensis* and *C. biporosa*.

The material described by Darteville is *C. canariensis* (Râs el-Amouch, 1899. 7. 1. 84, Busk Coll.), and shows the method of budding of zoecia from a broken fragment particularly well.

² For Smitt's authorship see Agassiz, 1888 : xxi.

³ Kirkpatrick (1890 : 612) only listed *C. guineensis* from the Torres Straits, his record is certainly not *C. canariensis* (see Hastings, 1930 : 714).

Much of the material listed by Silén (1942 : 13–14) has been re-examined, namely specimens from localities 2, 6, 7, 8, 9, 10, 15, 16 and 18. Of these, specimens 2 and 6, and one of the zoaria from 16, are *C. canariensis*. The remaining specimens belong to three other species, *C. biporosa* and *C. owenii* (see pp. 203 and 213 below), and *C. pyriformis* (Busk). Silén expressed doubt as to the identity of specimen 18, from Anguilla, West Indies; it is certainly referable to *C. pyriformis* (see Cook 1965 : 168).

The figures given by Canu & Bassler (1928) of specimens from the Gulf of Mexico are all of *C. canariensis* with the exception of text-fig. 2, of an operculum, which shows the elongated appearance typical of *C. biporosa*. Presumably their Recent material consisted of both species.

The figures of *C. canariensis* given by Manzoni (1869, Pliocene, Italy), Manzoni (1877, Miocene, Austria and Hungary) and Canu (1917, Lower Miocene, France) all show steeply descending cryptocysts and long basal sectors. Neviani (1895) recorded large colonies (2 cm. diameter) from the Italian Miocene, and (1891) had mentioned the elongated basal sectors with numerous pores of his post-Pliocene specimens. Both the specimens from the European Pliocene and Miocene lent by Dr. Lagaaij, and his description and figures (1952 and 1953) have the same consistent characters and thus contrast significantly with the figures of American Miocene specimens given by Canu & Bassler (see p. 206), all of which are attributable to *C. biporosa*. Buge (1957 : 177) stated that the figure of the basal side (as "face supérieure non zoéciale") of *D. umbellata* given by D'Orbigny (1853, pl. 717, fig. 4) was in reality of *C. canariensis*, and showed "secteurs radiaux avec pores". D'Orbigny's figure shows radial grooves typical of *D. umbellata*, and irregular tubercles, with no sign of tangential sector boundaries or biserial pores. It is, moreover, in outline, a mirror image of figure 3, which shows the frontal surface of *D. umbellata*, and the two figures were obviously drawn from the same colony with great attention to detail, as the budding pattern of the regenerated fragment from which the zoarium originates (see p. 193), may be seen to correspond on the frontal side, with the shape of the fragment visible on the basal side. D'Orbigny's explanation of pl. 717 (p. 473), however, gives the Plate number as "747" (which contains drawings of Cyclostomes only), and the descriptions of figures 2 and 3 have been interchanged. Buge found that d'Orbigny's material of *D. umbellata* contained one zoarium of *C. canariensis*. The frequent association of this pair of species has been noted, (see p. 209), and may have occurred in Buge's material from the Redonian, as his figure (pl. 10, fig. 3) of the frontal surface of his "*C. canariensis*" shows a well-developed vestibular arch and wide zooecia, and is perhaps a worn fragment of *D. umbellata* or *C. haidingeri*; it has not the character of *C. canariensis*, but the basal surface of a specimen figured on pl. 9, fig. 5, has irregular sectors with 4–8 pores, and is similar to other Miocene specimens of *C. canariensis*.

The figure given by Faura & Canu (pl. 3, fig. 8) shows evidence of a worn denticulate cryptocyst in some zooecia and is not of a specimen of *C. canariensis*. Their text-figures 4a, b, are reproductions of those of Pliocene specimens given by Angelis (1899), and do not represent their own material. Canu & Lecointre (1925, pl. 3) figured *C. canariensis* from the Burdigalian of the Gironde, but the photographs have

been retouched (in fig. 11 sector boundaries have been drawn in through basal pores), and little of the character of the specimens can be deduced.

The measurements given by Gautier (1962 : 53) show that the zooecia of his specimens had wide opesia. The zoaria were large (12.5 mm. in diameter), and were thus very probably of *C. canariensis*.

Lagaaij's extremely full and detailed study of *C. canariensis* (1963), includes a bibliography which combines references to both *C. canariensis* and to *C. biporosa*, as limited here.

Zoaria from west Africa are generally larger than those from the Gulf of Mexico, and of a flattened cone shape. In all the specimens examined the sides of the opesia are curved and the lateral cryptocyst descends steeply, and is so little salient that in cleaned specimens the pores in the lateral walls can be seen from a frontal view.

The ancestrula is frequently slightly larger than the zooecia of the primary circle budded from it (see Canu & Bassler, 1928, pl. 1, fig. 7), and the zooecia of the ancestrular area never show any thickening of the cryptocyst as in *C. biporosa* and *C. monotrema*. The zooecial vibracula of Recent specimens of *C. canariensis* are of two distinct kinds. The majority are similar to those found in all other species of the family; they have auriform opesiae, rounded proximally, and long vibracula setae. A proportion of between 1 : 10-1 : 30 individuals are small, have short, hooked setae, and more symmetrical opesiae, with prominent narrow rostra pointing proximally (see pl. 3, fig. 4). This kind of zooecial vibraculum has been found to occur in the lectotype, the majority of west African colonies, and in a few zoaria from the Gulf of Mexico. The occurrence thus differs from that of the vicarious vibracula with hooked setae (see below). No other species of Cupuladriidae has been seen in which two such types of vibracula occur. Canu & Bassler (1929 : text-fig. 13C) figured a second type of seta in *C. grandis*, but did not describe it. Their figure is somewhat similar to that of a regenerating seta in *D. umbellata* (subsp. *depressa*), given by Marcus & Marcus (1962, pl. 2, fig. 7). The opesiae of regenerated vibracula are not of the narrow, symmetrical type described above.

Vicarious vibracula are commonest in the central area of zoaria in which they occur, but may also be present among zooecia budded from a regenerating edge. They completely replace a zooecium and each has an ordinary small, distal vibraculum, like the zooecia. The opesia of the vicarious vibraculum of *C. canariensis* is quite unlike that of *C. biporosa*, which is auriform (see below). In *C. canariensis* a long, acute, raised, beaked rostrum protrudes proximally beyond the short gymnocyst. It supports a wide, short, strongly hooked seta, which is slung between the asymmetrical condyles. The basal sclerite differs slightly from that of the normal vibracular seta, but the individual is still basically a vibraculum (see Hastings, 1963 : 180).

The basal sectors of *C. canariensis* are unlike those of *C. biporosa*, being irregular in length and rarely square in outline. The majority are elongated rectangles, with 6-12 pores, and occasionally more (see Text-fig. 2f). Interspersed with these sectors are short wide ones with 3-6 pores, these occur at the origin of an intercalary row of zooecia. In basal view colonies of *C. canariensis* do not show the regular concentric series of sectors which is so striking in *C. biporosa*. At the growing edge, the minute

pores in the basal wall can be seen in the developing zoecia to be without any surrounding kenozoocelial chamber. Further toward the centre of the colony, a crescent of calcification with the concavity pointing distally grows round the pore; when the arms of the crescent meet, this forms the first kenozoocelial chamber. In young colonies the tangential divisions between the radial sector boundaries are not developed until at least 4 radial series of zoecia have been budded. Thus even young colonies

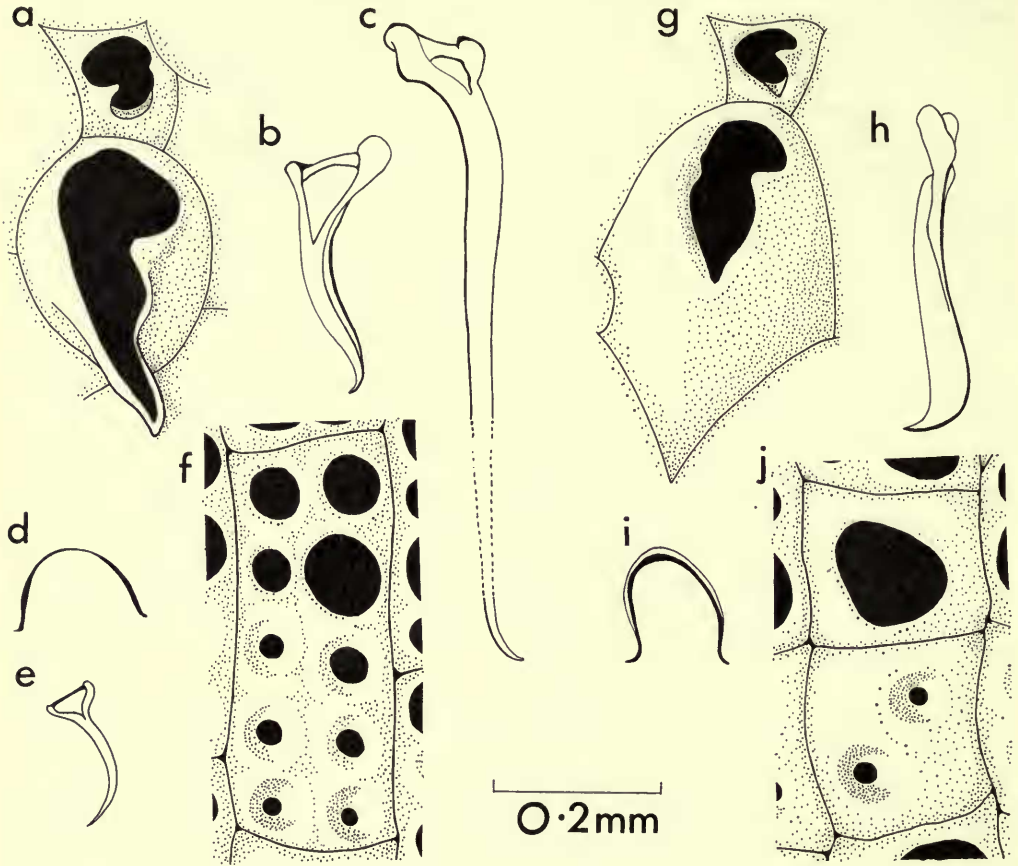


FIG. 1. *Cupuladria canariensis* and *C. biporosa*. a-f, *C. canariensis*. a. Vicarious vibraculum and normal distal vibraculum, treated with eau de javelle. Marche-Marchad Coll., I, 39 C. b. Hooked seta of vicarious vibraculum. c. Seta of normal vibraculum, central part omitted. d. Operculum. b-e, "Calypso" Coll., I, C 56 J. f. Basal surface, treated with eau de javelle, showing elongated sector with porous kenozoocelial chambers. Marche-Marchad Coll., I, 39 C. g-h, *C. biporosa*. g. Vicarious vibraculum and normal distal vibraculum, treated with eau de javelle. 1962. I, 26. I. h. Scimitar-shaped seta of vicarious vibraculum, in lateral view. i. Operculum. j. Basal surface, treated with eau de javelle, showing small, square sectors with porous kenozoocelial chambers. Marche-Marchad Coll., III, 24 G.

may be distinguished from those of *C. biporosa* where the tangential sector boundaries are seen as soon as the zoecia grow out beyond the original substrate.

Waters (1921 : 411) gave the number of tentacles as 14, but this is the number found in sections of *C. biporosa* (1929. 4. 26. 85 pt.). Waters's material included both *C. canariensis* and *C. biporosa*, and the number of tentacles in *C. canariensis* sections (MM II, 3A) is 17-19. *C. doma* (see Waters, 1921 : 411, and Cook, 1963 : 409) and the *D. umbellata*-complex (see Marcus & Marcus, 1962 : 295, and Cook, 1963 : 409) have 13-16 tentacles, and the same number has been seen in sections of *C. owenii disciformis* ("Calypso" Coll. C47A).

Thus *C. canariensis* differs from *C. biporosa* chiefly in the character of the basal surface, the cryptocyst, the number of tentacles, in the possession of two kinds of zoecial vibracula, and the form of the vicarious vibracula. The distribution of the two species also appears to have been completely distinct in the Miocene (see below). *C. canariensis* does not occur south of Barbados in Recent collections, all Brazilian records being of *C. biporosa* or *C. monotrema*.

