

NOTES ON THE CUPULADRIIDAE
(POLYZOA, ANASCA)



BY

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I INTRODUCTION

RECENT work on the rich west African fauna of species belonging to the Cupuladriidae, has led to an examination of other species and to a general review of the characters of the family. The following notes are an attempt to define the limits of variability of some of these characters, and to delimit groups of species which appear to be related.

Specimens in the Zoological Department of the British Museum are referred to by registered number thus, 1899. 7. 1. . . . ; in the Palaeontological Department thus, D 6474. Measurements of zooecial length have been made from the distal rim of one zooecium to that of the next succeeding radial zooecium, so including the vibraculum.

Measurements are given thus :

Length of zoecium	Lz	Length of operculum	Lo
Width of zoecium	lz	Width of operculum	lo
Length of vibracular opesia	Lvo	Length of zoecial opesia	Lop
Length of vibracular seta	Ls	Width of zoecial opesia	lop

DEFINITION OF TERMS USED. The majority of the terms used may be found defined by Lagaaij (1952 : 12) and Bassler (1953 : 7).

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

Vestibular arch. The distal, crescentic, raised portion of the aperture.

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

2 CUPULADRIIDAE Lagaaij

Cupuladriidae Lagaaij, 1952 : 31.

Lagaaij defined the family to include only the genus *Cupuladria*. A series of species is now known to exist (Cook (in press)) which links the membraniporan forms such as *C. canariensis* (Busk) with the microporan forms like *Discoporella umbellata* (Defrance). Both genera have therefore been included in the Cupuladriidae, the diagnosis of which has been accordingly slightly modified.

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

Lagaaij (1953 : 13) defined the term "lunulitiform" to include conical and discoid zoaria such as those of *Cupuladria*, *Discoporella*, *Lunulites* and *Selenaria*. For reasons given below, the term is here restricted to the first three of these genera, which all bud radially, although it is not assumed that the Cupuladriidae and *Lunulites* are closely related. The term "selenariiform" used by Harmer (1926 and 1957) for both Anascan and Ascophoran conical colonies, is here restricted to zoaria with spiral budding, e.g. *Selenaria*, *Setosellina* and *Heliodoma*. The term "conical" is used here for all the remaining forms described by Harmer, some of which may be attached to the substrate by rootlets, e.g. *Conescharellina*.

It must be stressed that, whereas the combination of characters found in the Cupuladriidae is exclusive, and the limits defining the species are generally well marked, the division of the family into two genera, *Cupuladria* and *Discoporella*, is somewhat arbitrary, depending upon only one character, namely, the extent of the development of the cryptocyst. Until work can be done on the life-histories and breeding of the Cupuladriidae, the importance of this character in relation to, for example, the size of the eggs, the larvae, and the other zoecial structures, cannot be assessed, and *Discoporella* is therefore retained here.

3 STRUCTURE AND DEVELOPMENT OF THE ZOARIUM

Although many free-living colonies are similar in appearance, they differ considerably in structure and development. In the Cupuladriidae both the early astogeny and subsequent growth of the zoarium are distinct from that found in other lunulitiform, selenariiform or conical colonies.

a. *Early astogeny.* The ancestrular area is here defined as comprising the ancestrula and the primary circle of zooecia budded from it. The single ancestrula buds a distal vibraculum, a pair of proximal-lateral zooecia and then one proximal zooecium (see Marcus & Marcus, 1962 : 287). A pair of lateral zooecia follows, and a pair of distal-lateral zooecia is the last to be formed (see Text-fig. 1B). Lagaaij (1963a : 182, text-fig. 10) found that secondary proximal buds were developed before this last pair, but colonies seem to be variable in development at this stage. Evidence has been gained from very young colonies of *Cupuladria* sp. (Gulf of Mexico, 1959. 8. 20. 3, Lagaaij Coll.) and *D. umbellata* (Madeira, 1963. 2. 28. 9, and S. Africa, 1949. 11. 10. 668, Burrows Coll.). Waters (1926 : 426) described a double ancestrula in *C. canariensis*, but none have been seen in any of the many specimens examined, and I agree with Lagaaij (1963a : 184) that it is possible that Waters regarded the proximal bud as the second member of a paired ancestrula.

In one group (*C. canariensis*, group A, see p. 167), the entire ancestrular area may consist of vicarious vibracula (see Smitt, 1873, pl. 2, fig. 70 ; Hastings, 1930 : 714 ; Marcus & Marcus, 1962 : 289 ; Lagaaij, 1963a : 183 ; and Cook (in press)). Although vicarious vibracula in the ancestrular area may sometimes be the result of regeneration of a normal zooecium, most of those found in *C. biporosa* (Canu & Bassler) and *C. monotrema* (Busk) are budded primarily as vibracular individuals. The "special area" described by Canu & Bassler (1923 : 81, pl. 2, fig. 18) is not an ancestrular area, but the growing edge of a regenerating, broken fragment (see below).

The pattern of budding outside the ancestrular area appears to be variable. Another variable character is found in *C. pyriformis* (see 168) and a few colonies of *C. canariensis*, where the vibracular seta of the ancestrula, when closed, is directed towards the right side (viewed frontally) (see Text-fig. 1C). In all specimens of

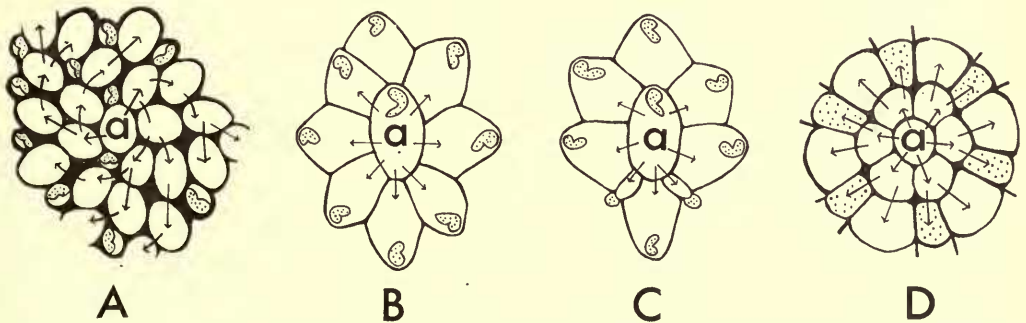


FIG. 1. Early astogeny. a, ancestrula ; vibracula stippled. A. *Setosellina*. Spiral budding. B. Cupuladriidae. Radial budding. C. *Cupuladria pyriformis* (Busk). 1st pair of zooecia aborted. D. *Lunulites*. Radial budding.

other species the seta is directed toward the left side, the seta of the zooecium budded from the proximal end of the ancestrula having the same orientation (see Text-fig. 1B). The seta of the right-proximal-lateral bud is directed to the right, that of the left-proximal-lateral bud to the left (see also Marcus & Marcus, 1962 : 297).

b. *Growth.* Each zooecium and vibraculum develops radially as a unit which arises as a common bud, the vibracular chamber being divided off from the cavity of the zooecium in the later stages of development. The relationship of the vibraculum with the zooecium distal to it is comparable with that of the "recumbent" ovicell of *Crepidacantha* (see Brown, 1954 : 244, footnote). Here the ovicell is fully formed before the development of the next distal zooecium, which grows round it from below. The vibracular chamber in the Cupuladriidae is not terminal and does not reach the basal surface of the zoarium. Thus, although apparently inserted between the zooecia at the frontal surface, the vibracula are not strictly interzooecial, nor are they adventitious or dependent.

The common bud is rarely present, even in specimens preserved in alcohol, as in its peripheral position it is particularly susceptible to damage when the colony is dead, and it is no longer protected by the extended peripheral vibracular setae (see Marcus & Marcus, 1962, and Cook, 1963). The bud arises between peripheral zooecia. The membranous ectocyst is closely applied frontally and basally to the neighbouring zooecia, but over the bud it is convex and free from the underlying structures. A line of demarcation occurs basally where the ectocyst is no longer in contact with the calcareous basal walls (see Text-fig. 2A). On the basal side the bud originates from the distal end of the proximal zooecium, below the vibracular chamber. On the frontal side the upper surface of the bud appears at the distal wall of the vibracular chamber. The membranous frontal part of the bud becomes the frontal membrane of the zooecium, the basal part the endocyst lining the zooecial cavity (see Marcus & Marcus, 1962, pl. 2, fig. 5). This can be seen in well-preserved specimens of *C. indica* (1899. 5. I. 267); *C. multispinata* (1949. II. 10. 617); *Discoporella umbellata* (MM I 39A); and *D. u. depressa*, (Terra Nova Coll., Stn. 42). The relationships of the young common bud have also been observed in living colonies of *D. umbellata* from Madeira.

As the bud enlarges and grows up between the two adjacent lateral zooecia, the basal wall is covered by a calcified lamina, which develops from the point of origin of the bud (see Text-fig. 2A, B). The polypide is first differentiated at the proximal end of the bud before it is completely covered basally by the lamina. As the lamina advances distally, the cryptocyst develops beneath the frontal membrane growing inward from the lateral walls. The lamina curves upward and inward, and the vibracular chamber develops as an inner compartment from the distal end of the bud. The walls of the chamber are thus double-layered laterally, with connecting bars of calcification. Large pores are present in the outer layer (= "chambers" of Marcus & Marcus, 1962 : 295). These calcify further, become smaller, and eventually communicate with the next distal-lateral zooecia to be developed. The vibracular chamber is connected with its proximal zooecium through a large pore in the dividing

wall. An uncalcified area, which is left in the lamina as it curves up sharply distally to the vibracular chamber, calcifies, but leaves a small pore which eventually communicates with the succeeding radial zoecium (see Text-fig. 2). Specimens clearly showing these structures are *C. multispinata* (S. Africa, 1949. II. 10. 94 B, Burrows Coll.) and *D. u. depressa* (Rio de Janeiro, Terra Nova Coll., Stn. 42).

Transverse sections of zoaria frequently show the stem-like extension of the zoecium, below the vibracular chamber of the previous zoecium. Each zoecium thus has a large distal pore communicating with the vibracular chamber, and 2-3 lateral pores communicating with the adjacent distal-lateral zoecia. No pores enter the vibracular chamber laterally, but it communicates with the next distal zoecium in a radial row. Specimens showing the interzoecial pores clearly are: *C. indica* (1899. 5. 1. 267 pt.) and *C. canariensis* (section, 1929. 4. 26. 85 pt.); see also Marcus & Marcus, 1962, pl. 2, fig. 1.

Large colonies of *D. umbellata* (e.g. coast of Ghana, 50B, Achimota Coll.) and *C. canariensis* (Senegal, MM II 3) show rings of growth (see Harmer, 1926 : 267). Apparently these zoaria have grown evenly for a period and then ceased to grow. New budding has been resumed simultaneously all round the periphery, so that a series of concentric ridges may be seen on the basal side.

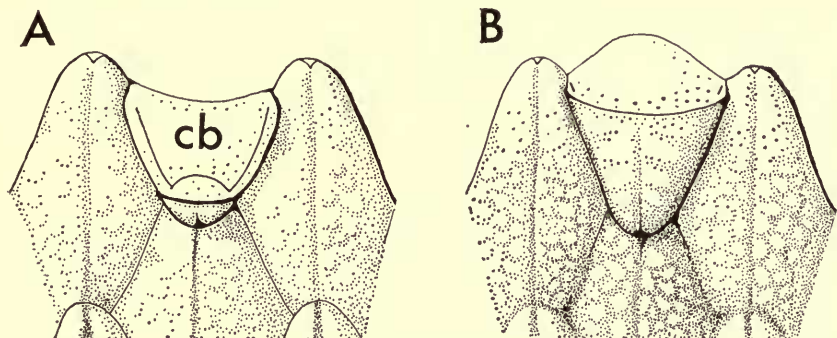


FIG. 2. Growth of the membranous common bud (*c.b.*) and calcareous basal lamina, viewed from the basal side. A. Transparent, membranous common bud developing between two peripheral zoecia. Note the uncalcified area in the distal wall of the vibracular chamber. B. Calcareous curved basal lamina developing over the growing common bud. Note the increased calcification of the previously developed proximal-lateral basal laminae, and the development of the radial median groove.

c. Regeneration and deformation. A large number of colonies are regenerated from broken fragments, and the budding by which a symmetrical colony is re-formed follows a characteristic pattern. Stach (1936a : 63-65) and Darteville (1933 : 70-72) have discussed the fragmentation of colonies, and the ecological significance of this form of regeneration. Darteville (1935 : 559-561) also described the form of budding in *C. canariensis*. He mentioned regeneration as occurring from "calcified zoecia" (see below), and examination of many colonies shows that these closed zoecia are, in fact, the primary buds regenerated from a broken edge of a fragment. The original fragment can usually be seen on the basal side of such colonies, as secondary

calcification at the centre does not seem to occur. The broken zooecia which were distal in position in a fragment regenerate zooecia distally, those which were proximal, regenerate zooecia proximally, in which the zooecial orientation is reversed. Zooecia growing from the lateral walls of old zooecia, are at right angles to the previous direction of growth of the fragment. Each broken zooecium produces one bud laterally from the mid-line of its basal wall, and another bud arises from beneath the vibracular chamber. These zooecia are wide and often slightly distorted (see p. 175). Subsequent budding of radial series, including intercalary rows, is exactly the same as in zoaria developing from an ancestrula. The usual radial alternation in the asymmetry of the vibracular opesia is established in the primary and secondary series of buds (see Text-fig. 3A). The colony of *C. elongata* Sakakura mentioned as distorted by Marcus & Marcus (1962 : 288) is, in fact, such a regenerating fragment.