7 *Cupuladria biporosa* Canu & Bassler

(Pl. 1, figs. 2A, B, 3A, B, 4A, B, 5, 6A, B, Text-figs. 1g-j)

Cupularia canariensis Busk (part) 1859a : 66, pl. 23, figs. 7, 8, Madeira and Canaries.

Cupularia canariensis Busk : Busk, 1859 : 87, pl. 13, figs. 2 a-e, Coralline Crag, Pliocene, Britain.

Membranipora canariensis (Busk) Smitt, 1873 : 10, pl. 2, figs. 69-71, 10-14 fath. Florida. (?part), 1888 : 79, 120 fath. and over, Florida.

?*Cupularia canariensis* Busk : Angelis (part), 1899 : 33, pl. B, fig. 6 only, Pliocene, Spain.

Cupularia canariensis Busk : Canu, 1908 : 275, pl. 5, figs. 8, 9, 10, Pampean, Pliocene, Argentina.

Cupularia guineensis Busk : Norman (part), 1909 : 289, pl. 37, figs. 4, 5, Madeira (not figs. 3, 6 = *C. canariensis*).

?*Cupularia guineensis* Busk : (part) Osburn, 1914 : 195, Tortugas Islands, Florida, 10 fath.

Cupularia canariensis Busk : Canu & Bassler, 1918 : 119, pl. 53, figs. 5-7, Miocene, Costa Rica and Jamaica.

Cupuladria canariensis (Busk) Canu & Bassler, 1919 : 78, pl. 1, figs. 8-10, Lower Miocene, Costa Rica, 1920 : 103, text-fig. 24D. 1923 : 28, pl. 1, figs. 7-9, Lower Miocene, Florida, Jamaica, Santo Domingo, Costa Rica ; Miocene and Pliocene, Florida.

Cupularia canariensis Busk : Waters (part), 1921 : 410, pl. 29, fig. 5, Madeira.

Cupuladria biporosa Canu & Bassler, 1923 : 29, pl. 47, figs. 1-2, Miocene, Santo Domingo.

Cupuladria canariensis (Busk) : Canu & Bassler, 1928 : 16, text-fig. 2, Pliocene Panama ; and Recent, Gulf of Mexico.

Cupuladria canariensis (Busk) : Hastings, 1930 : 714, pl. 8, figs. 38, 40, Gorgona, Colombia, 15-30 fath.

Cupuladria canariensis Busk (sic) McGuirt, 1941 : 46, pl. 1, figs. 1-3, 5-6, 8, Miocene & Pliocene, Louisiana.

Cupuladria canariensis (Busk) : Silén (part), 1942 : 13, text-fig. 8, West Indies.

Cupuladria canariensis (Busk) : Osburn, 1950 : 33, pl. 3, figs. 2, 3, Lower California to the Galapagos Islands, shallow water to 40 fath.

Cupuladria canariensis (Busk) : Soule, 1959 : 8, California, 7-40 fath.

Cupuladria canariensis (Busk) : Galopim de Carvalho, 1961 : 97, pl. 1, figs. 1-3, Pliocene, Portugal.

Cupuladria canariensis Marcus & Marcus, 1962 : 285, pl. 1, figs. 1-3, off Sao Paulo, 150 m., near Cabo Frio, 3 m., off mouths of the R. Amazon, 70 m.-71.5 m., dead.

Cupuladria canariensis (Busk) : Lagaaij, part, 1963, pl. 26, figs. 4, 5.

Cupuladria sp. Cheetham & Sandberg, 1964 : 1021, Quaternary, Louisiana.

MATERIAL. Holotype U.S.N.M. 68425. (Photographs, B.M.N.H. 1963. 1. 2. 1, 2) Miocenè, Bowden Marl, Santo Domingo.

"Calypso" Coll. I. Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m., C41(V). Stn. 29*, 4° 3' N., 6° 12' E., 26.v.56, 32 m., C49G (V).

Coll. II. Stn. 26, 15° 16' 30" N., 23° 47' 31" W., 18.ii.59, 50-65 m., C65R. Stn. 75, 16° 04' 20" N., 22° 58' 10" W., 45 m., C109A.

Marche-Marchad Coll. I. Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3E (V). Sud de Gorée, 27.x.53, 38-42 m., 7D. Sud de presque l'île de Cap Vert, 95 m., 33Q. S.W. Madeleines, 21.i.54, 46-48 m., 46G (V).

Coll. II. S.W. Madeleines, 9.i.54, 77.5 m., 31R.

Coll. III. Dragage 5, "Gerard Freca", 18.ii.54, 15I; Dragage 4, 97-98 m., 28K (V). 33-34 m., 27.ii.53, 29I (V). No information, 24R (V).

British Museum Coll. Canaries, M'Andrew, 1899. 7. 1. 4697B, Busk Coll. Canaries, M'Andrew, 1899. 7. 1. 4702, 1962. 1. 24. 4 and 5, Busk Coll. Madeira, 1879. 5. 28. 6. Bay of Funchal, Madeira, 1962. 1. 24. 6, 1963. 1. 16. 73, Madeira, 1962. 1. 24. 7, and 9 (V), Norman Coll; Funchal, 50 m., 1963. 2. 28. 6, Cook Coll., mud.* Râs el-Amouch, Algiers "Porcupine", 4 fath. and upwards, 1962. 1. 24. 1. Tangier Bay "Porcupine", 1911. 10. 1. 646, Norman Coll. Barbados, 73 fath., 9.iii.79, and 23° 13' N., 89° 10' W., 84 fath., "Blake", 1962. 1. 24. 8, Norman Coll. (V) West Indies, 1962. 1. 24. 2, Norman Coll (V). Gulf of Mexico, 91° W., 28° 6' 25" N., 37 fath., 1959. 8. 20. 3, Lagaaij Coll. (V). 89° 9' W., 28° 58' N., 1961. 11.2. 49B, Cheetham Coll. Gorgona, Colombia, 1929. 4. 26. 85. 86, 263 (V), 87 (V). St. James coast, Barbados, 1962. 1. 26. 1, Saunders Coll. (V). Miocene, Santo Domingo, 1899. 7. 1. 1259, Busk Coll. (V).

B.M. Palaeontological Dept. Coll. Coralline Crag, Pliocene, Britain, D 39968, 39969, D 6767, 6762, 6764, B 1624. Astigiana, Pliocene, Italy, 1848. 6. 12. 3-7.

U.S. National Museum Coll. Holotype, see above (V). 80747, Miocene, Bowden Marl, Jamaica (V).

Dr. A. Cheetham Coll. Forest Hill Clay, Alabama, L. Miocene. Oak Grove, Yellow River, Okaloosa County, Florida, L. Miocene. Cercado de Mao, Santo Domingo, L. Miocene (V). Tambo Trace, Shell Bed, nr. Talparo, Trinidad, L. Miocene (V). Manzanilla, Manzanilla coast, Trinidad, Miocene (V).

Dr. R. Lagaaij Coll. Miocene, Limestone Creek, Missouri. Miocene, Cubagua, Venezuela. Miocene, Bowden Marl (V), Jamaica. Pleistocene, Gulf of Mexico "Neptune" 1. Gulf of Mexico, "Atlantis" Stn. 163, 20 fath. (V).

Naturhistoriska Riksmuseet, Stockholm Coll. (Nos. in Silén, 1942: 13-14 in parentheses). Atlantic, 27° 16' N., 23° 21' W. at the surface, FBS 321 (No. 7). (One of the 9 specimens is *C. owenii* qv) West Indies, S.W. off Tortugas 40 m., FBD 239 (No 8) (V). As above, East Key, 20 m., FBD 258 (No. 9) (V). As above, nr. Rebecca shoal, 15 m., FBD 281 (No. 10) (V). Yucatan, 35 miles, N.N.E. off C. Catocla, 40 m., FBD 696 (No. 15) (V). 52 miles off Florida, 40 m., FBD 548 (No. 16) (V) (One colony of *C. canariensis* present).

C. biporosa is not present in the Achimota Collection.

Zoarium generally smaller than that of *C. canariensis*, not exceeding 16 mm. in

diameter, zooecia also smaller. Operculum frequently longer than wide with no basal sclerite. Cryptocyst descending gently, sides of opesia straight. Vicarious vibracula frequent, usually present in ancestrular area, occasionally throughout zoarium; seta straight, elongated, broad, slightly hooked, scimitar shaped. Basal surface divided into concentric series of small, nearly square sectors with 1-6 pores, usually 4. Basal concavity flattened and filled by many layers of kenozoecial chambers. Tentacles 14-15 (see above).

DIMENSIONS. Lz 0.40-0.65 mm., lz 0.25-0.35 mm., La 0.40-0.47 mm., Lvo 0.07-0.13 mm., Lv 0.45-0.55 mm., Ls 0.40-1.40 mm., Lvs 0.25-0.30 mm., Lo 0.10-0.11 mm., lo 0.09-0.10 mm., Lop 0.25-0.32 mm., lop 0.15-0.19 mm.

Dr. R. S. Boardman (*in litt.* 13.ii.1962) has found that the only specimen referred to *C. biporosa* in the U.S. National Museum Collection, is the holotype-fragment of which part was figured by Canu & Bassler (1923, pl. 47, figs. 1, 2). Enlarged photographs of the entire fragment show that one vicarious vibraculum is present, and that the opesiae of the zooecia in the published figure (fig. 1) have been enlarged by retouching of the photograph. This was presumably done to erase the image of detritus lodged in the opesiae, but has unfortunately given the impression that the cryptocyst descends more steeply than it in fact does.

Specimens of complete young zoaria labelled "*C. canariensis*", from the same horizon in Jamaica as the holotype (U.S.N.M. 80747) are strikingly similar in all characters to young Recent colonies from the West Indies (see pl. 1, figs. 4, 6).

Busk's description (1859a: 66) of the occurrence of 2-4 pores in the sectors on the basal side of his specimens, and his figures (pl. 23, figs. 7, 8) showing the small square basal sectors (fig. 7), and well-developed cryptocyst (fig. 8), are certainly of *C. biporosa*. The major part of the material from the Canaries collected by M'Andrew in the Busk Collection (see Busk, 1859a: 67) is also of *C. biporosa*, but specimens of *C. canariensis* are mixed with it, and it is probably these which Busk described as 0.5 in. in width, as none of his specimens of *C. biporosa* reach this size. The specimens on slide 1899. 7. 1. 4697 A + B, of *C. canariensis* and *C. biporosa*, are mounted on glass, and the distinctive characters of both surfaces of the colonies of the two species can be seen clearly.

Busk's figures of specimens from the British Crag (1859: 87, pl. 13, figs. 2a-e), show typical *C. biporosa* characters, namely the straight sides of the opesiae and the gently descending cryptocyst. The figure of the basal side shows some irregular sectors, but specimen D 6764 has square sectors, with 4 pores, and many layers of kenozoecial chambers, as well as the frontal character of *C. biporosa*. Busk's specimens are particularly interesting as the only other records of *C. biporosa* from the Pliocene of Europe are from Spain, Portugal and Italy. Pliocene specimens from the Netherlands are all referable to *C. canariensis*.

Smitt (1873: 10) described the "inner lamina" (i.e. cryptocyst) of his specimens as being similar to that of *Farcimia cereus* (p. 3, pl. 1, figs. 55, 56), which has a well-developed cryptocyst. His figure 69 shows the slightly elongated operculum, figure 70 the cryptocyst, and the vicarious vibracula in the ancestrular area (see Hastings, 1930: 714). Figure 71 shows the basal sectors, some of which have 4

pores, although others are shown bearing more. The specimens listed by Silén (1942, Nos. 8, 9 and 10) have been examined; they include those described and figured by Smitt. No. 8 (FBD 239) is the original of figure 71 and the actual sectors have been recognized. The basal sectors are square and more regular than in Smitt's drawing and the long irregular sectors do not occur, but are composed of several smaller sectors. Figure 70 is also drawn from this specimen and confirms that the irregular opesia shown in the figure are those of vicarious vibracula. In fact, not only the ancestrular, but all the 7 individuals surrounding it are of this type. This development is not unusual in *C. biporosa* and also occurs in colonies from FBD 696, FBD 548, Dr. Lagaij's specimen from the Gulf of Mexico, and 1962. 1. 26. 1. from Barbados. Specimen FBD 281 is the original of Smitt's figure 69; it is a large colony, 10 mm. in diameter.

The figures given by Angelis (1899, pl. B, figs. 7, 8) of the basal surface of his specimens from the Pliocene of Catalonia, show long irregular sectors, and are attributable to *C. canariensis*. Figure 6 (in which the zooecia are shown upside-down) has the appearance of *C. biporosa*, with a wide cryptocyst and straight-sided opesia. The figure is very similar in appearance to that of Busk's Crag specimens. Angelis's descriptions however, are taken from that of Manzoni (1877) and refers to *C. canariensis*. No fossil Spanish material has been seen, but specimens figured by Galopim de Carvalho (1961, pl. 1, figs. 1-3, Pliocene, Portugal) also show the straight-sided opesia and small basal sectors of *C. biporosa*. Pliocene material from Italy also consists of both *C. canariensis* and *C. biporosa*, (see pp. 198 and 204), and the correlation of the characters present is respectively consistent with the diagnoses of the two species.

The specimens figured from the Pliocene of Argentina by Canu (1908, pl. 5, figs. 8, 9, 10) were extremely worn, but figure 8 perhaps shows 2 vicarious vibracula (in the bottom right-hand corner).

Both Norman (1909, pl. 37, figs. 4, 5), and Waters (1921, pl. 29, fig. 5), who received his Madeiran material from Norman, show 2-4 pores on the basal sectors of their specimens. Examination of the plentiful Madeiran colonies in the Norman Collection shows that they, too, consist of a mixture of both *C. biporosa* and *C. canariensis*. Norman and Waters both stated that they considered *C. canariensis* and *C. guineensis* (Busk) to be synonymous. In view of the mixed nature of their material it should be noted that the salient lateral cryptocyst and small square basal sectors of *C. biporosa* are very similar to some specimens of *C. guineensis*, which was, however, distinguished and defined by Hastings (1930: 714).

The material from Costa Rica figured by Canu & Bassler (1918, 1919) as *C. canariensis*, belongs to *C. biporosa*. The same set of photographs was reproduced in both these papers and was again used to illustrate American fossil "*C. canariensis*" in 1920 and 1923. The photographs show 1) small colonies, natural size, with flattened bases; 2) zooecia with well-developed lateral cryptocysts, and with one vicarious vibraculum at the lower right-hand edge; 3) the basal sectors, each with 2-4 pores. The introduction of *C. biporosa* was illustrated by material from Santo

Domingo (1923). The fossils from the Gulf of Mexico region (1928), were illustrated by photographs of Recent *C. canariensis* from the same area.

The specimens described by Hastings (1930 : 714) from Gorgona, consist of colonies, the majority of which have regenerated from broken fragments. Where an ancestrula is present, the vicarious vibracula near it have smaller, more auriform opesia than those occurring elsewhere in the colony.

McGuirt (1941 : 46) mentioned the difficulty in distinguishing his Miocene material from Louisiana, attributed to *C. canariensis*, from *C. biporosa*. The specimens figured show vicarious vibracula (pl. 1, figs. 1, 3) and the small, square basal sectors (figs. 2, 5), and are certainly of *C. biporosa*. The zooecia in figure 8 have unusually narrow cryptocysts, and may have been worn.

Of the colonies collected at the surface of the Atlantic off the west coast of Africa (see Silén, 1942 : 13, specimen FBS 321 above, and p. 194), 8 colonies belong to *C. biporosa*. The ninth is a specimen of *C. owenii* (see p. 213).

Osburn's figure (1950, pl. 3, figs. 2, 3) shows small, square sectors with 1-3 pores (fig. 3), the zooecia in figure 2 have the well-developed lateral cryptocyst of *C. biporosa*, and Soule (1959 : 8) mentioned vicarious vibracula in his Californian material.

Marcus & Marcus (1962) gave a short description of the central vicarious vibracula, and, on pl. 1, fig. 2, illustrated the basal surface of one of their colonies with small segments arranged concentrically. Their material was collected from the northern and southern coasts of Brazil, no specimens being found in the intermediate area. The shallow depths at which some specimens occurred (3 m. near Cabo Frio) were at "sheltered localities", where there must have been little turbulence.

Lagaaij's figures (1963, pl. 26, figs. 4, 5) of material from the Gulf of Mexico are of *C. biporosa*, as is the unnamed species mentioned by Cheetham and Sandberg (1964).

The zoarium rarely attains a diameter of more than 10 mm.; fragments of large colonies estimated at 16 mm. diameter were found in fossil material from the U.S. Nat. Mus. Collection, 80747, and a colony of 11 mm. diameter, covered with 3 small colonies of *Onychocella angulosa* (Reuss) occurs in material from Madeira, 1962. I. 24. 7.

Unlike *C. canariensis*, the sides of the opesia are almost straight, and in the great majority of specimens the cryptocyst descends gently forming a salient lateral shelf and obscuring the pores in the lateral walls, which are not seen in frontal view as in *C. canariensis*. In some fossil specimens the cryptocyst descends more steeply, but this seems to be confined to zooecia of fragments of large zoaria, and does not occur in the smaller, whole colonies. The cryptocyst of the zooecia of the central area are sometimes slightly thickened by secondary calcification, but a lamina is never formed as is found in *C. guineensis* (see Cook, 1965 : 172); a similar thickening is found in *C. monotrema*.

The ordinary vibracula are of one kind only and vicarious vibracula are nearly always present, especially near the centre of the colony; their opesia are auriform, and there is a distinct, prominent gymnocyst. The setae of Recent specimens have the same type of basal sclerite and are similar to those of the ordinary vibracula (see also Hastings, 1930 : 714); they have no sigmoid curve, however, and in lateral view

they are broad, scimitar-shaped, and hooked at the tip (see Text-fig. 1h). They thus differ from the short, hooked setae of the vicarious vibracula of *C. canariensis*. Both Marcus & Marcus (1962 : 288, pl. 1, fig. 2) and Lagaaij (1963 : 183) described the vicarious vibracula of the ancestrular area as regenerated. Although the original zooecia may regenerate as vibracula in some cases, many specimens (notably those from Gorgona and the Gulf of Mexico), show that the vicarious vibracula are budded primarily as part of the normal development of a colony. Vicarious vibracula are often associated with areas of regenerating growth (see Cook, 1965 : 160), and here also, they are some of the first individuals to be budded, not the results of regeneration of the older zooecia.

The development of the basal porous sectors in *C. biporosa* differs from that of *C. canariensis* in that the chambers appear to develop more quickly, and large pores are rarely seen at the growing edges of young colonies. The tangential sector boundaries are always present on the basal side of the young peripheral zooecia, unlike *C. canariensis* (see above).

The layers of kenozoecial chambers are more numerous than *C. canariensis*, even in young colonies. They frequently conceal the original substrate, and in many colonies are so thick that the basal surface is flattened. In section these zoaria show successive rows of chambers up to 14 deep. A slide of sectioned colonies of *C. biporosa*, where the species is mounted with *C. guineensis* for comparison (1879. 5. 28. 6, Madeira + 1929. 5. 10. 1, Australia), was figured by Hastings (1930, pl. 8, fig. 38, as *C. canariensis*). The identity of the species in no way affects her description of the chambers as a distinction from *C. guineensis*, as those of *C. canariensis* are exactly the same in appearance, although they rarely reach a comparable number of layers, even in large colonies of this species.

One of the specimens from the Miocene of Santo Domingo (U.S.N.M. Coll.) shows a form of growth similar to normal colonies of *C. doma* (see Cook, 1965 : 162). The zoarium is small and high, the basal side is half filled by secondary calcification, and there are 3 rows of peripheral vibracula, the last of which encroaches on the basal side (see Pl. 1, fig. 5).

The geographical distribution of specimens of *C. canariensis* and *C. biporosa*, with and without vicarious vibracula, falls into distinct groups. The first, northerly area, consists of records from the S.W. Mediterranean, Spain, Portugal, and the Canaries ; no vicarious vibracula have been found in colonies of either species from these localities. Material of both species from Madeira, the Cape Verde Islands and the coast of Senegal has colonies both with and without vicarious vibracula ; whereas all the specimens from the southerly localities in the Gulf of Guinea and the Bay of Biafra have vicarious vibracula. Recent and fossil specimens of *C. biporosa* from the Gulf of Mexico are rarely without vicarious vibracula, whereas none have been found in the Recent colonies of *C. canariensis* from this area.

C. biporosa differs from *C. canariensis* consistently in the character of the basal surface, of the cryptocyst, in the number of tentacles, in the absence of a second kind of ordinary vibraculum, and in the form of the vicarious vibraculum. The fossil record shows whereas there are apparently no certain descriptions of *C. biporosa*

occurring before the Pliocene in south-western Europe, the only American records of *C. canariensis*, from the Gulf of Mexico and Florida, are Recent. The Miocene faunas of the eastern and western Atlantic were distinct.

C. canariensis and *C. biporosa* have similar geographical distributions, live in similar depths, under the same ecological conditions, and are thus frequently associated in Recent collections. There is a similar correlation between their occurrence and that of the *D. umbellata*-complex (see Canu & Bassler, 1918: 119), and as many as 5 lunulitiform species occur together at Konakrey and Cape Verde, and Stn. 45, "Calypso" Coll. I, off Cape Lopez, in the Bay of Biafra.

The confusion between *C. canariensis* and *C. biporosa*, and the occurrence of vicarious vibracula in both species, make it advisable to compare them with the only other species with similar characters, namely *C. monotrema* (Busk).

8 *Cupuladria monotrema* (Busk)

Cupularia monotrema Busk, 1884: 207, pl. 14, figs. 5, 5a, 5b, off Bahia, 10-20 fath.

Cupularia canariensis Busk: Waters, 1888: 36, pl. 3, fig. 2, Bahia, 10-80 fath.

Cupuladria monotrema (Busk) Hastings, 1930: 715.

MATERIAL. LECTOTYPE (chosen here), B.M., 1887. 12. 9. 820. British Museum Coll. Off Bahia, 10-20 fath., 1887. 12. 9. 820, 820A, Challenger Coll. (V). As above, 1944. 1. 8. 346, Busk Coll. (V). As above, 10-80 fath., 1889. 12. 12. 9 (V) Suppl. Challenger Coll. As above, 1890, 3. 22. 11 (V). Bahia and Pernambuco, 11° 45' S., 37° 15' W., 16-28 fath., 1890. 1. 30. 33-44 pt., and 13° 50' S., 38° 46' W., 32 fath., 1890. 1. 30. 33 pt. (VV).

British Antarctic Expedition Coll. Stn. 42, off Rio de Janeiro, 40 fath., 878A.

C. monotrema does not occur in any of the west African Collections.

Zoarium fairly large, maximum diameter 10 mm. Zooecia with cryptocyst descending quite steeply, lateral pores just visible in frontal view. Operculum opening within a strongly chitinized area of the frontal membrane, which is surrounded by a thickened band. Operculum frequently heavily chitinized, but proximal sclerite absent. Basal surface with only one layer of kenozoecia. Sectors small and square, with 1-3 pores. Vicarious vibracula numerous, nearly as large as the zooecia, with auriform opesia and long proximal gymnocyst. Vicarious vibracula often intercalary, reaching the penultimate peripheral circle of zooecia. Setae scimitar-shaped, similar to those of *C. biporosa*.

DIMENSIONS. Lz 0.40-0.50 mm., lz 0.26-0.37 mm., La 0.40-0.45 mm., Lvo 0.09-0.12 mm., Lv 0.35-0.45 mm., Ls 0.50-1.00 mm., Lvs 0.30-0.40 mm., Lo 0.10-0.11 mm., lo 0.12-0.13 mm., Lop 0.25-0.30 mm., lop 0.15-0.20 mm.

The opesiae of the zooecia of the central area are slightly reduced by secondary thickening as in *C. biporosa*. The vicarious vibracula are similar to those of *C. biporosa*, but are far more numerous. The opercular area is unlike that of other species, although the operculum itself is like that of *C. biporosa* in shape. Frequently its dark brown colour ends abruptly at the junction with the frontal membrane, giving the appearance of a curved proximal sclerite. In many colonies, a band of thickening

surrounds the distal part of the operculum and then extends proximally and across the frontal membrane. This whole area, with the operculum opening within it, is more heavily chitinized than the remaining frontal membrane surrounding it. It is particularly noticeable in dry specimens (such as those seen by Busk), that the area enclosed by the thick chitinous band shrinks differentially in relation to the rest of the frontal membrane, producing the "hippocrepiian" shape described by Busk, who was thus misled into thinking that this part of the whole frontal area was the operculum. In his explanation of terms (p. xvi), Busk did not give a definition of "hippocrepiian", but his "coarctate" form of orifice is similar to the lepra-lloid shape of the frontal area in *C. monotrema*. The chitinized band is not present in all specimens, nor in all zooecia of the zoaria in which it may occur.