Marcus & Marcus (1962 : 301) have described a second form of regenerative or "zoarial budding", in which small, fan-shaped zoaria are produced from a single zooecium at the periphery of the parent colony. This form of budding has been seen so far only in the *D. umbellata*-complex (e.g. Madeira, 1912. 12. 21. 1004, Norman Coll.) and in *C. multispinata* (Madeira, 1963. 1. 2. 3 and 4, Norman Coll.). Marcus & Marcus described the results of the fracture of the initial zooecium ("pseudoancestrula"), which frees the young zoarium from the parent colony. It then continues its development, eventually assuming a circular shape by the budding of intercalary series. Colonies arising in this manner have no central substrate present, e.g. a sand-grain or foraminiferan. They may also be recognized by the reversed orientation of the regenerated zooecium developed from the broken pseudoancestrula, and by their early fan-shaped budding.

The pseudoancestrula does not calcify fully on the basal side, and when still attached to the zoarium has been seen to fold frontally when its vibracular seta closes (see Cook, 1963 : 411). When fracture occurs, the basal lamina is detached with the new zoarial bud, but the proximal part of the cryptocyst remains with the parent colony (see Marcus & Marcus, 1962 : 302). The distal part of the pseudoancestrula then regenerates a zooecium orientated in the opposite direction. In the Madeiran material the fracture has not always occurred, and buds have continued to develop attached to the parent colony. Deformed colonies have resulted, some of which have been described as *C. lowei* by Busk (1854 : 99 = *D. umbellata*) and "*C. deformis*" by Waters (1921 : 413 = *C. multispinata*).

Other deformed zoaria, especially of these two species, originate from regenerating fragments, and here, deformation is the result of failure of development of one or more radial rows of zooecia. The cause is unknown, but in some cases it appears to be correlated with the growth of associated Sponges, belonging to the Plocamiidae, on the basal side of the Polyzoan colony. The Sponge appears to have inhibited growth at the origin of the chitinous zooecial bud, just below the penultimate series of vibracular chambers. The radial rows of zooecia adjacent to the affected zooecium or zooecia, produce intercalary series until the radial slit in the colony is closed when the two sides touch. Frequently, these zooecia are unable to form interzoecial connections, and a slit or furrow continues radially through the colony, which, as the

associated Sponge develops, becomes lined with spicules. No example of a spiral slit has been seen in deformed colonies of the Cupuladriidae, and the budding pattern should be compared with that of one deformed specimen of *Selenaria maculata* (Bass's Straits, 1899. 7. 1. 1497), where the slit is distinctly spiral (compare Text-figs. 3C, D). The basal surface of this zoarium also shows traces of a Sponge colony, and although it is possible that the Sponge is a secondary and unrelated growth, the correlation with this type of deformation is interesting.

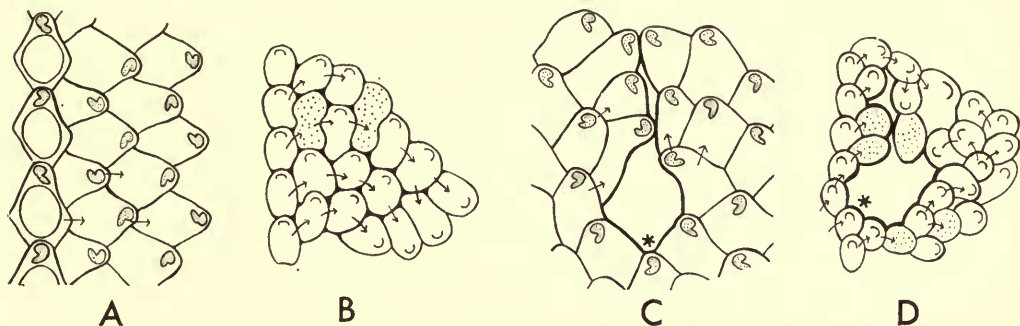


FIG. 3. Regeneration and deformation. Vibracula stippled. A. *Cupuladria*. Regeneration from lateral walls of a radial series. B. *Selenaria*. Spiral regeneration. C. *Discoporella*. Deformation (*), point where distal radial bud has not developed. D. *Selenaria*. Deformation (*), point where lateral distal bud has not developed.

4 CHARACTERS OF SYSTEMATIC VALUE

a. *The central area* is here defined to include the ancestrular area and the centre of the colony where the budding of intercalary radial rows is most frequent and closed zooecia are found. In all groups of species but one (group A, see p. 167), the opesia of the zooecia of the central area become occluded by secondary calcareous growth; these zooecia do not then contain polypides (see Harmer, 1926 : 267). Closed zooecia are often present even in fairly young colonies, and are also found in areas of rapid budding at the edges of regenerating fragments (see above).

In the membraniporan group B (see below) the lamina is formed as a thin sheet originating just below the level of the slight shelf formed by the descending cryptocyst. It develops in a proximal direction from the distal end of the opesia, later also growing out from the lateral walls. Although the lamina thickens it rarely approaches close to the frontal membrane. Irregular pores are left, especially at the lateral edges. In the denticulate forms (Group C, see p. 167), the lamina is formed by extension and fusion of the existing cryptocystal denticles and first develops proximally, spreading progressively to the sub-opercular region. It is closer to the frontal membrane in origin than the lamina in Group B, and when thickened by further deposition may almost obscure the mural rims of the central zooecia. In *Discoporella* where the opesia is restricted to a small sub-opercular area, the central cryptocystal pores calcify first, the opesia then becoming occluded by denticulate growth. The opesiules frequently remain uncalcified or only partially closed. The lamina in these

last two groups is rarely complete, irregular pores usually being present, but in contrast to the first group, no pores are present in the subopercular area.

The existence and type of central area closure may be evidence of the group to which a species belongs, and the association of closed zooecia with ancestrular and regenerative budding in groups B, C and D is comparable to the occurrence of vicarious vibracula in group A.

b. *The cryptocyst* is present in all species and, in well-preserved material, is a useful specific character, especially when its form can be correlated with other characters, such as those of the basal surface. Unfortunately, the cryptocyst is among the first structures to be damaged or worn, although there are usually one or two zooecia present in which it can be seen, even in fossil specimens.

The type of cryptocyst forms a series in the Cupuladriidae from the membraniporan *C. canariensis* to the microporan *D. umbellata*. In the *C. canariensis* and *C. guineensis* groups (see below), it is simple, though variously extensive. In the *C. owenii* group it is denticulate, the form and extent of the denticles being specific. In *Discoporella* it is so extensive that it has been regarded as a generic character. In development, however, the cryptocyst of *D. umbellata* shows great similarity to that of the *C. owenii* group, as it is formed from the fusion of irregular denticles (see Marcus & Marcus, 1962, pl. 1, fig. 4). In *Discoporella* the final development of the cryptocyst results in a pair of distal opesiules or opesiular indentations, through which pass a pair of muscles. Other opesiular pores are present, but the opesia is always limited proximally by a complete bar, formed by part of the cryptocyst.

c. *The opercula* of the majority of species of Cupuladriidae are similar to one another. They are membraniporan with a strong, curved distal sclerite. Their mean dimensions or proportions may give additional information toward the definition of a species, but generally their range of variation is large. Furthermore, opercula are absent not only in fossil specimens, but frequently from dead, Recent material which is a little worn.

Groups C and D (see below) each include species in which the operculum has a partial or complete proximal sclerite. In *C. doma* (Group C), the proximal sclerite is variable, and may be incomplete. Its presence may be useful in distinguishing small fragments from those of *C. owenii*, which may have similar zooecial characters, but the basal surface is here more certain as a determinant of the species. *Discoporella* (group D), has hitherto been distinguished by the possession of a proximal sclerite in the operculum, but there is evidence (Cook (in press)) that even in this group the opercula are not all of the same type and include at least one species in which they are without a proximal sclerite.

d. *The vibracula* are also similar in character in all species of the family. The opesia is auriform, with distinct condyles, which are alternately asymmetrical to right or left in each member of a radial row of zooecia. The vibracular setae are long and usually follow a sigmoid curve, they increase in length toward the periphery of the colony. The setae have an asymmetrical basal sclerite, to which are attached powerful muscles which fill the vibracular chamber. Although there are differences between the setae of various species, especially in the size and shape of the basal

sclerite, the variation within the colony is large and they appear to be of little use in specific determination. The basal sclerites of group A seem generally to be less tuberculate and robust than those of the other groups. The detailed morphology of the vibraculum was discussed by Marcus & Marcus (1962).

The seta is able to move in two directions and in one plane. Owing to its asymmetrical articulation and curvature, these movements cover nearly half of the frontal surface of the zooecia proximal and distal to any vibraculum. Live colonies examined by me have not been seen to use their setae like tweezers, as described by Marcus & Marcus (1962 : 299). The distribution of the setae, and their range of movement, is such that they rarely come into contact (see Text-fig. 4). Those near the centre of the colony may touch each other when closed, owing to the convergence of radial rows, but should any detritus be held between two setae in this position, they automatically lose all contact as soon as an opening movement begins. Particles on the frontal surface are dislodged by the movement of individual setae. They roll down the sloping surface of the colony, passing between the peripheral, supporting setae. The zoarium is thus kept clear of deposits settling upon it (see Cook, 1963 : 410).

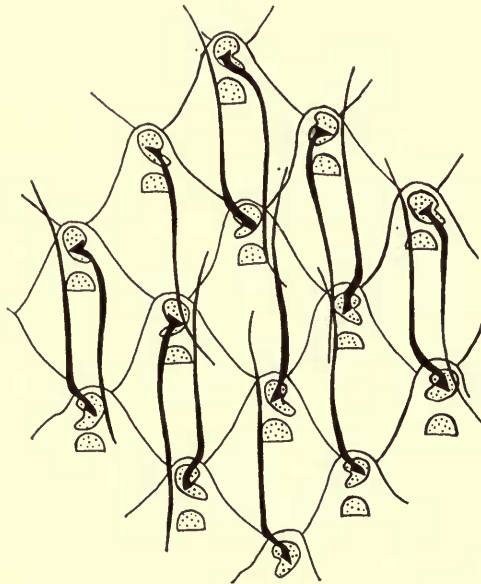


FIG. 4. Distribution of vibracular setae in *Discoporella umbellata*. Membrane of vibracular opesia and opercula stippled. Setae pointing distally are in the "open" position; those pointing proximally are in the "closed" position.

e. *The basal surface.* Lagaaij (1952 : 34, 1953 : 13) stressed the importance of the character of the basal surface in specific determination of fossil specimens, where the frontal surface may have suffered wear. In those groups (A and B below) in which rectangular or hexagonal sectors are present, the thickening consists of layers of

calcification, pierced by regular series of kenozoecial chambers, or by small pores. The shape and arrangement of the sectors, and the number of pores or chambers may be specific, within defined limits. For example, the basal sectors of *C. canariensis* s. s. consist of several layers of long irregular units, interspersed with occasional short sectors; whereas those of *C. monotrema* are single layered and invariably short and square. The sectors of *C. guineensis* (see Hastings, 1930: 714, and p. 170) may vary, especially in large colonies, from square to hexagonal. In the first case the characters of the basal surface are correlated with other distinguishing features, in the second, the variability of the character is found within a single colony, and is not correlated with any other character, and is therefore not specific. In the remaining groups the basal surface consists of a series of alternating radial grooves and ridges, the characters of which may also be specific, although they are variable, affected by wear, and similar forms occur in both *Cupuladria* and *Discoporella*.

The ridges and grooves are the result of the form of growth of the zooecia. Each curved basal lamina is grooved in the mid-line (see Text-fig. 2). As secondary calcification increases the groove may be filled in, and in some cases may be marked by a protuberant "thread" of heavier calcification. The tuberculation of the basal surface may increase with calcification, but may also become changed by wear. In some species, however, the form of tuberculation may be correlated with other characters, and be specific. For example, in *C. owenii*, the tubercles are consistently small and regular, and in *C. multispinata*, they are large, coarse, and coalescent (Cook (in press)).

5 THE EFFECTS OF ZOARIAL FORM ON CHARACTERS

The extreme variation in zoarial and zooecial characters of specimens attributed to *D. umbellata* has been discussed by several authors, and Silén (1942: 16) noted variation in the shape of zoarium of his specimens and grouped his material into localities where one type of zoarium was dominant. The type of zoarium appears to have little effect on the zooecial characters except where the form of the colony is the same as that found normally in *C. doma* (d'Orbigny) or that found in zoaria described as *C. peyroti* by Duvergier (1924: 19).

Doma-type zoaria occur in several species of Cupuladriidae (Cook (in press)) and perhaps correspond to the *Trochopora*-habit of *Lunulites* (see Lagaaij, 1953: 17). Specimens belonging to the *D. umbellata*-complex (see p. 175), frequently produce *doma*-type colonies, and before discussion of specific differences, the effects of form of growth must be considered.

The *doma*-type zoarium is small and usually high (diameter range 3-7 mm.) The zooecia are small, and the basal surface solid or nearly filled in by secondary calcification. In the majority of zoaria the peripheral zooecia are closed, and there may be from 1-3 rows of enlarged peripheral vibracula.

In all lunulitiform zoaria the angle of the axis of the polypide cavity approaches a right angle with the zoarial axis, and the planar intercept of the frontal of each zooecium is thus longer in flatter colonies than in the *doma*-type zoarium, where there is therefore a reduction of the zooecial dimensions usually found in the species, and

consequent changes in the development of the cryptocyst and the proportions of various other characters. The basal surface is also frequently non-typical, owing to the large amount of secondary calcification.