As stated by Hastings (1930 : 715), *C. monotrema* is clearly distinct from *C. canariensis*. It is very similar to *C. biporosa*, and may indeed be synonymous, but until more material is available, it is distinguished by the opercular area, the more numerous vicarious vibracula, and the single layer of basal kenozoecial chambers.

Marcus & Marcus (1962 : 286) found no specimens of *C. monotrema* in collections ranging from São Paulo north to the mouths of the Amazon. *C. biporosa* was found only at the extreme North and South of the collecting area, not in the Bahia area.

9 *Cupuladria multispinata* (Canu & Bassler)

(Pl. 2, figs. 2A, B, Text-figs. 2d)

Cupularia owenii (Gray) Busk, 1884 : 207, St. Vincent, Cape Verde Islands, 11 fath., mud (not *C. owenii* (Gray) see p. 213).

Cupularia johnsoni Busk ; Norman part, 1909 : 290, pl. 38, figs. 5, 6, Madeira (not figs. 1-4 = *C. doma*, see p. 216).

Cupularia denticulata Waters, 1921 : 413, listing specimens labelled "*C. deformis*" by Busk, in the British Museum, from Portugal and the Mediterranean, 50 m. to 45 fath.

Cupularia multispinata Canu & Bassler, 1923 : 78, text-fig. 13H, Oran, 105 m. (not text-fig. 13 I = *D. umbellata*, see p. 221). 1928 : 22.

?*Cupularia haidingeri* (Reuss) : Canu & Bassler, 1923 : 77, pl. 1, figs. 13-17, Miocene, Europe (not *C. haidingeri* (Reuss) see Lagaij, 1952 : 35).

Cupularia denticulata var. *multispinata* Waters, 1926 : 427, pl. 18, figs. 2, 4, 7, Oran (*C. denticulata* in the explanation of the plate).

Cupuladria owenii (Gray) : Silén, 1942 : 15, Madeira.

MATERIAL. "Calypso" Coll. I. Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m. C4E.

Coll. II. Stn. 26, 15° 16' 30" N., 23° 47' 31" W., 18.xi.59, 50-65 m., C65H.

Marche-Marchad Coll. I. Konakrey, Guinée Ise., 2E. S.W. Madeleines, 15.ix.53, 20A ; 9.i.54, 45-46 m., 26E. Sud de presque l'île du Cap Vert, 18.ii.54, 95 m., 33A. Baie de Seminoles, Gorée, 8.xii.53, 38 m., 39A (C) (+ *Hippoporina lacrimosa* Cook)

Coll. II. S. Baie de Gorée, 18.ii.54, 95 m., 30C. Baie de Seminoles, Gorée, 8.xii.53, 38 m., 36A.

Coll. III. Sud de Gorée, 13.ii.53, 33-35 m., 9C ; 34-37 m., 17C. Either S.W. Madeleines, 15.ix.53, 48., or Sud de Gorée, 13.ii.53, 34-37 m., 16G. Dragage 1 "Gerard Freca", 18.ii.54, 23G ; Dr. 4, 97-98 m., 28I ; Dr. 5, 27C. 33-34 m.,

27.ii.53, 29E. Mission Guinée Pte. 50, Parages des Fles de Los, Konakrey, 21.i.53, 19 m., 30C (C). No information, 24I.

British Museum Coll. St. Vincent, Cape Verde Islands*, 11 fath., mud, 1887. 12. 9. 82I, Challenger Coll. Port of Oratava, Canaries, 1899. 7. 1. 1224, Busk Coll. Bay of Funchal, Madeira, 1963. 1. 16. 4, Busk Coll; 50 m., 1963. 2. 28. 11. Cook Coll., mud*. Madeira, 1963. 1. 16. 2 and 3, Norman Coll. Mediterranean, 1899. 7. 1. 1236, and on 1223 with *C. canariensis*, "Porcupine", Busk Coll. Spain, 1899. 7. 1. 1239, Busk Coll. Cape Rosa, Algeria, 1899. 7. 1. 1233, Busk Coll. Ràs el-Amouch, Algeria, 45 fath., 1963. 1. 16. 1. Tangier Bay, 1890. 4. 15. 23. Cape of Good Hope, 1842. 12. 2. 19, Belcher Coll. South Africa, False Bay, 50 m., fine sand*, 1963. 1. 16. 5, Univ. Cape Town Coll. S. Africa, False Island N. 8.5 miles, 53 fath., 1949. 11. 10. 669B; Bakhoven Rock W., $\frac{1}{2}$ N. $\frac{3}{4}$ mile, 22 fath., 1949. 11. 10. 617; Cape St. Blaize, 7.5 miles N. 37 fath., 1949. 11. 10. 94B, 625B, 626B, 627B; Cape Infanta N.E. by N. 19 miles, 46 fath., 1949. 11. 10. 622B, 623B; N.E. by N. $\frac{1}{4}$ N., 45 fath., 1949. 11. 10. 621B; Stalwart Point, N.N.W. 9 miles, 53 fath., 1949. 11. 10. 652B; Nanquas Peak N. 46° E. 9 miles, 63 fath., 1949. 11. 10. 674B. Burrows Coll.

Discovery Coll. Stn. 299, 14.x.27, 7-11 m., Tarrafal, S. Antonio, Cape Verde Islands, 86A.

Naturhistoriska Riksmuseet, Stockholm, Madeira, FBD 36.

C. multispinata is not represented in the Achimota Collection.

Zoarium frequently large, (maximum diameter measure, 16 mm.), zoecia with a large range in size. Sides of vestibular arch straight, salient distal denticles absent. Operculum without a proximal sclerite. Descending lateral cryptocyst tuberculate, with 4-8 irregular denticles, themselves ending in fine spinules; proximal spinules infrequent. Central zoecia closed. Basal surface with large, irregular, coalescent tubercles and grooves frequently marked by a salient calcareous thread.

DIMENSIONS. Lz 0.55-0.76 mm., lz 0.32-0.47 mm., La 0.45-0.52 mm., Lvo 0.15-0.21 mm., Ls 0.60-1.90 mm., Lo 0.12-0.14 mm., lo 0.15-0.19 mm.

Busk's specimen from the Cape Verde Islands (Challenger Collection) differs slightly from the other west African specimens of *C. multispinata*. The colony is 7.5 mm. in diameter, but the peripheral zoecia are smaller than in other colonies of comparable size. The sides of the vestibular arch are straight, however, with no evidence of a distinct pair of distal denticles, as in *C. owenii*. The basal surface is worn, and almost smooth, but two areas show large irregular tubercles and faint threads marking the radial grooves. The specimen certainly belongs to *C. multispinata*.

Norman (1909: 290) remarked that specimens of *Cupularia oweni* (sic) were not found by him from Madeira. The Madeiran specimens which he referred to *C. johnsoni* are, however, a mixture of *C. multispinata* and *C. doma*. He included *C. reussiana* Manzoni and *C. doma* Smitt (sic) in his synonymy of *C. johnsoni* (= *C. doma* (d'Orbigny)). Part of the material which he referred to *C. lowei* (= *D. umbellata*, see p. 221), is also *C. multispinata*, as is the "variety" of *C. johnsoni* he described in which "the radiating ridges are greatly developed, and bear two rows of tubercles

regularly placed and of much larger size than those of the type". These specimens were figured on pl. 38, figs. 5, 6, and show the typical character of *C. multispinata*.

Waters (1921 : 413), in discussing *Cupularia lowei* (see p. 221), listed several British Museum specimens of another species, which had similarly deformed zoaria. He proposed to place these "under *denticulata*". Waters's publication of the manuscript name on the labels of Busk's specimens in the British Museum was not accompanied by a description, definition nor an indication (see International Code of Zoological Nomenclature, 1961, Articles 12 and 16). The specimens he listed are all identical with *C. multispinata*, as was suggested by Canu & Bassler (1923 : 78). Waters later (1926 : 427) confirmed this, and although in the explanation of pl. 18, on p. 432, he still referred to the species as *Cupularia denticulata*, he added the note "This is the *C. multispinata*, Canu & Bassler". On p. 427 he referred to it as "*Cupularia denticulata* var. *multispinata*". *C. denticulata* is a synonym of *C. owenii* (see below). The distribution of *C. multispinata* given by Canu & Bassler (1928 : 23) was derived from Waters's list of specimens given in 1921.

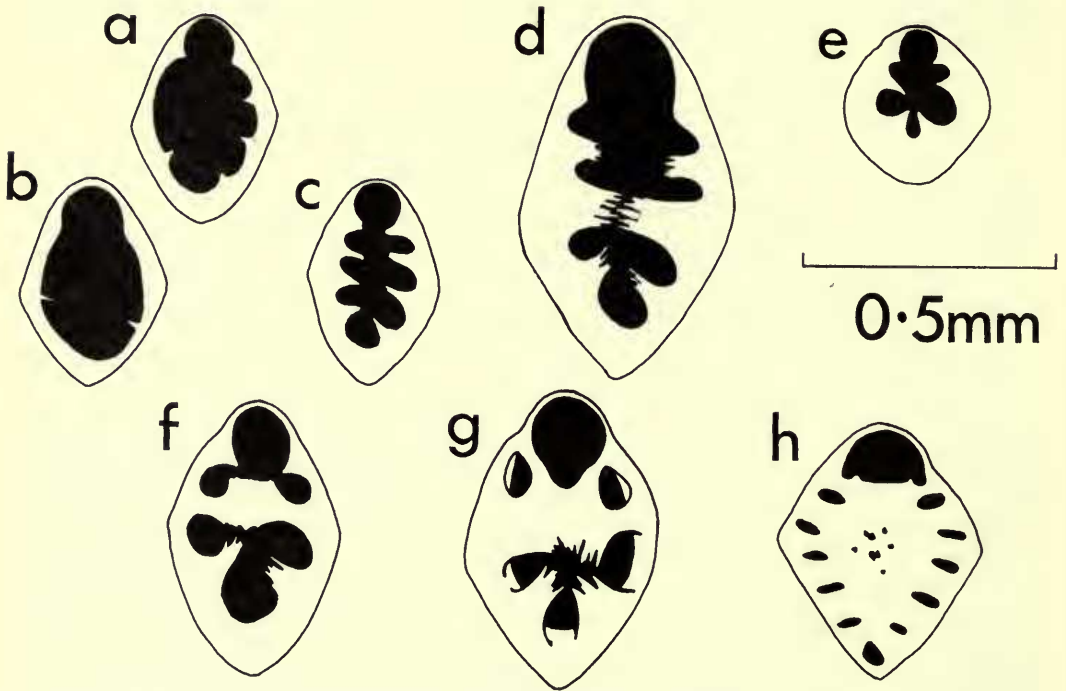


FIG. 2. Development of the cryptocyst in *Cupuladria* and *Discoporella*. Drawings semi-diagrammatic. a-e, *Cupuladria*. a, b, *C. owenii disciformis*. a. Form with vestibular arch with convergent sides, and several cryptocystal denticles. b. Form with vestibular arch with divergent sides, and very reduced cryptocystal denticles. c. *C. owenii*. d. *C. multispinata*. e. *C. doma*. f-h, *Discoporella* f. *D. reussiana*. g. *D. ocellata*. h. *D. umbellata*.

Nearly all the deformed colonies originate from regenerating fragments, and the irregularities are due to one or more radial rows failing to develop (see p. 195). Canu & Bassler's figure purporting to be of the frontal surface of *C. multispinata* with chitinous parts intact (1923, text-fig. 13 I) shows opercula with a strong basal sclerite and a horizontal cryptocyst with opesiules in one of the zooecia; it is almost certainly referable to *D. umbellata* (see p. 221).

Canu & Bassler (1923 : 77) described, as *C. haidingeri*, fossil specimens from Europe, in which the zooecia were large, like those of *C. multispinata*. *C. haidingeri* as defined by Lagaaij (1952 : 35) has small zooecia like *C. owenii*. Canu & Bassler gave a Lz of 0.60 mm., and measurements taken from their pl. 1, fig. 15 give an average length of 0.58 mm. It should be noted here that whereas the measurements given by Canu & Bassler for their *C. haidingeri* apparently include the vibraculum, those given for their *C. multispinata* are found (when compared with text-figure 13H), not to include it.