Canu & Bassler (1930 : 12) stated that specimens from abyssal depths of the Pacific reported in 1929 (p. 142), were stunted. Photographs of these specimens (1963. 3. 14. 14) show that they are not, however, either particularly small, or of the *doma*-type. Canu & Bassler also mentioned that colonies of " var. *conica* " had been found in the Helvetian of Touraine, but these colonies were not specifically mentioned by Canu (1909 : 448) in his description of the zoaria from this locality. Marcus & Marcus (1962 : 304) described colonies from the coast of Brazil as *D. umbellata* var. *conica* Canu & Bassler. These are certainly the same form as those listed below as *doma*-type zoaria (see p. 181).

The number of specimens examined of *doma*-type colonies is not at present sufficient to determine whether they should be considered a subspecies of *D. umbellata*. It appears more likely that they are a variant developed in response to specific, but unknown, ecological conditions. The specimens examined fall roughly into 3 groups, each corresponding to one of the 3 major forms in the *D. umbellata*-complex (see p. 176). The ecological factors involved in the occurrence of *doma*-type colonies are probably not simple. There is, for example, no correlation with depth in the material examined, although *C. doma* itself extends in distribution to greater depths than other species of the Cupuladriidae. One *doma*-type specimen from Cape Frio, off Angola, is the sole record from the south west coast of Africa, where the temperatures are lower than, for example, east of the Cape of Good Hope. At Möwe point, just south of Cape Frio, in 400 m., a temperature of 9° C. has been recorded (see Hart & Currie, 1960 : 173, text-fig. 29). The conditions producing *doma*-type growth may perhaps be related to temperature.

In the *D. umbellata*-complex the *doma*-type colonies are very small and the number of opesiules is reduced. The size of opesiæ and opercula are not, however, reduced in the same proportion. The peripheral zooecia are closed and the peripheral vibracula enlarged, as in *C. doma*. Generally, the effect is of a suppression of the characters normally separating the populations in the complex. In nearly all cases, however, the specimens retain traces of features consistent with those found in the larger, more normally developed colonies (see pp. 180, 182).

Peyroti-type growth is similar to *doma*-type growth, and may also be caused by ecological conditions at present unknown. Some colonies combine features of both forms of growth (see p. 180), but whereas *doma*-type zoaria occur in all 3 populations of the complex, Recent *peyroti*-type colonies are the characteristic form of one geographical area, namely the south-eastern coast of Africa. Duvergier (1924 : 19) described, as *Cupularia peyroti*, colonies similar in character to *Discoporella umbellata*, from the Miocene of France, in which the basal surface (described as " face superieur ", following Canu's theoretical orientation of lunulitiform and selenariiform colonies) was covered by kenozoocia and vibracula. Recent specimens from south and east Africa (see p. 177) show stages in the development of the same form of growth, which was briefly described by O'Donoghue (1924 : 39) and discussed by Hastings (1930 :

719), who doubted whether her south African specimens could be included in *D. umbellata*. The large number of colonies now available show that although the zoarial form is markedly different, the zooecial characters have much in common with *D. umbellata* s.s.

The modifications to a specific character produced by *peyroti*-type growth are principally in the appearance of the basal surface. Zoaria are usually large, unlike *doma*-type colonies, and have a smooth, slightly pitted base, which may be concave or solid. There is no sign of the tuberculate, grooved basal surface usually found in *D. umbellata*. In most zoaria the base is covered by a layer of kenozooecia and vibracula proliferated from the peripheral zooecia and vibracula (see Pl. 3, fig. 6). The vibracular opesia are as large as those of the peripheral vibracular zooecia but their setae are not as long. The kenozooecia have no polypides and resemble the closed zooecia of the frontal central area except that there are pores in the distal part of the lamina which in normal closed zooecia is the solid, sub-opercular region (see p. 160).

The peripheral frontal zooecia are also closed as in *doma*-type zoaria, but the peripheral vibracula are not greatly enlarged nor do several rows of them occur.

The basal vibracula presumably act in a similar manner to those at the periphery, and assist in stabilizing the zoarium and maintaining it just above the surface of the substrate (see Cook, 1963).

The conditions determining *peyroti*-type growth do not seem to be related to temperature, as similar ranges occur east of the Cape of Good Hope to those off west Africa (i.e. warm temperate to tropical, see Stephenson, 1947). No Cupuladriidae have been reported from the colder waters immediately to the west of the Cape of Good Hope.

6 COMPARISON WITH THE STRUCTURE OF OTHER FREE-LIVING ZOARIA

Silén (1942 : 1-22) examined many free-living zoaria and considered that their growth was spiral i.e. that the zooecia of each apparently radial row were budded from the nearest proximal-lateral, not proximal, zooecium. Examination of many lunulitiform, selenariiform and conical colonies has confirmed Silén's observations for *Setosellina*, *Setosella* (principally an encrusting form) and *Heliiodoma*, and Stach's observations (1936a) for *Selenaria*, but has also shown that the method of growth in the Cupuladriidae and the genus *Lunulites* is entirely different. The evidence is summarized below.

a. In the spirally growing forms the ancestrula buds off both a distal and a proximal (or proximal-lateral) vibraculum, each with an adjacent zooecium. A good example was figured in *Vibracellina caribbea*¹ by Osburn (1947 : 11, pl. 1, fig. 2). Two spirals of zooecia and vibracula develop from these foci, so that although the ancestrula is eventually surrounded by zooecia, unlike that of *Lunulites* and the Cupuladriidae, it has not directly budded all of them (contrast Text-fig. 1A with Text-figs. 1B, C and

¹ Lagaaij (1963b : 172) also describes and figures the ancestrula region of this species, which he refers to *Setosellina goësi* (Silén).

D). The spiral budding is well illustrated in 5 zoaria of *Selenaria squamosa* (N. Zealand, 1947. 8. 16. 1), where the spiral is anti-clockwise. All colonies of other species seen are developed in a clockwise direction. In *Lunulites* the budding pattern is radial, not spiral, but differs from that of the Cupuladriidae in that the ancestrula buds 6 zoecia, each of which then gives rise to a zoecium and a vibraculum. The ancestrula does not therefore directly bud a vibraculum (see Text-fig. 1D).

b. Silén based his conclusions as to the spiral nature of the zoaria of the Cupuladriidae on the assumption that morphologically the vibraculum was the distal bud formed by each zoecium, and that a vibraculum could not bud off a zoecium distal to itself. The zoecium and vibraculum of the Cupuladriidae originate as a unit, and although there is evidence that the vibraculum is a modified zoecium (see Marcus & Marcus, 1962 : 298), it is produced within the confines of the common bud, and is not itself the product of distal budding. In spirally developed colonies (e.g. *Setosellina*), the vibracular chamber can be seen to reach the basal side of the zoarium, and the distal-lateral origin of the next zoecial bud can be seen.

c. In spirally developed colonies, the parent zoecium of an intercalary series forms the second bud consistently on the side opposite to the direction of spiral growth. In the Cupuladriidae the intercalary zoecia are produced from either distal-lateral wall of the parent zoecium, in a random manner. The vicarious vibracula in the *C. canariensis* group (see below) may be intercalary or may themselves produce intercalary zoecia or further vicarious vibracula. Their appearance is also entirely random, and has no spiral pattern. In *Lunulites* the radial rows of zoecia alternate with those of the vibracula. There is no direct lateral relationship between the budding of the types of individual, which are developed radially, not spirally. Successive vibracula enlarge in a series and finally one buds a distal zoecium. New intercalary rows of vibracula are produced from bifurcations of series distal to a zoecium, not a vibraculum. In the central area the first vibracular rows are all budded from the proximal zoecium in the same lateral relationship to the zoecial buds (see Text-fig. 1D). In subsequent bifurcations the vibracular bud arises to the right or left of the zoecial bud in a random manner.

d. The growing edge of *Selenaria bimorphocella* (off Adelaide, 1928. 9. 13. 81), shows no basal curved laminae, but a series of groups of young zoecia alternating with developing vibracula, similar in appearance to the growing edge of an encrusting colony. Similarly, the growing edges of colonies of *Setosellina* have no basal curved laminae. The peripheral zoecia of *Lunulites* arise in a similar manner to those in the Cupuladriidae and basal laminae have been seen. The resulting basal grooves mark the junction of the lateral walls and do not have the alternating pattern of the Cupuladriidae (see below). In Recent *Lunulites* the cavities of the vibracula reach the basal surface, in the fossil specimens described by Lagaaij (1953), they do not.

e. As in the Cupuladriidae, the regenerative budding in *Lunulites* is at right angles to the lateral walls of broken fragments. This is in contrast to colonies of *Selenaria* regenerated from fragments (New Zealand, Discovery Coll., Stn. 936), which show spiral budding from the lateral walls of old zoecia. Each new bud is consistently

distal-lateral, and no zoecium produces new zoecia at right angles to its long axis (see Text-fig. 3B). The budding of deformed colonies of *Selenaria* is also spiral (see p. 159)

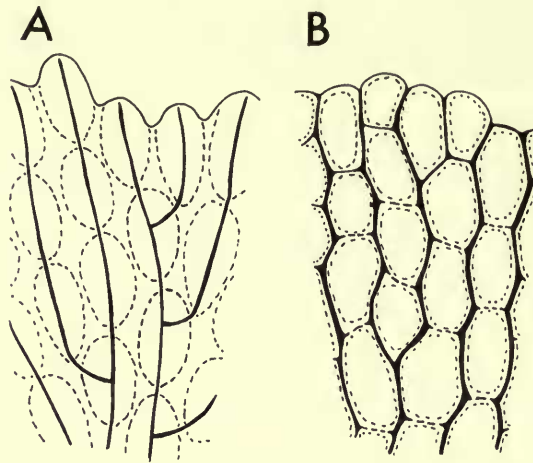


FIG. 5. Relationships of basal grooves. Broken lines indicate the position of the frontals of the zoecia on the upper surface. A. Cupuladriidae. Grooves running radially in the mid-line of the zoecia, branching at the beginning of an intercalary series. B. *Selenaria*. Grooves running between the zoecia, branching around the first zoecium of an intercalary series.

f. The basal radial threads and radial sector boundaries branch frequently. The origin of a branch may be traced and found to correspond exactly with the occurrence of the first zoecium of an intercalary row on the frontal surface. The budding of an intercalary row must be of the same nature as that of all other zoecia, and thus the radial nature of the threads and sector boundaries may also be presumed to reflect the radial development of the zoarium (see Text-fig. 5A). The formation of the basal surface in the Cupuladriidae is exclusive, but apparently similar forms are present in other families. An unnamed species of *Lunulites* described and figured by Lagaaij (1953: 18, pl. 2, figs, 6a, b), has a basal surface superficially like that of *C. guineensis*, and specimens of *Lunulites radiata* show alternating tuberculate ridges and grooves similar to those of *C. owenii*. *Selenaria bimorphocella* (S. Australia, 1928. 9. 13. 80, and off Adelaide, 1928. 9. 13. 81, Siboga Coll.), shows radial undulating grooves with large pores, which are occluded at the centre of the zoarium, except beneath the vicarious vibracula, where they remain open. In section, these pores do not show the serial kenozoecial structure found in Group A of the Cupuladriidae (see below). The grooves exactly outline the position of the zoecia above them, and, at the periphery, show indications of distal and proximal links, which correspond in position to the distal and proximal walls of the zoecia. Thus the grooves are entirely different in nature to, and do not have the alternating relationships of, the grooves, threads, or radial sector boundaries of the Cupuladriidae, and are only secondarily radial in appearance (see Text-fig. 5B).

7 GROUPING OF SPECIES

The groups defined below do not include all the species which have been described, but formulate the correlation of various characters found to be common to some species. *C. pyriformis* and *C. indica* (see below) combine some of the characters of more than one of these groups.

The groups are arranged in order of increasing extent of cryptocystal development.

A. *C. canariensis* group. Cryptocyst simple, without denticles, central zoecia without closures by calcareous laminae. Vestibular arch absent. Basal surface consisting of rectangular sectors, with successive series of porous kenozoocial chambers. Vicarious vibracula sometimes present. (Examples: *C. canariensis* (Busk), *C. monotrema* (Busk), *C. biporosa* Canu & Bassler).

B. *C. guineensis* group. Cryptocyst simple, without denticles, central zoecia closed by calcareous lamina developing proximally from below level of cryptocyst. Vestibular arch absent. Basal surface of hexagonal or quadrilateral sectors, with very small pores. Vicarious vibracula not present. (Examples: *C. guineensis* (Busk), *C. elongata* Sakaura².)

C. *C. owenii* group. Cryptocyst with denticles, central zoecia closed by lamina developing distally from fusion of denticles. Vestibular arch present. Basal surface with alternating ridges and grooves, tuberculate. (Examples: *C. owenii* (Busk), *C. haidingeri* (Reuss), *C. multispinata* (Canu & Bassler), *C. doma* (d'Orbigny), ? *C. misrai* (Tewari *et al.*³.)

D. *D. umbellata* group. Horizontal cryptocyst lamina complete proximally, with pores. Opesia with opesiules or opesiular indentations. Opesiae of central area closed by a complete lamina. Vestibular arch present. Basal surface with alternating grooves and ridges, or short grooves and lozenges, tuberculate. (Examples: *D. reussiana* (Manzoni), *D. umbellata* (Defrance), *D. umbellata* subsp. *depressa* (Conrad)).

There are two species which cannot be included in the groups defined above. Although superficially alike, they are probably not closely related. *C. pyriformis* has a similar cryptocyst to that found in groups A and B, but differs from both in the character of its basal surface, and in the possession of a distinct vestibular arch. *C. indica* is close to *C. guineensis*, but differs completely in the character of its basal surface; its geographical distribution is also distinct.

Cupularia capriensis Waters differs from the Cupuladriidae in important respects and is here referred to *Setosellina* (see p. 182).

² *Cupuladria elongata* Sakakura (1935: 6, pl. 1, figs. 1-3) was described with extremely elongated basal sectors, with small pores, from the Pleistocene of the Bôzô peninsula, Japan. Recent specimens from Japanese waters are all attributable to *C. guineensis*.