The specimens from Madeira referred by Silén to *C. owenii* have been re-examined, they belong to *C. multispinata*.

In west African collections where both *C. multispinata* and *C. owenii* are found, the basal surface of unworn colonies is so different that the two species may be distinguished by it even in young specimens.

The distribution of Recent specimens of *C. multispinata* is restricted to two areas: the northerly, from the south west Mediterranean to the coast of Senegal, and the southerly, off the the South African coast. Although there are differences between the two populations, the South African colonies being larger and more domed in shape, the characters of the zooecia are similar. *C. multispinata* has been recorded from depths of 7–105 m.

10 *Cupuladria owenii* (Gray)

(Pl. 2, figs. 3A, B, Text-fig. 2c)

Lunulites owenii Gray, 1828 : 8, pl. 3 figs. 15, 15a, 15b Coast of Africa.

Lunulites denticulata Conrad, 1841 : 348, Miocene, N. Carolina.

Lunulites denticulata Conrad : Lonsdale, 1845 : 503, text-figs. a, b, Miocene, N. Carolina.

Cupularia owenii (Gray) Busk, 1854 : 99, pl. 115, figs. 1–5, Coast of Africa.

Not *Cupularia denticulata* (Conrad) Busk, 1859 : 85 (= *C. haidingeri* (Reuss), see Lagaaij, 1952).

Cupularia denticulata (Conrad) Canu & Bassler, 1923 : 79, pl. 15, figs. 6–10, Miocene, N. Carolina and Florida, Pliocene, S. Carolina and Florida.

Lectotype, see Hastings (in press).

MATERIAL. "Calypso" Coll. I, Stn. 7*, 9° 40' N., 13° 53' W., 17.v.56, 18 m., C4H (C). Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C55G.

Marche-Marchad Coll. I. Konakrey, Guinée Ise., 2E (C). Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3A. S.W. Madeleines, 21.i.54, 46–48 m., 46C.

III. Au sud de presque l'île du Cap Vert, 18.ii.54, 46–50 m., 1E. Mission Guinée Pte 50, Parages des Fles de Los, Konakrey, 21.i.53, 19 m., 30A (C).

British Museum Coll. West coast of Africa, 1899. 7. 1. 4879, received from Gray,

Busk Coll. Canaries, M'Andrew, 1899. 7. 1. 1249, Busk Coll., and 1892. 6. 17. 1-4. Port of Oratava, Canaries, 1899. 7. 1. 1224, Busk Coll. South Africa, 1963. 1. 16. 12, O'Donoghue Coll. S. Africa, Cape Infanta N.E. by N. 19 miles, 46 fath., 1949. 11. 10. 622C, 623C, N.E. by N. $\frac{1}{2}$ N., 13 miles, 43 fath., 1949. 11. 10. 618B, N.E. by N. $\frac{1}{4}$ N., 14.5 miles, 45 fath., 1949. 11. 10. 621A; Great Fish River lighthouse N.E., 9 miles, 51 fath., 1949. 11. 10. 653A, Burrows Coll. Palaeontological Department, 2 miles S.W. Magnolia, S. Carolina, Duplin marl, Miocene, D 34410-18 and D 34419-30.

Naturhistoriska Riksmuseet, Stockholm. Atlantic, 27° 16' N., 23° 21' W., at the surface, FBS 312 part, (No. 7) (see p. 194).

Philadelphia Academy, Conrad Coll. Wilmington, N. Carolina.

U.S. Nat. Mus., Bassler Coll. Pliocene (Waccamaw marl), Waccamaw River, S. Carolina, No. 80710, Plesiotypes *C. denticulata*, fig'd. Canu & Bassler, 1923. Caloosahatchee marl, Pliocene, Florida.

C. owenii is not represented in the Achimota Coll.

Zoarium small (average diameter 5 mm.), zoecia small. Sides of vestibular arch curved, convergent, with a pair of well developed distal cryptocystal denticles. Operculum longer than wide, without a proximal sclerite. Descending cryptocyst finely tuberculate, with 4-6 denticles varying from wide, irregular denticles to narrow spinules. Central zoecia closed. Basal surface grooved, finely and regularly tuberculate or smooth and glassy.

DIMENSIONS. Lz 0.37-0.47 mm., lz 0.20-0.37 mm., La 0.32-0.35 mm., Lvo 0.08-0.13 mm., Ls 0.60-1.40 mm., Lo 0.07-0.09 mm., lo 0.09-0.10 mm.

The slide, 1899. 7. 1. 4879, which is labelled " West coast of Africa ", was received by Busk from Gray. It consists of two fragments, one of which was figured by Busk (1854, pl. 115, fig. 3), see Hastings (in press). The frontal of Gray's specimen is worn, but shows the small zoecia and convergent vestibular arch. The basal surface is smooth, glassy and grooved, a condition found in many specimens from the Marche-Marchad Collection. Specimens from the Achimota Collection have a finely tuberculate basal surface, but also show that the smooth type is not an effect of wear. Some colonies have the more central parts smooth and the later growth tuberculate; whilst in others the position of these types of surface is reversed.

The identity of *L. denticulata* Conrad with *L. owenii* Gray was suggested by Lonsdale (1845: 503), who also described the closed, central zoecia. Specimens of *C. denticulata* from Conrad's Collection, from Wilmington, N. Carolina, and from Bassler's Collection, from S. Carolina and Florida, agree in all respects with the type of *C. owenii* and thus extend its range in time and space to the Miocene and Pliocene of North America. The fossil material shows a similar range in variation of characters of both frontal and basal surface to that of Recent zoaria from west Africa. The specimens from the Caloosahatchee marl are small, the largest zoarium having a diameter of 4 mm., the smallest of 2 mm.; and those from the Waccamaw marl are generally larger and flatter. A few zoaria from Caloosahatchee have a growth form approaching that of *C. doma*; the basal concavity being nearly filled by secondary

calcification. However, the surface is still finely tuberculate, and there are no peripheral closed zooecia or enlarged vibracula (see below).

Generally, the small size of the zooecia distinguishes colonies of *C. owenii* from those of *C. multispinata*, even to the naked eye. In young colonies, the size of some of the zooecia may be similar, but the zoaria may then be separated by the basal surface (see above). In well preserved colonies of *C. owenii*, the strongly incurved vestibular arch, with the distinct distal denticles, is completely unlike that of *C. multispinata*, and resembles that of *C. doma*, from which *C. owenii* is distinguished by the absence of any trace of proximal sclerite on the operculum, the basal surface, and by the absence of peripheral kenozoecia or enlarged vibracula. *C. owenii* is very similar to the European fossil *C. haidingeri* (Reuss) (see Lagaaij, 1952 : 35, 1953), but differs in its finely tuberculate or smooth basal surface. A specimen of *D. owenii* (Marche-Marchad Coll. III, 30A) has a regenerated zoarium where many of the first zooecia budded from the edge of the fragment have become closed in the same manner as the ancestrular zooecia of other colonies.

The S. African zoaria are slightly larger and more domed than those from west Africa, and the distal pair of denticles is less well developed. The small zooecia and the glassy basal surface distinguish them from S. African colonies of *C. multispinata*.

The Recent distribution of *C. owenii* appears to be restricted to the African coast where it is known from the Canaries to the Bay of Biafra, and off S. Africa. It has not been found from depths of more than 95 m., and for this reason is unlikely to have been the species listed by Calvet (1907 : 393) from 1900 m., Cape Verde Islands, as "*Cupularia umbellata* . . . a la forme de *denticulata* de Conrad" (see p. 222).

II *Cupuladria owenii* subsp. *disciformis* n. subsp.

(Pl. 2, figs. 1A, B, Text-figs. 2a, b)

HOLOTYPE. Museum d'Histoire naturelle, Paris, C43A, pt.

PARATYPES. "Calypso" Coll. I. Stn. P1, entre Pta da Mina et I. S. Ana, 21.vi.56, 10-12 m., C44A. Stn. P7*, entre Pta da Mina et P. Novo Destino, 26.vi.56, 6 m., C47A. Stn. P8, I. S. Ana, 27.vi.56, 2-4 m., C43A.

C. owenii disciformis is not present in the Marche-Marchad nor the Achimota Collections.

Zoarium flattened, disc-like, average diameter 7 mm. Zooecia small, narrow, Cryptocyst descending steeply, with 2-4 small, simple denticles. Sides of vestibular arch not strongly convergent, distal denticles weakly developed. Central zooecia closed. Opercula wider than long. Basal surface with grooves and fine tubercles. Tentacles 13-16 (see p. 203).

DIMENSIONS. Lz 0.37-0.53 mm., lz 0.20-0.35 mm., La 0.40 mm., Lvo 0.09-0.10 mm., Ls 0.60-0.90 mm., Lo 0.05-0.06 mm., lo 0.11-0.12 mm.

At first sight, this form is so unlike *C. owenii* that it might be thought to be a distinct species. Detailed examination of the colonies shows, however, that some zooecia have a vestibular arch with convergent sides, and more numerous cryptocystal

denticles, than others. These zooecia approach those of *C. owenii* in appearance. The vestibular arch varies in character in *C. owenii* (see above), and it is possible that a series of forms might be found linking the two extremes of variation.

This population was collected from one small area in the Bay of Biafra, from very shallow water. The zoaria all have polypides, and chitinous parts intact. They were associated with many specimens of *Caulibugula* sp., which were not, however, attached to the lunulitiform zoaria.

C. owenii disciformis is separated here because each of the large number of colonies examined (over 100), shows a high level of consistency of correlation of the characters distinguishing them from typical *C. owenii*. These characters are: the flattened shape; the slightly larger zooecia and coarser basal tubercles; the shallow opercula; and the reduction in cryptocystal denticles. In some zoaria, this reduction is such that the zooecia resemble those of *C. pyriformis* (Busk).

Studer (1889: 7, 13) listed *C. pyriformis* from west Africa, but it seems unlikely that it occurs anywhere in the eastern Atlantic (see Cook, 1965, 169). Although Studer's record may have belonged to *C. canariensis* or *C. biporosa*, it is also possible that the specimens were of *C. o. disciformis*, which, like *C. pyriformis*, has a ridged, finely tuberculate basal surface.

Five unnamed fossil specimens from France have similar characters to those of *C. o. disciformis*. Two zoaria are from the Burdigalian of Léognan (Lower Miocene, S. of Bordeaux, Gironde, D 25002 and 25004); they are very flat, regenerated fragments. The remaining three zoaria are from the Pliocene of Biot (near Antibes, D 49301-3); they are slightly more domed, and originate from ancestrula. The zooecia of all the specimens are slightly larger than those of *C. o. disciformis* (Lz 0.40-0.57 mm.), but like them, nearly all have a vestibular arch with divergent sides, and rarely more than 3 small lateral cryptocyst denticles. The basal surface of all the colonies is finely tuberculate. No reference has been found in the literature to this form, and further material would have to be examined before its relationship with *C. o. disciformis* could be established.

12 *Cupuladria doma* (d'Orbigny)

(Pl. 1, fig. 7, Text-figs. 2e, 3)

Discoflustrella doma d'Orbigny, 1853: 561, Recent, Algeria.

Cupularia johnsoni Busk, 1859a: 67, pl. 23, figs. 1-5, Madeira. Norman (part), 1909: 290, pl. 38, figs. 1-4, Madeira (not figs. 5-6 = *C. multispinata*, see p. 210). Canu, 1917: 139. Waters, 1921: 413, pl. 29, fig. 17, pl. 30, figs. 23, 30, 31, Oran, Madeira.

Cupularia doma (d'Orb.) Smitt, 1873: 15, pl. 3, figs. 81-84, Florida, 29 fath. Canu & Bassler, 1923: 77, pl. 1, fig. 15, pl. 15, figs. 1-5, Miocene, N. Carolina. 1928: 64, pl. 6, figs. 2-5, Florida, 56 fath. 1928a: 23, pl. 2, figs. 1-4, Cap Blanc, 20-30 m.

?*Cupularia reussiana* Manzoni: Neviani (part), 1895: 102, Recent, Algeria.

Discoporella doma (d'Orbigny) McGuirt, 1941: 64, pl. 2, figs. 1, 4, Miocene, Louisiana. Maturo, 1957: 41, figs. 48, 49, N. Carolina. Cheetham & Sandberg, 1964: 1022, text-fig. 15, Quaternary, Louisiana.

Cupuladria doma (d'Orbigny) Gautier, 1962: 54, Algeria, 75-80 m.

MATERIAL. "Calypso" Coll. I, Stn. 1*, 21° 05' N., 17° 14' W., 10.v.56, 43-45 m., CIH.

Marche-Marchad Coll. I, Konakrey, Guinée Ise, 2D. Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3D. Sud de Gorée, 27.x.53, 38-42 m., 7A; 24.xi.53, 40 m., 8A; 39.5 m., 9F; 40-41 m., 11G. Baie de Seminoles, 8.xii.53, 38 m., 39B. S.W. Madeleines, 15.ix.53, 48 m., 22A; 9.i.54, 45-49 m., 26F; 21.i.54, 46-48 m., 46D. Sud de presque l'île du Cap Vert, 18.ii.54, 95 m., 33B.

Coll. II. Alignment Gorée, Cap Manuel, hauteur de Madeleines, 19.x.56, 35-42 m., 9A. S.W. Madeleines, 9.i.54, 47.5 m., 31C. Baie de Seminoles, 8.xii.53, 38 m., 36B.

Coll. III. Sud de presque l'île du Cap Vert, 18.ii.54, 46-50 m., 1F. Sud de Gorée, 13.xi.53, 33-35 m., 9D. Either as above or S.W. Madeleine, 15.ix.53, 48 m., 16H and 17D. Dragage 1 "Gerard Freca", 18.ii.54, 23H; Dr. 4, 97-98 m., 28F; Dr. 5, 15D, 27E. 27.xi.53, 33-34 m., 29F. No information, 24J.

British Museum Coll. Madeira, 1879. 5. 28. 6, and 1911. 10. 1. 649, 650, 1912. 12. 21. 1003, Norman Coll; Bay of Funchal, 50 m., 1963. 2. 28. 5, Cook Coll., mud*. Canaries, 1899. 7. 1. 1240, Busk Coll. Mediterranean, 1899. 7. 1. 1243, 152 fath.; 1242, 5-51 fath.; 1245, 151 fath., Busk Coll. Tangier, 1899. 7. 1. 1244, 164, Busk Coll. Râs el-Amouch, Algeria, 1899. 7. 1. 1247; 1245, 45 fath., Busk Coll. Oran, 1903. 3. 6. 1-4, and 1911. 10. 1. 645, Norman Coll. Gulf of Mexico, 28° 45' N., 85° 2' W., 30 fath., Stn. 2405, "Albatross", 1932. 3. 7. 102, Canu & Bassler Coll. S.S.W. John's Pass, Florida, 34 fath. 1959. 1. 6. 5, Lagaaij Coll.

C. doma is not represented in the Achimota Collection.

Zoarium small (average diameter 4.5 mm.), steep-sided, sometimes solid basally. Zoecia small, vestibular arch strongly curved, with well developed distal cryptocystal denticles. Operculum with a complete or partial proximal sclerite. Cryptocyst descending gently, with wide denticles which occasionally fuse proximally. Basal surface frequently solid, grooved or smooth, or with a small central cavity with elongated spiny tubercles. Central zoecia and those at the periphery closed in fully grown colonies. Peripheral vibracula enlarged, occasionally more than one series developed. Tentacles 13-16 (see p. 203).

DIMENSIONS. Lz 0.34-0.42 mm., lz 0.30-0.37 mm., La 0.34-0.37 mm., Lvo 0.09-0.19 (peripheral) mm., Ls 0.50-1.70 mm. (peripheral), Lop 0.07-0.10 mm., lop 0.10-0.12 mm.

D'Orbigny's description of *Discofustrella* mentions the "Gros pore spécial" (= vibraculum) in front of each zoecium, and his specimens of *D. doma* were examined and their identity confirmed by Smitt (see below). D'Orbigny also described and figured *Discofustrellaria doma* (p. 509, pl. 722, figs. 6-10), a Cretaceous fossil, probably referable to *Lunulites* (see Waters, 1921 : 408).

Unfortunately, Canu and Bassler (1923 : 77) confused the two references and quoted "*Discofustrellaria doma* d'Orbigny, p. 561" in their synonymy, a combination followed by Gautier (1962 : 54), and by Annoscia (1963 : 227, as *Discofustrellaria* (sic)).

Smitt compared his specimens from Florida with Algerian material from Busk ; he also examined specimens in d'Orbigny's Collection (see Canu & Bassler, 1923 : 78), as did Canu (1917 : 139), who, nevertheless, still placed *C. doma* in the synonymy of *C. johnsoni*. There has been some confusion of *C. doma* with *Discoporella reussiana* (see below). Specimens labelled "*C. reussiana*", some from Levinsen (1903. 3. 6. 1-4), others in the Norman Collection (1911. 10. 1. 645), are referable to *C. doma*.

The west African material shows a range in development of the proximal opercular sclerite, which is, for example, complete in Marche-Marchad Coll. I 39B, but only partial, and absent centrally in Coll. II 9A.

The basal surface of *C. doma* may consist of a concavity, with long spinous tubercles, or be flat, and smooth or tuberculate. Although the solid state is apparently an effect of age, it is not correlated with growth in a simple manner, as very small colonies may have flattened bases, whereas in larger zoaria they may be concave. There seems, however, to be a correlation between the occurrence of peripheral kenozoocia and a flattened, solid basal surface, and presumably a colony at this stage does not grow further, as no zoarium has been found with new zooecia budding from closed peripheral kenozoocia. In these fully grown colonies, there may be several series of peripheral vibracula ; they are enlarged, and their setae may be much longer than those of the rest of the colony. The intervening kenozoocia are still present, but have become progressively smaller, until the zoarium has the appearance of possessing two or three rows of vibracula only at the periphery. A section through a zoarium shows that the cavity of each zooecium is present, but that the angle of its longitudinal axis in relation to the axis of the colony is such, that its projection on to the plane of the zoarial surface is very small. Thus, when the opesia is closed by calcification, the kenozoecial frontal is hardly noticeable, and the enlarged vibracular chambers appear to be adjacent to each other (see Text-fig. 3).

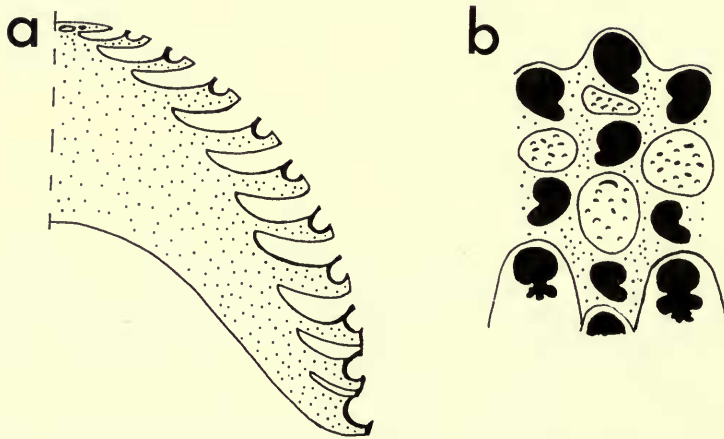


FIG. 3. *Cupuladria doma*, closed peripheral zooecia, drawings semi-diagrammatic. a. Section through a zoarium, $\times 20$. b. Frontal view of enlarged peripheral vibracula and closed peripheral zooecia, $\times 40$.

There may be some relationship between the presence of closed peripheral kenozoecia and the form of the zoarium. Although the closed zoecia are typical of *C. doma* they may also occur in specimens of other species which develop apparently aberrant small, high zoaria with a solid base (see Cook, 1965 : 162, and p. 208). Duvergier (1924 : 20) mentioned that some specimens of *C. porosa* Busk (= *C. haidingeri* (Reuss), see Lagaij, 1952 : 36) had two rows of peripheral zoecia.

C. doma is very similar in many features to *C. owenii*, which occasionally develops small high colonies (see p. 215), but it may be distinguished by its slightly smaller zoecia, its basal surface, and the presence of a proximal sclerite on the operculum.

The African distribution of *C. doma* is confined to the more northerly coasts from Algeria to Senegal, and includes the Canaries and Madeira, but not the Cape Verde Islands. It extends to greater depths than *C. owenii*, and has been recorded from 8–369 m.

13 *DISCOPORELLA* d'Orbigny

Discoporella d'Orbigny, 1852 : 472. Hastings 1930 : 718. Cheetham & Sandberg, 1964 : 1022.

TYPE-SPECIES *Lunulites umbellata* DeFrance, 1823, Miocene, France.

Zoarium lunulitiform. Zoecia with a well-developed vestibular arch. Horizontal cryptocyst lamina complete, formed of fused denticles. Opesiular indentations or closed opesiules present. Vibraculum distal to each zoecium. Vicarious vibracula absent. Basal surface grooved and tuberculate, not divided into sectors. Central zoecia closed.

14 *Discoporella reussiana* (Manzoni)

(Pl. 3, fig. 1, Text-fig. 2f)

Cupularia reussiana Manzoni, 1869 : 27, pl. 2, figs. 19, 19¹ (as 18, 18¹ in text), Tertiary, Italy. Waters, 1878 : 16, Pliocene, Italy. Canu & Bassler, 1923 : 78, pl. 1, figs. 19–22, Pliocene, Italy.

Cupuladria reussiana (Manzoni) Annoscia, 1963 : 226, pl. 9, fig. 2, pl. 10, fig. 2, pl. 13, fig. 1, pl. 14, figs. 1a, 1b, Quaternary, Italy.

MATERIAL. "Calypso" Coll. Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48D (C), with *Cleidochasma porcellanum* (Busk), C55L.

D. reussiana is not represented in the Marche-Marchad nor Achimota Collections. Zoarium domed, sometimes higher than wide (average diameter 6 mm.). Zoecia wide, proximal part of vestibular arch strongly curved and flanged. Cryptocyst descending gently at first, coarsely tuberculate. Horizontal cryptocyst formed by fusion of wide, irregularly shaped denticles, with 2–4 pores. Distal pair of denticles forming a bar, with a wide tooth protruding distally into the opesia, forming two lateral opesiular indentations. Basal surface grooved with large tubercles, which obscure the slight threads marking the grooves in peripheral zoecia.

DIMENSIONS. Lz 0.48–0.60 mm., lz 0.30–0.42 mm., La 0.36 mm., Lvo 0.14–0.17 mm.

Norman (1909 : 290) included *C. reussiana* Manzoni in his synonymy of *C. johnsoni*, and Waters (1878 : 16) placed *C. doma* Smitt (sic) in the synonymy of *C. reussiana*. Neviani (1895 : 102) included *C. doma* in the distribution of *C. reussiana*, giving the localities of Recent specimens as Algeria and Florida.

There is no doubt that the "Calypso" specimens are referable to Manzoni's species, which has hitherto been described only from European Tertiary and Quaternary deposits. Manzoni's fig. 19 shows the large cryptocystal pores and the toothed distal bar which is not present in the majority of the zooecia figured by Canu & Bassler.

D. reussiana resembles *C. doma* and *C. owenii* in the strongly flanged vestibular arch, but the horizontal cryptocyst lamina is similar to that of *D. ocellata*, (see below) and forms a link in the series of species of which the end term is *D. umbellata*.

The specimens of *C. canariensis*, *C. owenii*, *D. reussiana* and *D. ocellata* from "Calypso" Stn. 45, in the Bay of Biafra, are all dark grey in colour, quite unlike those of the other west African localities, which are light brown. Those of *D. reussiana* have no chitinous parts and some are worn, but, as polypides are present in the zooecia of the majority of zoaria of the other 3 species, it is improbable that the specimens of *D. reussiana* are displaced fossils, and therefore it must be presumed that the species has existed continuously from Tertiary times.

15 *Discoporella ocellata* n.sp.

(Pl. 3, fig. 2, Text-fig. 2g)

MATERIAL. HOLOTYPE, Museum d'Histoire naturelle, Paris, C48C pt.

"Calypso" Coll. I, Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48C, C55K Lagaaij Coll., Nigeria D. 220.