³ *Discoporella misrai* Tewari *et al.* (1958: 234, pl. 46, figs. 1-4, pl. 47 fig. 2), a Miocene fossil, was described to include specimens from Kutch, India, and those previously reported from the Miocene of Travancore as *Cupularia* spp. (Jacob & Sastri 1953: 348, pl. 14, figs. 5a, b, pl. 15, figs. 7a, b, pl. 16, figs. 10, 11). The specimens appear to have a denticulate cryptocyst and tuberculate basal surface.

8 *Cupuladria pyriformis* (Busk)

(Pl. 1, figs. 3, 4, Text-fig. 1C)

Cupularia pyriformis Busk, 1854: 100, pl. 124, St. Vincent (Windward Is.).*Cupuladria canariensis* (Busk): Silén (part), 1942: 14, pl. 4, figs. 15, 16, text-fig. 9, Anguilla, Leeward Is., 40-150 m. (not text-fig. 8).

LECTOTYPE, chosen here, specimen on slide B.M. 1840. 10. 23. 80 (figured by Busk, 1854, pl. 124, basal surface), St. Vincent.

LECTOPARATYPE, 1840. 10. 23. 81, on the same slide.

OTHER MATERIAL. Naturhistoriska Riksmuseet, Stockholm, FBD 533, Anguilla, Leeward Is., 45-150 m., Göes Coll., 1 specimen.

Zoarium small (3.5-4.5 mm. diameter). Cryptocyst without spines or denticles. Vestibular arch well developed. Opercula without proximal sclerite. One pair of circum-ancestrular zooecia aborted. Central zooecia closed by irregularly perforated lamina. Vibracula raised, with salient condyles. Basal surface with deep grooves and raised ridges, with very small tubercles.

DIMENSIONS. Lz 0.35-0.40 mm.; lz 0.20-0.30 mm.; Lop 0.12-0.17 mm.; lop 0.18-0.27 mm.; Lvo 0.09-0.12 mm.

C. pyriformis has been reported twice with certainty, and only 3 specimens are at present known to exist in Museum collections.

The zooecia are narrow, tapering distally, with a vestibular arch distinctly raised above the zoarial surface. The vibracula are also prominent, with narrow opesia and slightly hooked condyles. The central zooecia are closed by a thin, minutely granular lamina, originating just below the salient, shelf-like part of the cryptocyst. The lamina is perforated by 4-7 irregular pores, which in several cases are arranged parallel to the edge of the cryptocyst, but which may also be scattered.

In all 3 specimens the circle of zooecia budded by the ancestrula is unlike that of other Cupuladriidae in that pair No. 1 is nearly aborted. Each minute zoecium has a small distal vibraculum (see Text-fig. 1C). Silén (1942, text-fig. 9) showed only one abortive zoecium and did not clearly indicate its relationship to the ancestrula, but the figure shows the salient character of the vibracula.

The basal surface is deeply grooved, with sharp alternating ridges. The surface is finely tuberculate but not porous. Busk described *C. pyriformis* with basal pores, but the faint markings are in fact very small tubercles; his figure shows the other basal characters well, and they are the same in the specimen from Anguilla; unfortunately Silén's photograph does not show the ridges which are in fact present (see Pl. 1, fig. 4).

The position of the locality given by Busk for his material, "St. Vincent" ("St. Vincents" on the slide label), is open to several interpretations. Although much of the material from "St. Vincent" described in the 1854 Catalogue was from St. Vincent, Cape Verde Islands, the specimens registered as 1840. 10. 22 . . . and 23 . . . consist almost entirely of slides labelled "St. Vincents, W.I.". There is a St. Vincent Island off the west coast of Florida but the most likely locality is St. Vincent Island in the Windward Islands. This supposition is strengthened by the

occurrence of the one other specimen from the neighbouring Leeward Islands. Silén only doubtfully included this colony in *C. canariensis*, and examination of the specimen shows certainly that it belongs to *C. pyriformis*.

Studer (1889) listed specimens identified by Kirchenpauer from Madeira as *Cupularia pyriformis* Busk, on p. 7 and from near Cape Verde as *Cupularia pyriformis* Gray (sic), on p. 13. It is possible that Studer's specimens belonged either to *C. canariensis* or to *Cupuladria* sp. (Cook (in press)), which, superficially, have similar zooecial characters. Prof. E. Voigt (Geologische Staatsinstitut, Hamburg), has informed me that Kirchenpauer's specimens were almost certainly destroyed during the 1939-1945 war.

Lagaaij (1963a : 182, pl. 25, figs. 2a, b) mentioned a species of *Cupuladria*, probably related to *C. pyriformis*, from the Miocene of East Venezuela.

The character of the basal surface and the presence of a distinct vestibular arch indicate an affinity between *C. pyriformis* and the *C. owenii* group of species ; but the absence of denticles on the cryptocyst and the form of the central closures show a similarity with the *C. guineensis* group.

9 *Cupuladria indica* sp. n.

(Pl. 2, figs. 1, 2)

Cupularia umbellata DeFrance : Hincks, 1887 : 125, Mergui Archipelago.

Cupuladria guineensis (Busk) : Hastings (part), 1930 : 714, 719 (specimens from Mergui, Burma).
Silén (part), 1942 : 8, pl. 4, figs. 13, 14 (specimens from locality 1, Gulf of Aden).

HOLOTYPE. Mergui, Burma, B.M. 1899. 5. 1. 23A, Hincks Coll.

PARATYPES, as above, 1899. 5. 1. 23B-H, 1899. 5. 1. 267, Hincks Coll.

OTHER MATERIAL. Mergui, 1963. 3. 18. 3, Anderson Coll.

" John Murray " Coll. (all specimens from a sandy or muddy substrate) : Stn. 80, S.E. of Muscat, 22° 13' 30" N., 59° 49' 42" E., 30.xi.33, 16-22 m., Z191A. Stn. 77, as above, 22° 13' 30" N., 59° 52' E., 421 m., Z196A. Stn. 178, N. of Somali Horn, 12° 00' 36" N., 50° 40' 06" E., 2.v.34, 91 m., Z201A (with *Anoteropora latiroitris* Silén). Stn. MB I d, Hanish Is., Red Sea, 13° 39' 30" N., 42° 43' E., 17.ix.33, 29 m., Z146A and Z41E. Stn. Mb I b, as above, Z139A. Stn. MB II c, Khorya Morya Is., 17° 33' 30" N., 56° 01' 30" E., 28.x.33, 26 m., Z161A.

Naturhistoriska Riksmuseet, Stockholm, FBD 822, Gulf of Aden, 30 m. (with *Setosellina* sp.), photograph registered B.M. 1963. 3. 14. 1.

Zoarium frequently flattened, discoid, average diameter 7 mm. Cryptocyst simple, well developed laterally, descending gently, edge serrate but not denticulate. Operculum without proximal sclerite. Central zooecia closed by irregular denticles forming a lamina at the level of the cryptocyst. Basal surface with radial ridges and large, regular tubercles, no rectangular or hexagonal sectors or pores present.

DIMENSIONS. Lz 0.40-0.50 mm., av. 0.45 mm. ; lz 0.30-0.40 mm., av. 0.35 mm. ; Lop 0.25-0.30 mm., av. 0.28 mm. ; lop 0.16-0.21 mm., av. 0.19 mm. ; Lvo 0.12-0.15 mm. ; Ls 0.50-0.70 mm.

Hincks described his specimens as *C. umbellata* and his material in the British Museum was originally labelled as this species. Hincks noted that the majority of the zooecia showed "no trace of a lamina", but that the central zooecia were closed by one. The peripheral pores in the cryptocyst of the closed central zooecia in *C. indica* do somewhat resemble the opesiules of *D. umbellata*, as does the basal surface with its tuberculate ridges and grooves, of which Hincks gave a very full description.

The specimens show little variation; just over half of the zoaria are extremely flat, the remainder slightly more conical. The central closures differ from those of *C. guineensis* in that they are formed from denticles or laminae which appear to originate from the salient shelf-like edge of the descending cryptocyst, not just below it (see p. 159). This is particularly noticeable at the proximal edge of the opesia, which is the last part to be occluded. However, the later thickening results in a very similar appearance in both species. Young colonies, and those formed from regenerated fragments, have no closed zooecia. Generally, the cryptocyst is narrower than that of *C. guineensis*.

The basal surface shows little variation in the size of the tubercles, and the radial grooves are marked by a slight thread in all specimens, which distinguish *C. indica* from those specimens of *C. guineensis* which have heavy basal tuberculation.

The basal structure of *C. indica* is similar to that of the *C. owenii* group. There are no sectors, and no pores in the basal lamina, which is not thickened as in *C. guineensis*. In other respects, *C. indica* closely resembles *C. guineensis*, and its zooecial dimensions fall within the range of variation of *C. guineensis*; they are, however, consistently at the smaller end of that range.

The two species also appear to be allopatric, their geographical distributions being mutually exclusive. The occurrence of the conical *Anoteropora latirostris* and the selenariiform *Setosellina* sp. from the same stations as the lunulitiform *C. indica* illustrates the correlation between various types of free-living zoaria with a sandy or muddy substrate, as discussed by Harmer (1957: 649).

10 *Cupuladria guineensis* (Busk)

(Pl. 1, figs. 1, 2, Pl. 2, figs. 3, 4, Text-fig. 6)

Cupularia guineensis Busk, 1854: 98, pl. 114, figs. 1-5, New Guinea. Busk, 1884: 206, pl. 14, fig. 6, N.E. Australia, 8 fath. Marcus, 1921: 8, 2° 30' S., 107° 10' E., 15 Fd.

Cupularia stellata Busk, 1854: 99, pl. 118, figs. 1-4, Philippines. Marcus 1921: 8.

Cupularia canariensis Busk, Waters, 1885: 308, Aldinga, Tertiary, S. Australia. 1887: 201, Princess Charlotte Bay, N.E. Australia, 12 fath. 1921 (part): 410. 1926 (part): 426, pl. 18, fig. 10, Princess Charlotte Bay.

Cupuladria guineensis (Busk) Harmer, 1926: 266, text-fig. 9, pl. 16, figs. 5-7, S. of Mindanau, 0-36 m. Canu & Bassler, 1929: 74. Hastings, 1930: 714 (not specimens from Mergui, = *C. indica*). 1932: 412, Great Barrier Reef. Silén, 1938: 366, pl. 17, fig. 119. 1941: 61, East China Sea, 90 m. (cf. locality 7 in 1942). 1942 (part): 8, text-figs. 5-6, pl. 3, figs. 10-12, localities 2-7 (not locality 1, pl. 4, figs. 13-14 = *C. indica*). Androsova, 1963: 23, 39, pl. 1, fig. 3, S. China Sea.

Cupuladria intermedia Canu & Bassler, 1929: 74. Hastings, 1932: 412.

Cupuladria brevipora Canu & Bassler, 1929: 74. Hastings, 1932: 412.

- Cupuladria transversata* Canu & Bassler, 1929 : 74, 75, pl. 3, figs. 3, 4. Stn. D 5579, Borneo 175 fath., sand.
- Cupuladria dentifera* Canu & Bassler, 1929 : 74, 75, pl. 3, figs. 5-8, Stn. D 5230, Limasaua Is. 118 fath., sand.
- Cupuladria tuberosa* Canu & Bassler, 1929 : 76, pl. 4, figs. 1-4, Stns. D 5134, Sulu Archipelago, 25 fath., sand, and D 5144, Jolo, 19 fath., sand.
- Cupuladria grandis* Canu & Bassler, 1929 : 77, pl. 4, figs. 10-13, Stn. D 5161, Sulu Archipelago, 16 fath., sand.
- Cupuladria granulosa* Canu & Bassler, 1929 : 74, 78, pl. 4, figs. 5-9, Stn. D 5358, Jolo Sea, 39 fath., mud. Kataoka, 1961 : 224, pl. 30, figs. 2, 5, Pleistocene, Japan.
- Cupuladria hexagonalis* Canu & Bassler, 1929 : 74 (as *hexagona*) 78, pl. 5, figs. 1-4, Stns. D 5141, Jolo, 29 fath., sand, and D 5147, Sulu Archipelago, 21 fath., sand.
- Cupuladria microdenticulata* Kataoka, 1961 : 225, pl. 29, figs. 1, 2, Pleistocene, Japan.

HOLOTYPE, B.M. 1842. 11. 30. 14, New Guinea.

OTHER MATERIAL. Where the predominant type of basal sector present is hexagonal (see Text-fig. 6B), the specimens listed below are marked "A", where it is nearly square (see Text-fig. 6D), they are marked "B"; where pores have been seen, and where tubercles are present, the letters "P" and "T" are added.

British Museum. New Guinea 1842. 11. 30. 14 (APT). 1859. 2. 25. 11 (BP). S. of Mindanau, 15 fath. 1928. 3. 6. 74 (APT). Torres Straits 1862. 6. 5. 14 (BP), 10 fath., sand. 1882. 2. 23. 37-40 (BP). ?N. Australia 1855. 12. 27. 38 (APT), 1872. 6. 21. 21 (B). Holothuria Bank, N.W. Australia, 34 fath., 1892. 1. 28. 125 (BPT). 1963. 2. 2. 1 (BP), 1891. 12. 16. 1-4 (BP). Cossack Is., N.W. Australia, 8 fath., 1891. 12. 16. 31-37 (BP), Baudin Is., 15 fath., 1891. 12. 16. 21 (BP), 22 (BP), 23 + 24 (B + AP), 25-30 (BP + BPT), 1892. 1. 28. 128. 8-15 fath., (B + APT). Cape York N.E. Australia, 10° 30' S., 142° 18' E., 8 fath., sand, Chall. Stn. 186, 1887. 12. 9. 819 (BP). Low Is. off Port Douglas, Gt. Barrier Reef, 1932. 4. 20. 112 (BPT). Bass's Straits, S. Australia, 1899. 7. 1. 1269. Busk Coll. (BPT) Australia 1929. 5. 10. 1 (AP), 1899. 7. 1. 1252 Busk Coll. (labelled *C. stellata*). Philippines, 1854. 11. 15. 147 (type of *C. stellata*), 1899. 7. 1. 1231, Busk Coll. (AT). Philippines, Stn. D. 5161, 1931. 12. 30. 9 (AP) and Stn. D 5156, off Tinakta Is., 18 fath., 1931. 12. 30. 10 (AP) (topotypes of *C. grandis*), Canu & Bassler Coll. Sulu Archipelago, "Albatross" Stn., D5134, 1963. 3. 14. 2 (AP); Suluade Is., Stn. D 5147, 1963. 3. 14. 3 (APT); and Philippines, 26 fath., Stn. D 5181, 1963. 3. 14. 4 (AT), Bassler Coll. Photographs of type specimens from the Bassler Collection, United States National Museum, all $\times 20$. *C. transversata*, Holotype, 1963. 3. 14. 5 and paratypes, 1963. 3. 14. 6 (AP). *C. dentifera*, Cotypes, 1963. 3. 14. 7 (APT). *C. grandis*, Syntypes, 1963. 3. 14. 8 (AP). *C. granulosa*, Syntypes, 1963. 3. 14. 9 (APT). *C. hexagonalis*, Syntypes, 1963. 3. 14. 10 (APT). *C. tuberosa*, Syntypes, 1963. 3. 14. 11 (AP).

Manchester, Museum, Waters Coll. Princess Charlotte Bay, 12 and 13 fath., Australia, (BP).

Naturhistoriska Riksmuseet, Stockholm. Forty-five miles W.S.W. off Cap Jaubert, N.W. Australia, 100 m., FBS 157 (BPT), FBS 109 (BPT). S. China Sea, between Nagasaki and Hongkong 75 m., mud, FBS 904 (BPT). Malayan Archipelago, Java Sea, 2° 30' S., 107° 10' E., 27 m., FBS 639 (AT).

United States National Museum. The Museum was unable to lend material named by Canu & Bassler, but made available photographs of the type specimens (see above) and also unnamed specimens from various "Albatross" Pacific Stations, 2 of which were the same as those from which some of Canu and Bassler's species were obtained. D 5134 Sulu Archipelago, 6° 44' N., 121° 48' E., (APT) (Locality for *C. tuberosa*). D 5147 Suluade Is., Sulu Archipelago, 21 fath., (APT) (Locality for *C. hexagonalis*). D 5145, Jolo, 23 fath. (APT). D 5159, Philippines (AP). D 5181, Philippines 26 fath. (APT). D 5314, China Sea nr. Hong Kong, 122 fath. (AT).

Zoarium frequently very large (maximum observed diameter 24 mm.). Zoecia with broad tuberculate cryptocyst, opesia often almost rectangular. Operculum without a basal sclerite. Central area of zoecia closed by growth of a lamina from beneath the shelf-like salient part of the cryptocyst. Basal surface smooth or tuberculate, divided into quadrilateral or hexagonal sectors, variable. Pores present in peripheral sectors, becoming sunk in pits, occluded or hidden by tubercles.

DIMENSIONS. Lz 0.40–0.75 mm., av. 0.60 mm.; lz 0.30–0.50 mm., av. 0.40 mm.; Lop 0.30–0.40 mm., av. 0.35 mm.; lop 0.15–0.25 mm., av. 0.20 mm.; Lvo 0.12–0.20 mm.; Ls 0.5–1.5 mm.

C. guineensis was defined by Hastings (1930 : 714–5), who distinguished it from the *C. canariensis*-complex of species (Cook (in press)) by the nature of the basal surface and the extent of the cryptocyst. Of the 8 species introduced by Canu & Bassler (1929 : 74–9), two, *C. intermedia* and *C. brevipora*, were placed in the synonymy of *C. guineensis* by Hastings (1932 : 412), who also agreed with Marcus (1921 : 8) regarding *C. stellata* Busk as the young form of *C. guineensis*.

Before considering the remaining species introduced by Canu & Bassler, the characters of the material described by Busk in 1854 and 1884 must be re-examined. Two groups are evident in the large number of specimens available (see list above); these differ principally in the pattern of the basal sector boundaries, and fall very roughly, but not exclusively, into two areas of geographical distribution.

The first, more northerly form (A), is that originally described by Busk. The basal sectors are hexagonal, pierced by very small pores, which are frequently obscured by tubercles. Busk described the basal surface as "divided into hexagonal areas, each corresponding to a cell", and his fig. 3 showed irregular, tuberculate, hexagonal sectors; he did not mention the pores, which are, however, visible at the periphery of the holotype. The sectors, as described above (p. 162) do not, in fact, each correspond to a zoecium, but do have a definite relationship with the zoecia frontal to them (see Text-fig. 6). Busk's specimen from the Challenger Collection is of a second type (B), the basal sectors being quadrilateral, and the surface smooth. Pores are visible in the peripheral zoecia, which become immersed in pits and finally occluded toward the centre of the colony. The basal surface of his specimen was described by Busk "with shallow radial sulci, ridges quite flat, divided into moveable quadrangular areas, each of which has four or five shallow pits". Figure 6b showed these, and (p. 207) Busk mentioned that they might "represent occluded pores".

Busk's description of "moveable" areas may have referred to a dry, loose, basal ectocyst, which, like the calcareous surface, shows the sector boundaries, although his specimen from the Challenger Collection has no ectocyst present. However, it may perhaps have been a reference to the variation in shape of the basal sectors of other specimens Busk had examined.

Both types of basal sector may be modified by tuberculation which obscures the sector boundaries and pores. Zoaria of the B-type tend to be less tuberculated, and are also usually larger than the A-type. In several cases they show central areas with irregular and hexagonal sectors (e.g. 1891. 12. 16. 23 + 24 and 1892. 1. 28. 128).

The variation in zoecial size and proportion, the extent of the cryptocyst, and the shape of the zoecial and vibracular opesiae appear to include all the forms listed in the synonymy above. Canu & Bassler introduced *C. intermedia* for *C. guineensis* Busk, 1884, which they distinguished from the holotype by the possession of porous basal sectors. As noted above, pores are present in both A and B forms, and this is not a specific distinction. *C. brevipora* was introduced for *C. guineensis* Harmer, but the Siboga specimens are not distinct (see Hastings, 1932 : 412).

The remaining 5 species described by Canu & Bassler all have hexagonal basal sectors and are only distinguished from each other by the form of the opesiae and the degree of basal tuberculation. Silén (1942 : 8-9) remarked on the variations within the limits of the species and on the similarity of character given in Canu & Bassler's descriptions. One species was introduced on the evidence of one fragment of a zoarium (see Canu & Bassler 1929 : 75), and examination of photographs of the type specimens, and of unsorted Philippine material, shows that all 5 species fall within a continuous range of variability.

C. transversata, which was described from a single fragment, showed "a great variety of aspect of the inner face", and had a smooth basal surface with some peripheral tubercles, and pores. The figure shows a somewhat worn, moderately tuberculate colony, and photographs of the holotype (1963. 3. 14. 5, which comprises only 32 zoecia), show that it has characters extremely like those of the photographs of *C. hexagonalis*.

C. dentifera was described as differing from *C. stellata* in its tuberoso basal surface. Busk's fig. 3 shows *C. stellata* without basal tubercles, but one of the specimens numbered 1854. 11. 15. 147, is mounted on glass, and it may be seen that fine tubercles are present. Specimens from the type-locality of *C. tuberosa* show similar ranges of variation in size of colony, zoecia, opesiae and tuberculation of basal surface, as those from the type-locality of *C. hexagonalis*. Canu & Bassler's figure of the frontal surface of *C. hexagonalis* is of a worn specimen, and while some of the zoaria from Stns. D 5147 and D 5314 resemble it, others are very similar to the figures of *C. transversata*. Photographs of the cotype specimens of *C. dentifera* show that Canu & Bassler's figure (pl. 3, fig. 7) has been retouched, and that the irregular shape of the opesiae is due to the development of the cryptocyst laminae closing the zoecia.

C. granulosa, in which the sector boundaries were "scarcely visible", is an extremely tuberculated form. The specimen FBS 639 shows this type of development, but the

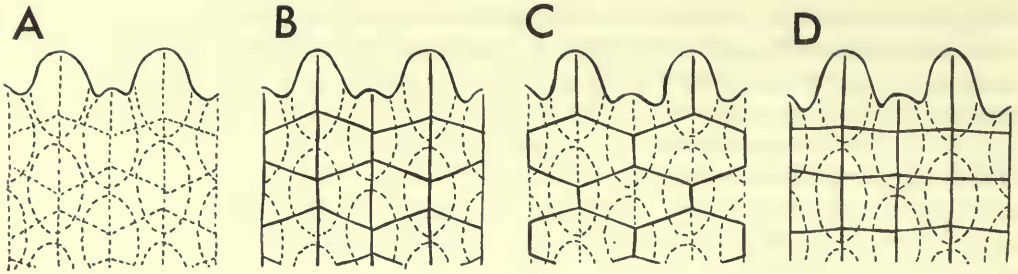


FIG. 6. Basal sectors in *Cupuladria guineensis*. Ovals in broken lines indicate the position of the frontals of the zoecia on the upper surface. A. "*C. dentifera*". Sector boundaries little developed. B. *C. guineensis*, "A" form. Hexagonal sector boundaries divided by radial boundaries. C. "*C. transversata*". Wide hexagonal sectors where the radial sector boundaries are intermittently obscured. D. *C. guineensis*, "B" form. Quadrilateral sectors.

sector boundaries may be seen at the periphery of the colony, and by lighting the surface obliquely. Heavily tuberculated variants of the *granulosa*-type are superficially similar to *C. indica*, but may be distinguished by the absence of any radial threads on the basal side (see above).

The features distinguishing *C. grandis* were its large zoarium and smooth basal surface. The largest zoaria of *C. guineensis* examined are all shallow, with square basal sectors; the topotypes of *C. grandis* are large, strongly domed, and have hexagonal sectors. Domed, B-type zoaria, of similar size (e.g. FBS 157, 18 mm.) and flatter, smaller, A-type colonies (e.g. 1928. 3. 6. 74) indicate that zoarial size and shape are not correlated with type of basal sector, although there is a tendency to reduction of tuberculation in large zoaria of both types. Canu & Bassler figured, but did not comment further on, two distinct forms of vibracular seta in *C. grandis*; "recurved" (text-fig. 13A) and "rectilinear" (text-fig. 13C). Two kinds of seta have been found in *C. canariensis* s.s., the differences in which are reflected in the calcareous parts (Cook (in press)). No sign of any such dimorphism has been seen in any of the many colonies with setae, or in the opesia of specimens of the topotypes of *C. grandis* and the other specimens attributed to *C. guineensis*. The seta in Canu & Bassler's text-fig. 13C somewhat resembles that of a regenerating seta figured by Marcus & Marcus (1962, pl. 2, fig. 7).

The variation in type and degree of calcification of the curved laminae may result in differing appearances of the basal surface. Where the hollows between the laminae are not filled in by secondary calcification, and where the pores are obscured, the surface is like that described in *C. dentifera* (see Text-fig. 6A). Where the radial sector boundaries are intermittently obscured, large, wide, hexagonal sectors are produced, as in *C. transversata* (see Text-fig. 6C). Differential development of tuberculation and pitted pores, together with the effects of wear, produce many other intermediate types of basal surface, but the characters of the zoecia are similar in all zoaria.

The specimens described as *C. granulosa* and *C. microdenticulata* by Kataoka (1961: 224, 5) appear to be referable to *C. guineensis*. The basal surface of both species had sectors, which were porous in *C. microdenticulata*, and the zooecia had the well-developed cryptocyst of *C. guineensis*.

The zoarium of *C. guineensis* attains a larger size than that of any other species in the Cupuladriidae. The largest colonies (Torres Straits 1862. 6. 5. 14 and S. China Sea FBS 904) are 24 mm. in diameter, and many of the other zoaria, especially those with square basal sectors, exceed 15 mm. in diameter.

The size of zooecia varies considerably, but the Lz does not seem to exceed 0.75 mm. and the lz 0.50 mm. The range of Lz given by Canu & Bassler for *C. transversata* includes the dimensions given for all the other species. Measurements taken from their figures indicate that the Lz for *C. dentifera*, *C. grandis* and *C. granulosa* may be as low as 0.50 mm., which is the figure given in the text for the Lz of *C. transversata*, *C. tuberosa* and *C. hexagonalis*. The opesia of these last 3 species are rectangular in contrast to the opesia of the first 3 species, which are often oval, but A-type zoaria having zooecia with both forms of opesia are present from Stn. D 5181, and B-type zoaria with the same degree of opesia variation from the Holothuria Bank 1963. 2. 2. 1, and Low Island, 1932. 4. 20. 112. Generally the more peripheral zooecia of the larger zoaria of both types tend to have more oval opesia and more steeply descending cryptocysts. Some zooecia have distinctly serrated cryptocysts.

As noted above, the vibracular setae appear to be of one kind, and are similar to those found in all other species of the family. Proportionately they are shorter than those of *Discoporella umbellata*, the larger zoaria of which approach those of *C. guineensis* in size.

Two forms of *C. guineensis* therefore exist, but the characters of each are not exclusively correlated and cannot be regarded as specific.