D. ocellata is not represented in the Marche-Marchad nor Achimota Collections.

Zoarium fairly large (average diameter 8 mm.). Zooecia with lateral cryptocyst descending moderately at first, then salient, forming a narrow shelf. Horizontal cryptocyst lamina formed by fusion of wide, irregular denticles originating on the frontal side of the shelf. Vestibular arch with two curved flanges uniting centrally with each other below the orifice, and with the fused distal lateral denticles, forming a sinuate opesia with two closed lateral opesiules. Operculum without a basal sclerite. Basal surface grooved, grooves marked by a thread, not obscured by the irregular tubercles.

DIMENSIONS. Lz 0.55-0.63 mm., lz 0.36-0.42 mm., Lvo 0.10-0.14 mm., Ls 0.70-2.00 mm., Lo 0.10-0.12 mm., lo 0.12-0.15 mm.

The zoaria are more flattened than those of *D. reussiana*. In worn specimens of *D. ocellata* the proximal bar between the opesia and opesiules may be broken, producing a trifoliate opesia very similar to that of *D. reussiana*. The slope of the cryptocyst and position of the origin of the cryptocystal denticles are then the only features distinguishing the species on the frontal surface. In *D. ocellata* the cryptocyst descends moderately at first, then becoming salient, forming a shelf, which may be seen distally and below the horizontal denticles which originate above the angle produced by the change of slope (see Text-fig. 2g). In *D. reussiana* the descent of the

cryptocyst is at first gentle and then, after the origin of the horizontal denticles, steep, so that no shelf is visible below them (see Text-fig. 2f).

There is a superficial resemblance between *D. ocellata* and the photographs of *Cupularia bioculata* Canu (1904: 10, pl. 2, figs. 21, 22, Miocene, Patagonia). *C. bioculata* is shown with a sinuate opesia and a pair of opesiules. None of the zooecia has a distal vibraculum, and the occasional large individuals may be broken vicarious vibracula. The absence of small vibracula excludes it from the Cupuladriidae, and it is perhaps referable to *Selenaria*.

D. ocellata is related to both *D. reussiana* and *D. umbellata* and forms an important link between those species. It differs from *D. reussiana* in its closed opesiules and basal surface, and from *D. umbellata* in its sinuate opesia, basal surface, and operculum, which has no proximal sclerite.

16 *Discoporella umbellata* (Defrance)

(Pl. 3, fig. 3, Text-fig. 2h)

Lunulites umbellata Defrance, 1823: 361, pl. 47, figs. 1a, 1b, Miocene, France.

Cupularia lowei Busk, 1854: 99, pl. 116, figs. 1-6.

Discoporella umbellata (Defrance): Lagaaij, 1953: 16, pl. 1, fig. 3, Miocene, Netherlands. Cook, 1965: 177, pl. 1, fig. 7, pl. 3, figs. 1, 3, 5, 6, text-fig. 4.

MATERIAL. "Calypso" Coll. I, Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m., C4G. Stn. 17, 5° N., 5° 28' 30" W., 21.v.56, 27 m., C56G (C). Stn. 18, 5° 2' 5" N., 5° 24' 4" W., 21.v.56, 20-25 m., C5D. Stn. 19, 5° 2' 30" N., 5° 24' 40" W., 21.v.56, 21-27 m., C57I. Stn. 29*, 4° 3' N., 6° 12' E., 26.v.56, 32 m., C49A. Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48A (with *Labioporella dipla* Marcus and *Cleidochasma porcellanum* (Busk)), C55H. Stn. 63, 0° 20' N., 6° 47' E., 17.vi.56, 54-40 m., C28A. Stn. 77, 0° 25' 40" N., 6° 40' 10" E., 21.vi.56, 50 m., C45A. Stn. 90*, 1° 36' 55" N., 7° 22' E., 26.vi.56, 30 m., C37B. Stn. P14*, Dans l'axe de la Baie, Principe, 29.vi.56, 15 m., C59A.

Coll. II. Stn. 73, C72A. Stn. 88, 16° 15' N., 22° 56' 5" W., 26.xi.59, 54 m., C80A.

Marche-Marchad Coll. I. Konakrey, Guinée Ise, 1G, 2F. Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3C. Sud de Gorée, 27.x.53, 38-42 m., 7C. S.W. Madeleines, 15.ix.53, 48 m., 20C; and 21.i.54, 46-48 m., 46F (C). Presque l'île du Cap Vert, 18.ii.54, 95 m., 33P (C). Baie de Seminoles, 8.xii.53, 38 m., 39D (C).

Coll. II, as above, 36C. Alignment Gorée-Cap Manuel, lantern de Madeleines, 19.x.56, 35-42 m., 9B (C), 20-25 miles au large de Saloum, 8.iii.55, 35-37 m., 26A (C).

Coll. III. Au sud de presque l'île du Cap Vert, 18.ii.54, 46-50 m., 1D. Either S.W. Madeleines, 15.ix.53, 48 m., or Sud de Gorée, 34-37 m., 13.xi.53, 16F. Dragage 4, "Gerard Freca", 97-98 m., 28H; Dr. 5, 18.ii.54, 15C, 27D. 33-34 m., 27.xi.53, 29D. Museum Guinée, parages de Flos de Los, Konakrey, 21.i.53, 9 m., 30B. No information, 24H.

Achimota Coll. I, Stn. 47*, Dredge Haul No. 1, 4.i.51, 44 m., 14d. Stn. 48*,

Dredge Haul No. 2, as above, 22C. Stn. 111*, Agassiz Trawl No. 2, 4.iv.51, 43 m., 49P. Stn. 132,* as above, 2.v.51, 44 m., 42E and 50B (C). Stn. 133*, Agassiz Trawl No. 3, as above, 51 m., 45H. Coll. II, Stn. 133*, see above, 7A. Stn. 111*, see above, 12A.

Zoarium frequently very large (maximum diameter measured, 30 mm.). Zooecia wide, opesia small, nearly straight proximally, with a pair of small denticles. Operculum with a stout proximal sclerite. Lateral cryptocyst descending gently, tuberculate, horizontal cryptocyst a complete lamina, with 8-14 small peripheral opesiules and small scattered central pores, which are frequently occluded. Vibracular opesia large, proximal edge denticulate. Basal surface with short grooves, irregular pits and tubercles. Tentacles 13-16 (see p. 203).

DIMENSIONS. Lz 0.60-0.70 mm., lz 0.45-0.65 mm., La 0.40-0.43 mm., Lvo 0.20-0.25 mm., Ls 0.90-1.65 mm., Lo 0.10-0.12 mm., lo 0.12-0.15 mm., Lop 0.13-0.15 mm., lop 0.15-0.20 mm.

C. lowei Busk differs from *D. umbellata* only in its deformed zoaria (see p. 195 and cf. *C. multispinata*, p. 212). The majority of the specimens from the Marche-Marchad Collections II and III are deformed, most of those from Collection I, the "Calypso" Collections, and the Achimota Collection, are not.

The tubules which extend from the basal wall of the cystid cavity to the basal surface of the zoarium have been described by Marcus & Marcus (1962 : 295, pl. 2, fig. 5). In decalcified specimens these appear as minute strands, and were first described by Waters (1921 : 412, pl. 30, figs. 3, 5, 6). Their presence in *D. umbellata* (subsp. *depressa*) was noted by Hastings (1930 : 719), and they are clearly seen in specimens from Rio de Janeiro (British Antarctic Expedition Coll., Stn. 42). The pore in the basal surface described by Waters is present in specimens of *D. umbellata* from Senegal (Marche-Marchad Coll. I 39D). It is present in all peripheral zooecia and remains open in the majority of zooecia of young colonies. In older colonies it becomes obscured by the increasing development of tuberculate secondary calcification. A short groove may be seen in peripheral zooecia running proximally and distally from the pore. As stated by Waters (who described them as muscles), the tubules appear to be inserted into the basal wall along or near the groove. Decalcified specimens from Rio de Janeiro show a small granular mass which corresponds in position to the basal pore.

Calvet (1907 : 393) recorded *D. umbellata* from Madeira (80 m.) and a specimen from the Cape Verde Islands (1900 m.) which was described as "à la forme de *denticulata* de Conrad". In view of the depth given, it seems unlikely to be *C. owenii* (see p. 213), which does not extend to great depths, and it may have been a colony of *D. umbellata*, in which the cryptocyst was worn away or damaged.

Specimens of *D. umbellata* from west Africa are consistent in character, and although larger, agree with the European fossil material. The wide zooecia, the nearly straight proximal edge of the opesia, with its two denticles, and the denticulate edge of the proximal vibracula opesia, are all features not found in the fossil and Recent specimens from the western Atlantic and eastern Pacific which have been separated

as *D. umbellata* subsp. *depressa* (Conrad) (see Cook, 1965 : 180). The development of the horizontal cryptocyst lamina in young peripheral zoecia, however, shows the close relationship of *D. umbellata* to both the subspecies *depressa* and to the denticulate species of *Cupuladria*.

The distribution of *D. umbellata* in these collections extends from Senegal to the Bay of Biafra, and includes the Cape Verde Islands. Recent specimens have also been recorded from Madeira and the Canaries. The recorded bathymetrical range is from 8–130 m.

Dr. R. Lagaaij (*in litt*) 20. x. 64 has drawn my attention to the two distinct species figured as *Lumulites rhomboidalis* by Münster (in Goldfuss, 1829 : 105, pl. 37, figs. 7a–c), from the German Tertiary deposits. Figure 7a greatly resembles a young colony of *Discoporella umbellata*, although no opesiules, and very few vibracula, are figured. Figures 7b and c are the frontal and basal views respectively of a regenerated fragment of a species of *Cupuladria*. Dr. Lagaaij remarks "Of the two localities mentioned on p. 106, that of Kassel is now considered the type locality of the Chattian (Upper Oligocene)" (see Drooger, 1964 : 372), "this would not fit with the presence of *D. umbellata* which first appears in the Aquitanian (Lower Miocene)". In this connection, it should be noted that neither Philippi (1844 : 3) nor Reuss (1865 : 685), who both listed *L. rhomboidalis*, had found specimens in their material.

17 ACKNOWLEDGMENTS

I should like to thank Dr. A. Andersson (Naturhistoriska Riksmuseet, Stockholm), Dr. R. Boardman (Smithsonian Institution, Washington), Prof. Dr. E. Voigt (Geologisches Staatsinstitut, Hamburg), and Dr. H. G. Richards (Academy of Natural Sciences, Philadelphia), for the loan and presentation of specimens and photographs. My thanks are also due to Dr. A. Cheetham (Louisiana State University) and Dr. R. Lagaaij (Shell Exploratie en Produktie Laboratorium, the Netherlands), both for stimulating discussion and criticism, and for the loan of specimens. The photographs were taken at the British Museum by Mr. J. V. Brown and Mr. P. Green. Finally, I am deeply indebted to Dr. A. B. Hastings and Dr. J. P. Harding (British Museum, Natural History) for their continual interest and encouragement.

18 SUMMARY

Nine species belonging to the family Cupuladriidae are described, eight of which occur in west African waters.

Cupuladria canariensis is defined and distinguished from *C. biporosa*; *C. monotrema* is also described, and the occurrence of vicarious vibracula in the three species is discussed.

Three species with denticulate cryptocysts, *C. multispinata*, *C. owenii* and *C. doma*, are defined and distinguished, and a new subspecies, *C. owenii disciformis*, characteristic of very shallow waters in the Bay of Biafra, is described.

The genus *Discoporella* is defined, and three species are described, in which the development of the horizontal cryptocyst lamina is increasingly complex. *D. reussiana*, hitherto recorded as a fossil only, shows similarities with both the denti-

culate species of *Cupuladria* and with *D. umbellata*. *D. ocellata*, a new species, links the zoecial characters of *D. reussiana* and *D. umbellata*.