11 THE DISCOPORELLA UMBELLATA-COMPLEX

The characters defining species in the Cupuladriidae, where the common zoarial form determines similarity in the development of all structures, must of necessity be judged using fine criteria. To define a species adequately there must be a recognizable degree of correlation between each character considered, morphologically, geographically, and if possible, palaeontologically. In each of these respects it is possible to divide records of *D. umbellata* into two distinct groups. The problem is whether these groups are of specific or subspecific rank, and the principal criterion applied below is that of character-consistency throughout the time range of the group considered.

Canu & Bassler (1923, text-fig. 13) noted the variability of their material assigned to *D. umbellata*, and figured wide zooecia in Miocene material from Santo Domingo (pl. 2, fig. 18). The part of the zoarium figured showed the growing edge of a regenerating fragment, where the zooecia of all species are frequently wide and slightly distorted (see pp. 155, 158). Photographs of this material (1963. 3. 14. 12) show that subsequent zooecia are narrower. Canu & Bassler's figures (including fig. 17) emphasized the different appearance of Recent specimens from Oran (p. 76, text-

fig. 13A) and the increase in size of the zooecia compared with those of Miocene material from France (text-figs. 13B-C).

C. robertsoniae was introduced by Canu & Bassler for specimens named *C. canariensis* by Robertson (1908 : 314). Her figures showed narrow zooecia with 5-7 opesiules and were certainly referable to the *D. umbellata*-complex (see Hastings, 1930 : 719). In renaming Robertson's specimens Canu & Bassler were apparently aware of basic differences between "typical" *D. umbellata* and their Pleistocene material from the Pacific coast, which was included in *C. robertsoniae*, as they gave the narrow zooecia and large, proximally curved opesia as diagnostic characters. Comparison of Canu & Bassler's figures of their Pacific Pleistocene material (1923, pl. 34, figs. 5-7) with those they gave of West Indian Miocene specimens (1923, pl. 2, figs. 15-19, as *C. umbellata*) shows striking similarities and indicates a strong affinity between the two groups of specimens.

Osburn (1950 : 113) concluded that the wide range of variation found in American specimens justified their inclusion in one species with European *D. umbellata*, but apparently he did not compare his specimens with European material.

Generally, fossil material from the Miocene of Europe and America shows consistently correlated differences in character, which have become even more divergent in Recent specimens from the two areas (see Pl. 3, figs. 1-4). Applying the criteria used in defining the other species described above, the American fossils cannot be included in typical *D. umbellata*, and, as the Recent specimens differ still further, all American records have been separated here as *D. umbellata* subsp. *depressa* (Conrad).

The constant characters of the European material are the wide zooecia, the presence of a pair of opesial denticles, the proportionately large size of the vibracular opesiae, and the numerous small opesiules. There has been an increase in size in Recent specimens, where the proximal edge of the vibracular opesia is denticulate, and the smaller pores in the centre of the horizontal cryptocyst persist.

The constant characters of the American material are the narrow zooecia, the non-denticulate opesiae, with curved proximal edge, the relatively small size of the vibracular opesia, which is never denticulate, and the smaller number of large opesiules. Some fossil specimens have central cryptocystal pores, but these are rarely persistent in Recent material. In contrast to *D. umbellata*, the zooecia of fossil specimens of *D. u. depressa* are, on average, larger than those of Recent colonies.

It might be argued that the narrower zooecia of *D. u. depressa* themselves directly result in the smaller number of opesiules and the lack of central cryptocystal pores, but, as the two species exhibit similar ranges in size and shape of zoarium, there must be some inherent difference producing the narrower zooecia of *D. u. depressa*. The nature of the zoecial and vibracular opesiae are, however, not affected by conditions of growth or width of zooecia, and these are the most important features which show correlated character-consistency in the two forms.

When the *peyroti*-type zoaria listed below are included, records of *D. umbellata* show three separate mean types of population. These forms may overlap at the ends of their ranges of variation, but the Recent forms of each group are geographically distinct. By the application of a discriminant function technique to

further morphometric studies, it is intended to investigate the nature and degree of relationship of the members of this complex.

12 *Discoporella umbellata* (Defrance)

(Pl. 1, fig. 7; Pl. 3, figs. 1, 3, 5, 6; Text-fig. 4)

Lunulites umbellata Defrance, 1823: 361, pl. 47, figs. 1, 1a, 1b. "Lunulite en-parasol" de Blainville, 1834: pl. 72, fig. 1a, 1b.

Discoporella umbellata (Defrance) d'Orbigny, 1853: 473, pl. 717, figs. 1-5. Lagaaïj, 1953: 16, pl. 1, fig. 3, Miocene, Netherlands. Buge (part), 1957: 177, pl. 10, fig. 4, Miocene, S.W. France.

Discoporella berardana d'Orbigny, 1853: 474, Recent, Algeria, 14 m.

Cupularia lowei Busk, 1854: 99, pl. 116, figs. 1-6, Madeira. *C. lowei* Gray (sic) Norman, 1909: 290, pl. 37, figs. 7-12, Madeira 50-70 fath. Waters, 1921: 412, pl. 30, figs. 1-6, 26-29, Madeira.

Cupularia umbellata (Defrance): Manzoni, 1869: 26, pl. 2, fig. 16, Pliocene, Italy. 1875: 39, pl. 5, fig. 67, Miocene Italy. Calvet 1907: 393, Canaries, 80 m., and Cape Verde Islands, 1900 m. Canu, 1909: 448, pl. 16, figs. 16, 17, Burdigalian, Helvetien, Miocene, S.W. France. Waters, 1921: 414, Pliocene, Italy. Canu & Bassler, 1923: text-figs. 13A, Oran, Recent; B. C. D. E France Miocene, ?I Oran, Recent (as *C. multispinata*).

Peyroti-type zoaria: *Cupularia peyroti* Duvergier, 1921: 124. 1924: 19, pl. 1, figs. 6-10, Helvetien, Miocene, France.

Cupularia umbellata Defrance: O'Donoghue, 1924: 39, Cape St. Blaize, S. Africa.

Discoporella umbellata (Defrance) part Hastings, 1930: 719, specimens from S. Africa.

MATERIAL. British Museum. Bay of Funchal, 1892. 8. 6. 1 (type material of *C. lowei*). Madeira, 1911. 10. 1. 648, 1004 and 1963. 1. 16. 10 and 11, Norman Coll. Madeira, 1932. 8. 23. 1. Canaries, 1899. 7. 1. 1250, Busk Coll. Near Cape Frio, Angola, 12° E., 18° 30' S., 1899. 7. 1. 1241, Busk Coll. (*doma*-type zoarium).

Palaeontology Dept. Coll. D. 25005, 25003, Burdigalian, L. Miocene, Bordeaux. D. 39047-96, Miocene, Reinbeck, Germany. D. 38947-9, Miocene, Beeringen. D. 39884-91 (pt), Albena, Bordighera, Pliocene, Italy.

Voigt Coll. Reinbeck, L. Miocene. Boring, Bockstedt, Middle Miocene (1 *doma*-type zoarium present).

Peyroti-type zoaria.

MATERIAL. British Museum. Cape St. Blaize, S. Africa, 1923. 7. 26. 9, O'Donoghue Coll. S. Africa, 1963. 1. 16. 9, O'Donoghue Coll. S. Africa, 34° 29' S., 21° 02' E., 26. 11. 59, 73 m., sand, SCD 114C, 1963. 1. 16. 6; 34° 29' S., 22° 18' E., 28. 8. 60, 106 m., sand, SCD 147D, 1963. 1. 16. 7; False Bay, 31. 1. 59, 50 m., FAL 341D (B), 1963. 1. 16. 8, Univ. Cape Town Ecological Survey Coll. Cape of Good Hope, 1842. 12. 2. 20, Belcher Coll. S. Africa, Cape Infanta N.E. by N½N, 13.5 miles, 43 fath., 1949. 11. 10. 618; Stalwart Point N.N.W. 9 miles, 53 fath., 1949. 11. 10. 652A; Nanquas Peak N. 46° E., 19 miles, 63 fath., 1949. 11. 10. 674A, and N.E. ¾N., 15 miles, 59 fath., 1949. 11. 10. 675 (including 2 *doma*-type zoaria), N.W. ¼N. 15 miles 49 fath., 1949. 11. 10. 668; Cape Infanta N.E. by N19 miles, 46 fath., 1949. 11. 10. 622A, 623A, N.E. by N¼N. 14.5 miles, 45 fath., 1949. 11. 10. 620; Cape St. Blaize N. 7.5 miles, 37 fath., 1949. 11. 10. 624A, 625A, 626A, 627A and 94A, N.E. ¾N. 11

miles, 40 fath., 1949. II. 10. 629; Tugela River mouth, N.N.W. 11.75 miles, 37 fath., 1949. II. 10. 644 (including 2 *doma*-type zoaria); Umtwalumi River mouth N. by W. 7 miles, 50 fath., 1949. II. 10. 651; False Island N. 8.5 miles, 53 fath., 1949. II. 10. 669A; Glendower Beacon N.½W. 6 miles, 39 fath., 1949. II. 10. 660, Burrows Coll. John Murray Coll. (all from sandy substrates). Stn. 103, 5° 39' 30" S., 39° 11' 30" E., N. of Zanzibar, II. 1. 34. 101 m., Z. 198 C. Stn. 104., 5° 37' 54" S., 39° 11' 36" E., II. 1. 34, 207 m. Z. 199A.

Zoarium usually large (maximum observed diameter 22 mm.). Zooezia often as wide as long. Opesia small, with straight proximal border with a pair of minute denticles. Operculum with a straight proximal sclerite. Descending cryptocyst wide, tuberculate, horizontal cryptocyst lamina with some small irregular central pores and 8-14 small opesiules, frequently slit-like. Vibracular opesia very large ($\times 1.75$ of Lop), finely denticulate proximally in Recent specimens. Basal surface with short grooves, pits and ridges, tuberculate, or smooth, with a layer of kenozooezia and vibracula encroaching from the frontal surface.

DIMENSIONS. Lz 0.50-0.70 mm.; lz 0.40-0.63 mm.; Lop 0.10-0.15 mm.; lop 0.12-0.20 mm.; Lo 0.10-0.11 mm.; lo 0.12-0.15 mm.; Lvo 0.18-0.25 mm.; Ls 0.6-1.45 mm.

The records of European Miocene and Pliocene specimens agree in describing and figuring *D. umbellata* with wide zooezia and a large number of opesiules. Although generally the zooezian measurements of fossils are smaller than those of Recent specimens, the proportions and general characters of the species seem constant, and are certainly distinct from those of *D. u. depressa*.

The majority of zooezia are as wide or occasionally wider than long, and the number of opesiules is most frequently between 8 and 10. Defrance figured 8-9, d'Orbigny 10, de Blainville 8-9, and Manzoni (1869), 10-11, although the number given in 1875 was 7. In Recent specimens the number is often as many as 14, and the opesiules are slit-like. D'Orbigny described, as *D. berardana*, Recent specimens from Algeria with denticulate cryptocysts, transverse, semi-lunar orifices, and very large vibracular opesia. *D. umbellata* was figured by Canu & Bassler (1923, text-fig. 13A) from Oran, and it is possible that d'Orbigny's record referred to worn specimens of this species. Canu & Bassler's photograph of *C. multispinata* (1923, text-fig. 13I.) showed opesiules and a basal sclerite in the operculum, and is perhaps also of *D. umbellata*.

The specimens described as *C. lowei* were distinguished from *D. umbellata* by the deformation of the zoarium (see p. 158, and Marcus & Marcus, 1962: 294).

The paired denticles on the proximal edge of the opesia are present in all well-preserved fossil and Recent material. Waters (1921: 415) noted their occurrence, and Lagaaij (1953: 16) included them in his diagnosis of the species.

The proximal edge of the vibracular opesia of Recent specimens is finely denticulate (see pl. 3, fig. 1), a character which has not been seen in fossil material. The vibracular opesia are extremely large, as noted by d'Orbigny (1853: 474, in *D. berardana*), their length being significantly greater than that of the zooezian opesia.

The operculum is strongly flanged laterally, with a straight, robust, proximal sclerite.

The specimen from Cape Frio has a *doma*-type zoarium. The basal surface is solid and there are peripheral kenozoecia, but the zoecia are worn, and the character of the opesia cannot be clearly seen. However, the width of the zoecia (lz 0.3–0.48 mm.) and the number of the opesiules (5–7), are nearer the higher end of the range of variation than those of many of the corresponding *doma*-type specimens from the west Atlantic (see below), and thus reflect the differences found in zoecia of normal zoaria of the two forms. One fossil zoarium (Voigt Coll.) is also extremely worn, but shows two rows of peripheral vibracula and a basal surface almost filled by secondary calcification.

The development of the cryptocyst in the young peripheral zoecia shows the close relationship of *D. umbellata* both to *D. u. depressa* and to the denticulate species of *Cupuladria* (group C). Fine, irregular denticles grow first from the proximal and lateral edges of the cryptocyst and then develop progressively in a distal direction. At this stage the zoecia greatly resemble specimens of *C. owenii* and *C. doma*. Further calcification produces a distal bar cutting off the opesia, and, as the more proximal denticles fuse, leaving a series of denticulate, irregular opesiules, and a number of pores in the centre of the horizontal cryptocyst lamina thus formed (see also Marcus & Marcus, 1962, pl. 1, fig. 4). The appearance of the zoecia at this stage is then very similar to that of Miocene specimens of *D. u. depressa* from Oak Grove, Florida, where this type of development was the final stage. Other specimens of *D. u. depressa* from the Miocene of Cercado de Mao, Santo Domingo, show more complete calcification, with rounded opesiules and no central pores. The calcification of eastern Atlantic fossil and Recent specimens of *D. umbellata* is even greater, and the opesiules are further reduced.

The distribution of *D. umbellata* s.s. is now confined to the northern and north western coasts of Africa, and the neighbouring islands.

D. umbellata and *C. haidingeri* are frequently associated in samples from the European Miocene. When worn they are extremely difficult to distinguish from each other. The basal surface of *D. umbellata* is not as regularly grooved as that of *C. haidingeri*, and generally the zoecia of *D. umbellata* are wider. Even when the central part of the cryptocyst lamina is broken, the vestibular arch surrounding the distal part of the opesia is smaller and more incurved in *D. umbellata* than in *C. haidingeri*. At the edge of the central area of closed zoecia the most recent closed frequently show the straight bar, proximal to the opesia, which is absent in *C. haidingeri*.

Recent specimens from south and east Africa correspond almost exactly with *C. peyroti* as described by Duvergier. The dimensions he gave fall within the range of those now obtained from a large number of specimens, and the photograph shows kenozoecia exactly like those of the Recent material. In one respect, Duvergier's account may be confusing, as he followed Canu in describing the frontal, convex surface of the colony as basal, and the concave or planar kenozoecial surface as frontal. O'Donoghue mentioned the invasion of the basal surface by kenozoecia

and vibracula, and Hastings, who examined some of O'Donoghue's material, expressed doubt as to its inclusion in *D. umbellata* s.s. The Miocene specimen of *D. umbellata* figured by Buge shows a hollow basal surface covered by kenozoecia and vibracula. The specimens from south Africa show the complete range of development, those from east Africa, the young stages only. Young zoaria are flat, with a solid, smooth base, and older colonies are more domed, with the basal surface either concave (e.g. 1963. I. 16. 6-9, 1949. II. 10. 625A) or completely filled with secondary calcification (e.g. 1949. II. 10. 669A and 652A). In neither state is the surface ridged or tuberculate. The budding of the basal kenozoecia appears to be random and irregular, and the calcified cryptocyst is developed like that of the zoecia, from the fusion of irregular denticles.

The zoecial opesiae are often slightly curved proximally, and the denticles are often reduced or absent, but the opesiae are never sinuate as in *D. u. depressa*. The horizontal cryptocyst lamina differs from that of typical *D. umbellata* in the large number of frontal pores, which are often indistinguishable from the marginal opesiules. The operculum is like that of *D. umbellata*, and is flanged laterally, with a strong, straight proximal sclerite.

A few colonies combine some characters of both *doma*- and *peyroti*-type growth. They are small (diameter 2 mm.) and high, with solid, smooth bases. The peripheral zoecia are closed, but only one row of peripheral vibracula is present, and there is no invasion of the basal surface by kenozoecia. The zoecia are small, approximately half the length of zoecia in a normal colony, but the opesiae are not reduced in proportion, being about $\frac{3}{4}$ of the length of normal opesiae. The zoecia have an average of 8 opesiules and a number of irregular frontal pores in the cryptocyst. The proximal edge of some vibracular opesiae are finely denticulate. The *doma*-type colonies thus have many of the characters of the normal zoaria from the south east African coast. Their occurrence does not seem in this case to be correlated with low temperature, as all the records are confined to warm waters, extending from the warm-temperate zone, eastward to the subtropical zone, as described and discussed by Stephenson (1947 : 215).

As noted above (p. 163), no specimens of typical *D. umbellata* have been found from the south and east coasts of Africa, nor have *peyroti*-type zoaria been recorded from the west African coast. Specimens of *Cupuladria owenii* (Gray) and *C. multi-spinata* (Canu & Bassler), both of which also occur from these two areas, show no examples of *peyroti*-type growth.

13 *Discoporella umbellata* subsp. *depressa* (Conrad)

(Pl. 3, figs. 2, 4)

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

Discoporella denticulata (Conrad) Gabb & Horn, 1862 : 142, pl. 20, fig. 25, Miocene, New Jersey to S. Carolina.

- Cupularia umbellata* (Defrance) Smitt, 1873 : 14, pl. 3, figs. 75-80, Cape Fear River, N. Carolina, 7 fath. *C. umbellata* (Manz.) (sic) : Verrill, 1878 : 305. Canu & Bassler, 1918 : 118, pl. 53, figs. 2-4, 1919 : 85, pl. 1, figs. 5-7, pl. 2, figs. 17-21. 1923 : 68, pl. 2, figs. 15-19, text-fig. 10G, Lower Miocene, west Indies. 1928 : 64, pl. 7, figs. 1-3, Gulf of Mexico. 1929 : 142, pl. 15, figs. 5-11, text-figs. 35A-K (as *C. lowei*), between California and Hawaii, 2723 fath. 1930 : 11, Galapagos and Hawaii. Silén, 1942 (part) : 15, text-figs. 10-12, localities 1-17.
- Cupularia punctata* Canu, 1904 : 10, pl. 2, fig. 23, Miocene, Patagonia.
- Cupularia canariensis* Busk : Robertson, 1908 : 314, pl. 24, figs. 90, 91, California.
- Cupularia lowei* Busk : Osburn, 1914 : 194, Florida, 12 and 22 fath.
- Cupularia robertsoniae* Canu & Bassler, 1923 : 82, pl. 34, figs. 5-7, Pleistocene, California.
- Discoporella umbellata* (Defrance) Hastings, 1930 : 718, pl. 11, fig. 54, Gorgona, Galapagos, Balboa, 15-30 fath. Mcguirt, 1941 : 65, pl. 1, figs. 4, 7, 9-11, Miocene, Louisiana. Osburn, 1950 : 113, pl. 11, figs. 7-10, California to Ecuador, 5-100 fath. Soule, 1959 : 34, Gulf of California, 5-46 fath. Soule & Duff, 1957 : 99, Pleistocene, California. Marcus & Marcus, 1962 : 290, pl. 1, fig. 4, pls. 2-5, Brazilian coast, 4-150 m.

MATERIAL. British Museum. Gorgona, 1929. 4. 26. 102, 103, 106 ; Balboa, 1929. 4. 26. 104 ; Galapagos, 1929. 4. 26. 105. "St. George" Coll. Galapagos, 1933. 12. 10. 15, Canu & Bassler Coll. Abrolhos Bank, off Brazil, 1899. 7. 1. 1260, 1261 and 1265 (*doma*-type zoarium). Berbice, British Guiana, 25 fath. (21 zoaria, 4 of *doma*-type). "Terra Nova" Coll. Stn. 42, off Rio de Janeiro.

Palaeontological Dept., D 33911, D 33912, D 33916, D 33910, Miocene, San Domingo. D 41118, Bowden marl, Miocene, Jamaica. D 34392-409, Miocene, Duplin, S. Carolina.

Cheetham Coll. Miocene, Oak Grove, Okaloosa Co., Florida.

Philadelphia Academy Coll., Wilmington, N. Carolina.

Zoarium large (maximum diameter observed 18 mm.). Zooecia generally narrower than in *D. umbellata*, lateral cryptocyst descending more steeply. Horizontal cryptocyst lamina not usually porous at centre (in Recent specimens). Opesia large, curved proximally or slightly sinuate, denticles absent. Opesiules large, 3-9 in number. Operculum with delicate basal sclerite curved distally. Vibracular opesiae little larger than zoecial opesiae, not denticulate proximally. Basal surface tuberculate with grooves, or short furrows and pits.

DIMENSIONS. Lz 0.45-0.7 mm. ; lz 0.22-0.35 mm. ; Lop 0.11-0.13 mm. ; lop 0.12-0.14 mm. ; Lo 0.07-0.08 mm. ; lo 0.10-0.11 mm., Lvo 0.15-0.18 mm. ; Ls 0.60-1.10 mm.

Conrad's description of *L. depressa* mentioned that "many of the larger pores" (i.e. zooecia) were "filled with a minutely porous plate or diaphragm, solid in the centre". Specimens examined from the Miocene of Wilmington, N. Carolina, have narrow zooecia, with 7 large opesiules and an opesia with a curved proximal edge. A few central pores may be seen from the underside of the cryptocyst, but most of these are occluded by secondary calcification. Natural Well, the type locality, and Wilmington, are near the Cape Fear River, from which Smitt described the first Recent specimens from Pourtales's Collection. Canu's figure of *C. punctata* showed the frontal surface of a worn specimen ; it had the characters of *D. u. depressa*, with 3-7 opesiules, and a rounded opesia.

The magnification of some of the figures of *D. u. depressa* (as *D. umbellata*) given in

two of the works of Canu & Bassler is confusing. The same series of photographs were used throughout; but those of 1919 (pl. 2, fig. 17 (nat. size), figs. 18 ($\times 25$), 19, 20 and 21 ($\times 19$)) are smaller than those of 1923 (pl. 2, figs. 15, 16, 17, 18, 19) which are described as having the same magnification.

Osburn (1950) confirmed that Verrill's record (1878) of *D. umbellata* from Fort Macon, N. Carolina, was correct, as he had examined material from the same locality.

The zooecia of *D. u. depressa* are generally narrower than those of *D. umbellata*. The figures of American material all agree in showing narrow zooecia with large, rounded opesia and opesiules, and Soule & Duff described the zooecia as "elongate". The opesia is always curved proximally, and may be distinctly sinuate; denticles are absent. The bars between the opesiules are narrow. The proximal sclerite of the operculum is delicate and slightly curved in a distal direction. The vibracular opesia are never denticulate proximally, as in *D. umbellata*, and proportionately, they are smaller; the setae do not appear to attain the length of those of *D. umbellata*.

Most of the 7 *doma*-type colonies examined have large, rounded opesia and narrow zooecia (lz 0.20–0.35 mm.), with 2–7 opesiules, and are thus similar to more normal specimens of *D. depressa*. They differ from the *doma*-type colony of *D. umbellata* principally in their narrower zooecia and larger opesia.

14 CUPULADRIIDAE, GENERAL COMMENTS

The number of species of Cupuladriidae from the Pacific Ocean is thus two, *C. guineensis* and *D. u. depressa*, which last is confined to the eastern part. Two species occur in the Indian Ocean; *C. indica* in the north and west, and *D. umbellata* (*peyroti* form) in the south-west. Ten forms may be distinguished in the Atlantic Ocean (Cook (in press)), only the subspecies *D. u. depressa* occurring in both the Atlantic and Pacific.

The family is sharply defined, its principal characters being the distinctive astogeny, radial development and type of vibracula. Species in which any character shows a major discrepancy should be assignable to other families. This is demonstrated by examination of the characters of *Cupularia capriensis* Waters.

HINCKSINIDAE Canu & Bassler 1927

Hincksinidae Canu & Bassler, 1927 : 3, Bassler, 1953 : G 159, Lagaaij, 1963b : 171.

SETOSELLINA Calvet, 1906 : 157

15 *Setosellina capriensis* (Waters)

(Pl. 1, figs. 5, 6)

not *Setosellina roulei* Calvet, 1907 : 395, pl. 26, figs. 5, 6, Cape Verde Is., 1900 m., Capo Blanco, 2330 m.

"*Cupularia minima* (Busk MS)" Waters, 1921 : 419, as *Heliodoma implicata* Calvet, specimens from the Aegean Sea. (not *H. implicata*, see below).

Setosellina roulei Calvet : Waters, 1925 : 350, pl. 21, fig. 4, Capri, 50 fath.; Gautier, 1962 : 69, Tunisia, 150 m., Rhone Delta, 120 m.

Cupularia capriensis Waters, 1926 : 432, pl. 18, figs. 8, 9, Capri.

Cupuladria capriensis (Waters) Marcus & Marcus, 1962 : 288.

LECTOPARATYPES, chosen here, Manchester Museum, Faraglione, Capri, 150 fath., Waters Coll.

OTHER MATERIAL. British Museum. Aegean Sea, 130 fath., 1899. 7. 1. 1253 and 5122 ; 100 fath., 1899. 7. 1. 1251, collected Spratt. Râs el-Amouch, 1899. 7. 1. 4701 ; Mediterranean, 30 fath., 1899. 7. 1. 1491, collected "Porcupine". Busk Coll.

Zoarium small, selenariiform, free, growing on a sand-grain. Zooecia with oval opesia. Each zooecium with a distal interzooecial vibraculum, reaching the basal wall of the zoarium. Opesia of ancestrular and central area closed by a calcified lamina with a single central pore. Ancestrula with one distal and one proximal-lateral vibraculum, and surrounded by 6 zooecia, budded spirally.

DIMENSIONS. Lz 0.45-0.60 mm., av. 0.54 mm. ; lz 0.30-0.34 mm., av. 0.32 mm. ; Lop 0.32-0.35 mm., av. 0.33 mm. ; lop 0.17-0.20 mm., av. 0.19 mm.

Waters (1921) described, as *Heliodoma implicata* Calvet (1906 : 157, 1907 : 396, pl. 26, figs. 7, 10), some specimens from the Aegean Sea in the Busk Collection (1899. 7. 1. 1253). He particularly noted that the form of the zoarial spiral differed from that figured by Calvet. The zooecia of the ancestrular area of *H. implicata* are not occluded by a lamina, which is however, present in the specimens on slide 1899. 7. 1. 1253. These zoaria are identical with those from Capri described by Waters in 1926 as *Cupularia capriensis*, which has almost complete opesial closures in the ancestrular area, a small central pore only remaining open.

Waters does not at any time appear to have considered the Aegean specimens either as distinct from *H. implicata* or as identical with his new species, *C. capriensis*. His quotation of Busk's MS name for them in 1921 cannot therefore be regarded as a specific designation.