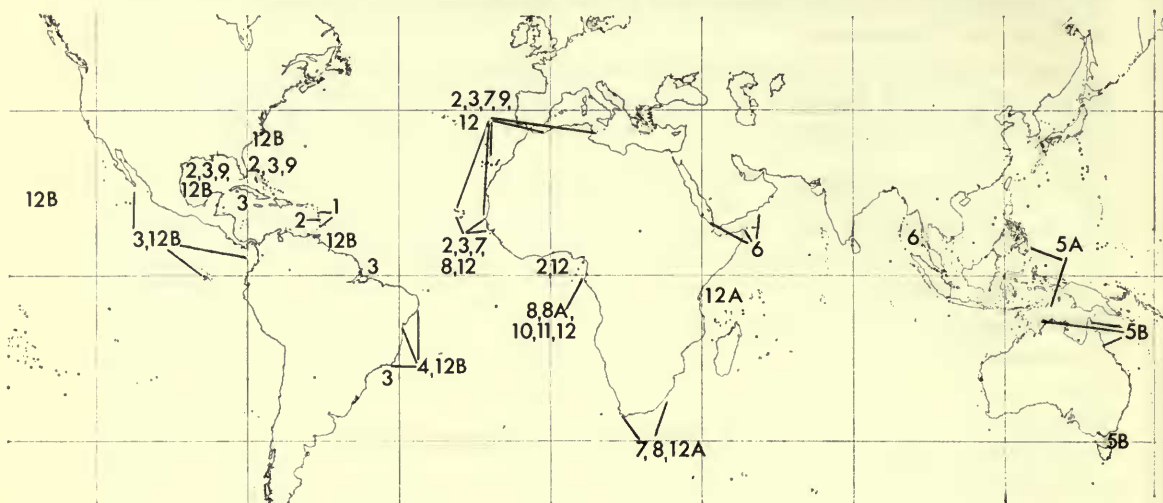


FIG. 4. Distribution of Recent Cupuladriidae. 1. *Cupuladria pyriformis*. 2. *C. canariensis*. 3. *C. biporosa*. 4. *C. monotrema*. 5. *C. guineensis*, A = A form, B = B form. 6. *C. indica*. 7. *C. multispinata*. 8. *C. owenii*. 8A. *C. owenii disciformis*. 9. *C. doma*. 10. *Discoporella reussiana*. 11. *D. ocellata*. 12. *D. umbellata*. 12A. *D. umbellata peyroti*-type zoaria. 12B. *D. umbellata depressa*. (For notes on species 1, 5, 6, 12A and B, see Cook, 1965).

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PLATE 1

Cupuladria, zoaria treated with eau de javelle

- FIG. 1. *C. canariensis* (Busk) Barbados, 1962. I. 26. 2. A. Frontal view. B. Basal view. $\times 7.4$.
- FIG. 2. *C. biporosa* Canu & Bassler. Barbados, 1962. I. 26. 1. A. Frontal view, showing zooecia with wide lateral cryptocysts, and large vicarious vibracula. B. Basal view. $\times 7.4$.
- FIG. 3. *C. biporosa*. Yucatan, Naturhistoriska Riksmuseet, No. FBD 696. A. Frontal view. B. Basal view, showing basal kenozoecia covering the original substrate, cf. *C. canariensis*, fig. 1B. $\times 7.4$.
- FIG. 4. *C. biporosa*. West Indies, Naturhistoriska Riksmuseet, No. FBD 548, a Recent specimen, cf. figs. 6A, B, of a Miocene colony. A. Frontal view. B. Basal view. $\times 7.4$.
- FIG. 5. *C. biporosa*. Jamaica, Miocene, Bowden marl, United States National Museum, No. 80747 pt. Colony with aberrant *doma*-type growth, basal view, showing rows of peripheral vibracula. $\times 7.4$.
- FIG. 6. *C. biporosa*. Jamaica, Miocene, Bowden marl, United States National Museum, No. 80747 pt., cf. figs. 4A, B. A. Frontal view. B. Basal view. $\times 8.1$.
- FIG. 7. *C. doma* (d'Orbigny). Senegal, Marche-Marchad Coll., I, 33 B. Lateral view, showing closed peripheral zooecia. $\times 12$.

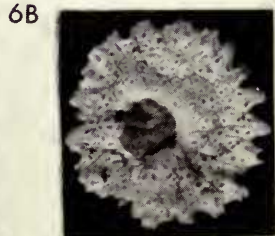
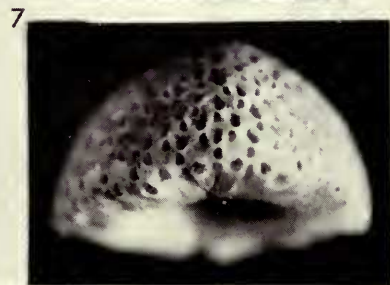
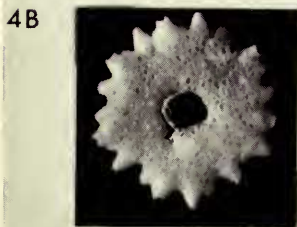
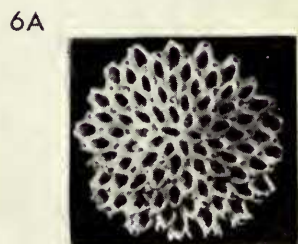
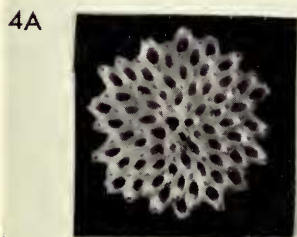
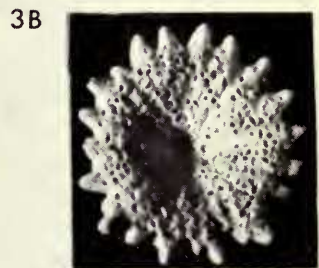
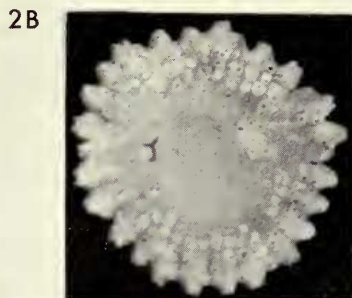
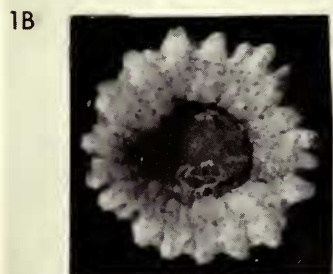
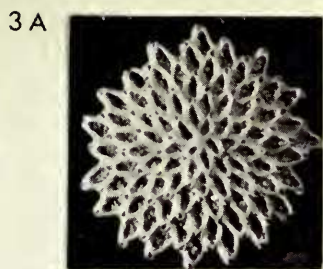
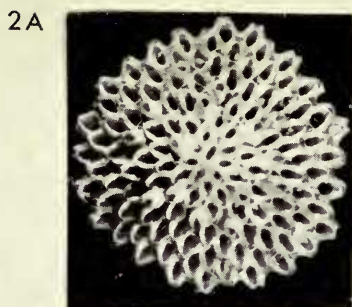
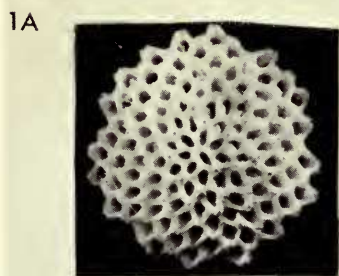


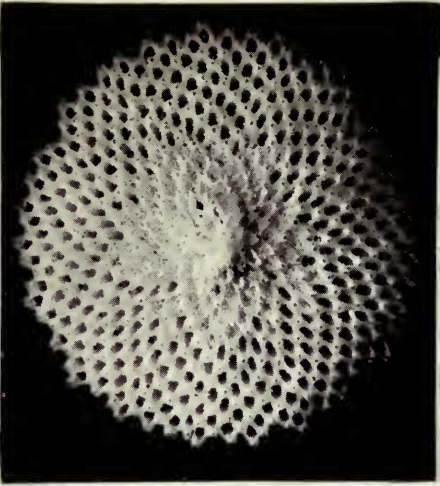
PLATE 2

Cupuladria, zoaria treated with eau de javelle

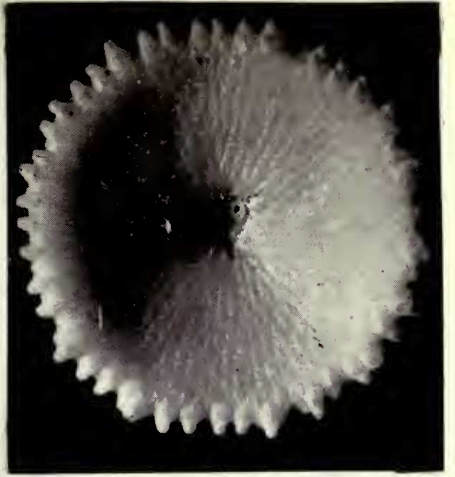
- FIG. 1. *C. owenii disciformis* n. subsp. Bay of Biafra, "Calypso" Coll., C47A. A. Frontal view, showing closed central zooecia, and reduced cryptocystal denticles of other zooecia. B. Basal view, showing fine tubercles. $\times 9$.
- FIG. 2. *C. multispinata* (Canu & Bassler). Senegal, Marche-Marchad Coll., I, 33 A. A. Frontal view, showing numerous cryptocystal denticles. B. Basal view, showing large tubercles and radial "threads". $\times 7.5$.
- FIG. 3. *C. owenii* (Gray). Senegal, "Calypso" Coll., I, C4H. A. Frontal view, showing closed central zooecia, and well-developed vestibular arches of other zooecia. B. Basal view, showing both smooth and finely tuberculate forms of basal calcification. $\times 10$.

N.B. Figures 2 and 3 are not reproduced at the same magnification, so that the marked difference in size between the zooecia of *C. multispinata* and *C. owenii* is not immediately apparent.

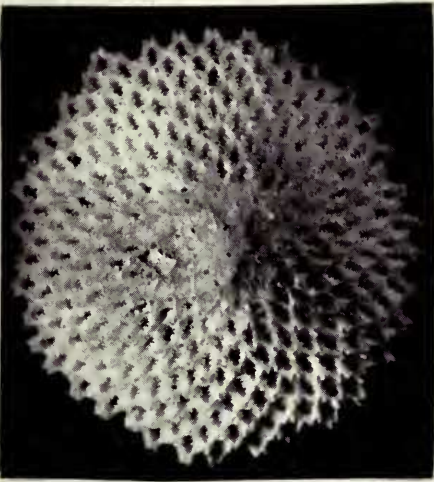
1A



1B



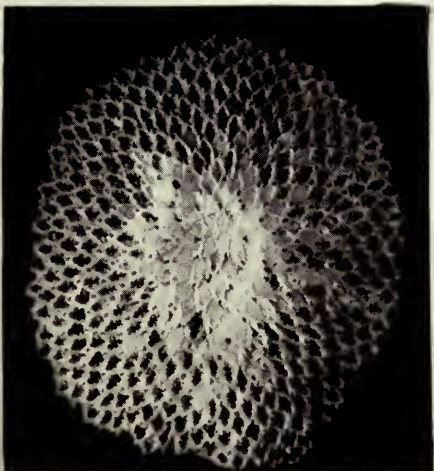
2A



2B



3A



3B

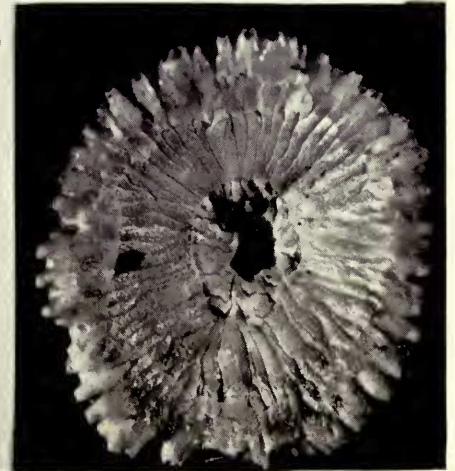


PLATE 3

Cupuladria and *Discoporella*, zooecia and vibracula treated with eau de javelle.

- FIG. 1. *D. reussiana* (Manzoni). Bay of Biafra, "Calypso" Coll., I, C48D. Zooecia showing toothed cryptocystal bar and opesiular indentations. $\times 49$.
- FIG. 2. *D. ocellata* n. sp. Bay of Biafra, "Calypso" Coll., C48C. Zooecia showing sinuate opesia and paired distal opesiules. $\times 53$.
- FIG. 3. *D. umbellata* (Defrance). Ghana, Achimota Coll., II, 7A. Showing the slit indicating the former presence of an Acrothoracid Cirripede. $\times 32$.
- FIG. 4. *C. canariensis* (Busk). Senegal, Marche-Marchad Coll., II, 3A. Showing position of small, hooked vibracula thus: ***. $\times 24$.