C. capriensis Waters is certainly referable to *Setosellina* Calvet. Calvet (1907 : 395) described *Setosellina roulei* with a salient calcareous lamina and figured (pl. 26, fig. 6) zooecia which were partially closed, with a small central pore. The early astogeny of specimens of *S. capriensis* was described (as *S. roulei*) by Waters (1925 : 350, pl. 21, fig. 4, Capri, 50 fath.). The budding is similar to that of *Otionella* and *Selenaria* figured by Stach (1936b : 64, text-figs. 1-7). The same type of spiral budding is found in *Setosellina constricta* (Borneo Bank, 1928. 3. 6. 75 and N. New Guinea, 1928. 3. 6. 76) described by Harmer (1926 : 264), and *S. goesi* (Silén) described by Lagaaij (1963b : 172). The basal surface of *S. capriensis* shows that the vibracular chambers are inserted between, and extend to the same depth as the zooecia. They are thus truly interzooecial, and completely unlike those found in the Cupuladriidae.

Gautier (1962 : 69) commented on the probable identity of *C. capriensis* Waters with *Setosellina roulei* Calvet. The dimensions of the abyssal specimens figured by Calvet are significantly smaller than those of *S. capriensis* given above. They average : Lz 0.36 mm. ; lz 0.25 mm. ; Lop 0.23 mm. ; lop 0.13 mm. Measurements taken from

Waters's figure of *S. roulei* from the Mediterranean (1925, pl. 21, fig. 4), combined with those given by Gautier, give a range of Lz 0.45-0.50 mm.; lz 0.32-0.35 mm.; Lop 0.25-0.28 mm.; lop 0.16-0.18 mm. These dimensions are far closer to those of *S. capriensis* given above than to those of *S. roulei* as originally described. The geographical and bathymetrical distributions of the two forms are also distinct; *S. roulei* occurring off the Cape Verde Islands at 1900 m., and off Capo Blanco at 2330 m. The larger *S. capriensis* has been recorded from the Mediterranean and Aegean only, at a greatest depth of 150 m. Until further material from both areas can be examined, all the Mediterranean records are here considered to be distinct and referable to *S. capriensis*.

S. capriensis differs from the Cupuladriidae in its early astogeny, and related to this, in the spiral development of the zoarium. The relationship of the vibracular chamber to the zooecium, and the type of opesial closure of the central zooecia, are also fundamentally different from those found in the Cupuladriidae.

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17 SUMMARY

The principal characters and mode of development of the Cupuladriidae are described and discussed, the family is defined, and groups of species with similar characters are listed. The effects of zoarial form of zooecial characters, and the occurrence and possible causes of abnormal zoaria similar to those found in *C. doma*, and those described as *C. peyroti*, are discussed. Descriptions are given of *C. pyriformis*, *C. indica* and *C. guineensis*. The complex of forms previously assigned to *D. umbellata* is examined in the light of character-consistency of fossil and Recent records. *Cupularia capriensis* Waters is described and referred to *Setosellina*.

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PLATE I

Cupuladria, *Setosellina* and *Discoporella*

- FIG. 1. *Cupuladria guineensis* (Busk). Philippines, United States National Museum. Syntype of "*C. granulosa*", 1963. 3. 14. 9. Photograph by courtesy of the United States National Museum. $\times 14.5$.
- FIG. 2. *C. guineensis*. Philippines, United States National Museum. Cotype of "*C. dentifera*", 1963. 3. 14. 7. Photograph by courtesy of the United States National Museum. $\times 16$.
- FIG. 3. *C. pyriformis* (Busk). Anguilla, Naturhistoriska Riksmuseet, FBD 533, frontal surface. $\times 10$.
- FIG. 4. *C. pyriformis*. The same specimen, basal surface. $\times 10$.
- FIG. 5. *Setosellina capriensis* (Waters). Aegean, 1899. 7. 1. 1253pt., Busk Coll., frontal surface. $\times 17.4$.
- FIG. 6. *S. capriensis*. The same specimen, basal surface. $\times 17.4$.
- FIG. 7. *Discoporella umbellata* (Defrance). *Peyroti*-type zoarium, S. Africa, 1949. 11. 10. 94, Burrows Coll., basal surface, showing kenozoocia and vibracula growing over the basal surface. $\times 4.3$.

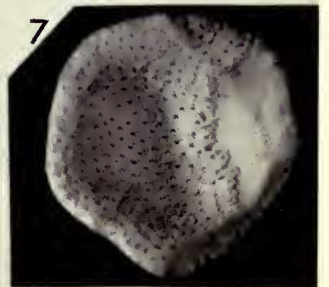
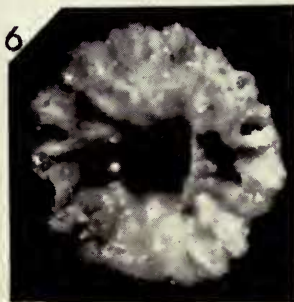
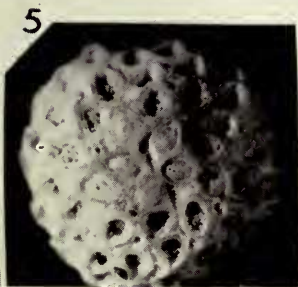
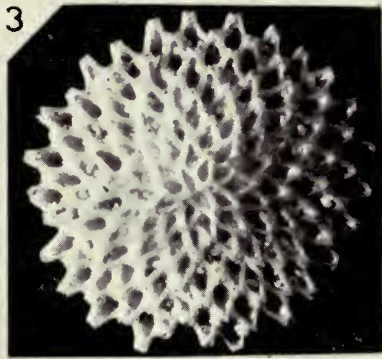
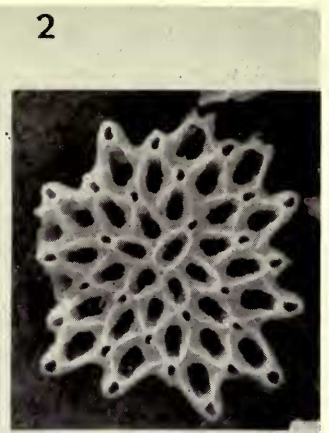
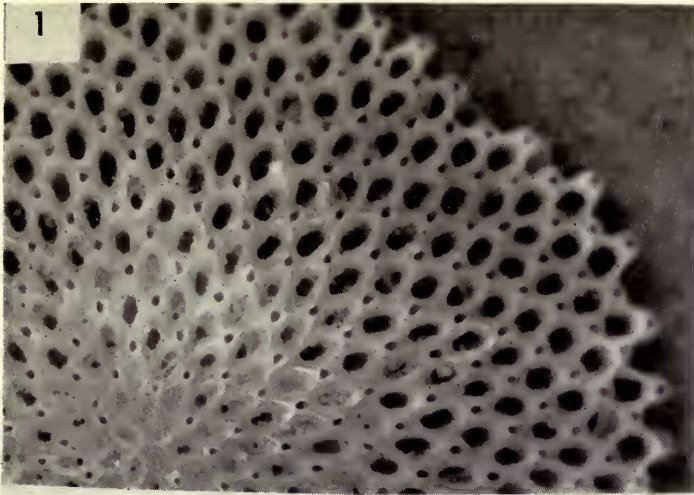


PLATE 2

Cupuladria indica and *C. guineensis*

- FIG. 1. *Cupuladria indica* n. sp. Burma, 1899. 5. 1. 267 pt., Hincks Coll., paratype, frontal surface. $\times 13.4$.
- FIG. 2. *C. indica*. The same specimen, basal surface. $\times 10.5$.
- FIG. 3. *C. guineensis* (Busk). Sulu Archipelago, 1963. 3. 14. 2, U.S.N.M. Coll. (from type-locality of "*C. tuberosa*"), frontal surface. $\times 9$.
- FIG. 4. *C. guineensis*. The same specimen, basal surface. $\times 9$.

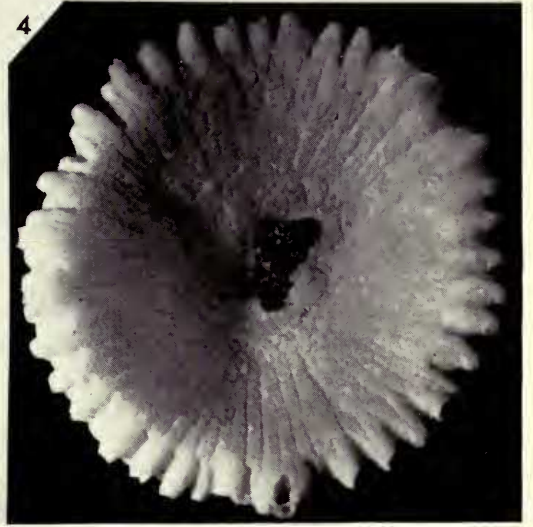
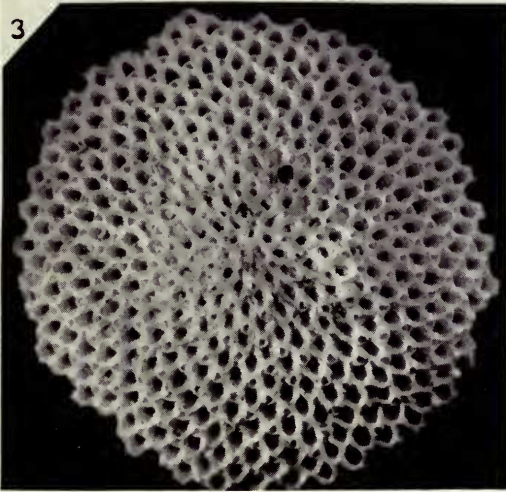
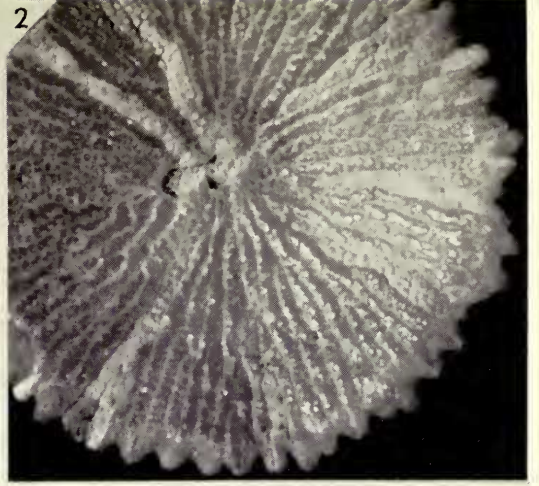
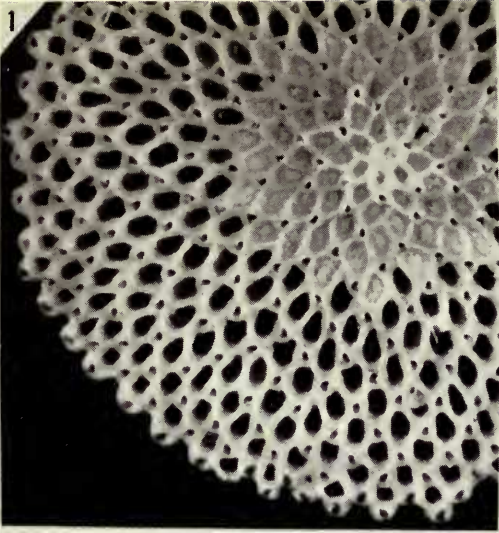


PLATE 3

The *Discoporella umbellata*-complex

- FIG. 1. *Discoporella umbellata* (Defrance). Ghana, Achimota Coll., II, 7A. Zooecia and vibracula. $\times 40$.
- FIG. 2. *D. umbellata* subsp. *depressa* (Conrad). Rio de Janeiro, Discovery Coll., 879A. Zooecia and vibracula. $\times 55$.
- FIG. 3. *D. umbellata*. S.W. France, L. Miocene, D25003. Zooecia and vibracula. $\times 31$.
- FIG. 4. *D. umbellata* subsp. *depressa*. Florida, Miocene. Zooecia and vibracula. $\times 18.5$.
- FIG. 5. *D. umbellata*. *Peyroti*-type zoarium. S. Africa, 1949. II. 10. 94 pt., Burrows Coll. Zooecia and vibracula. $\times 43$.
- FIG. 6. *D. umbellata*. *Peyroti*-type zoarium. The same specimen, basal surface, showing kenozoecia and vibracula. $\times 37$.

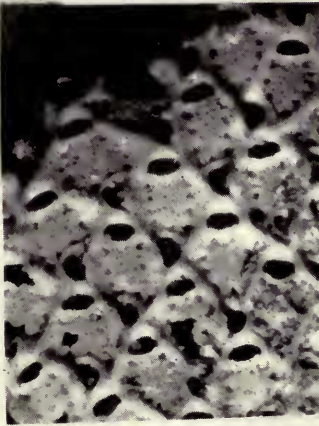
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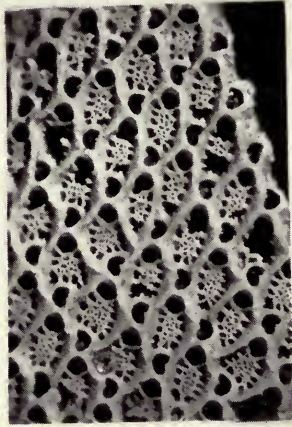
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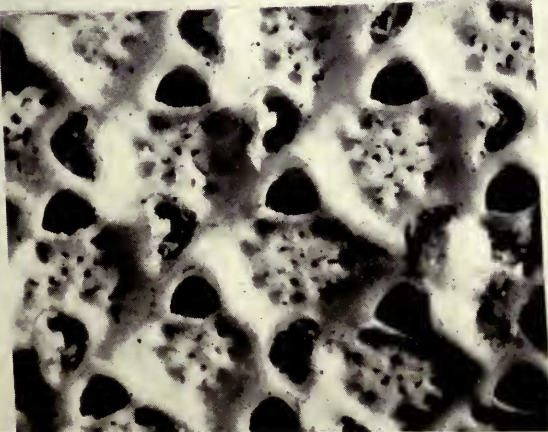
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