

*DIONELLA* GEN. NOV. (SUPERFAMILY  
MEMBRANIPORACEA) FROM THE UPPER  
CRETACEOUS OF EUROPE

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ABSTRACT. The new genus *Dionella* is proposed for membraniform Polyzoa from the Upper Cretaceous of Europe having slightly calcified frontal walls, diatellae, hyperstomial ovicells, and small interzoecial avicularia, which, when present, are distal to the ovicells. The type material of the seven species assigned to this genus is redescribed with the establishment of lectotypes, a neotype, and many synonymies. A possible evolutionary pattern for the group has also been given.

THE material, which forms the basis of this paper, is part of the large collection of Chalk Polyzoa made by R. M. Brydone and lodged in the Sedgwick Museum, Cambridge. With this material Brydone established numerous species of Cretaceous membraniform Polyzoa, and those which had encrusting zoaria he placed in the genus *Membranipora*. However, an encrusting zoarium is no longer accepted as the major diagnostic feature of this genus (Borg, 1931, p. 4) and all of the species, assigned by Brydone to this genus, must be transferred to other genera. The present paper is the first of a series attempting such a systematic revision, and is one of the topics studied for a thesis at the University of Cambridge.

The terminology and stratigraphy adopted in this paper follow that used by Larwood (1962). The text-figures are based on drawings made with the aid of a squared graticule and the measurements have been made with the aid of a micrometer scale.

Measurements are given below in an abbreviated form (text-fig. 1) for many of the type specimens, and they are all in hundredths of a millimetre. These measurements are given only for those autozoecia which occur in a longitudinal row and do not give rise to a new row. *N* represents the number of observations made for each character. The autozoecial measurements comprise three sets of figures for each character (for example: 54-67/60/4), which correspond to the observed range, the mean, and the standard deviation respectively. The standard deviation has not been calculated for the ovicells and so only the observed range and the mean are given (for example: 54-67/60).

SYSTEMATIC DESCRIPTIONS

Superfamily MEMBRANIPORACEA Busk 1854

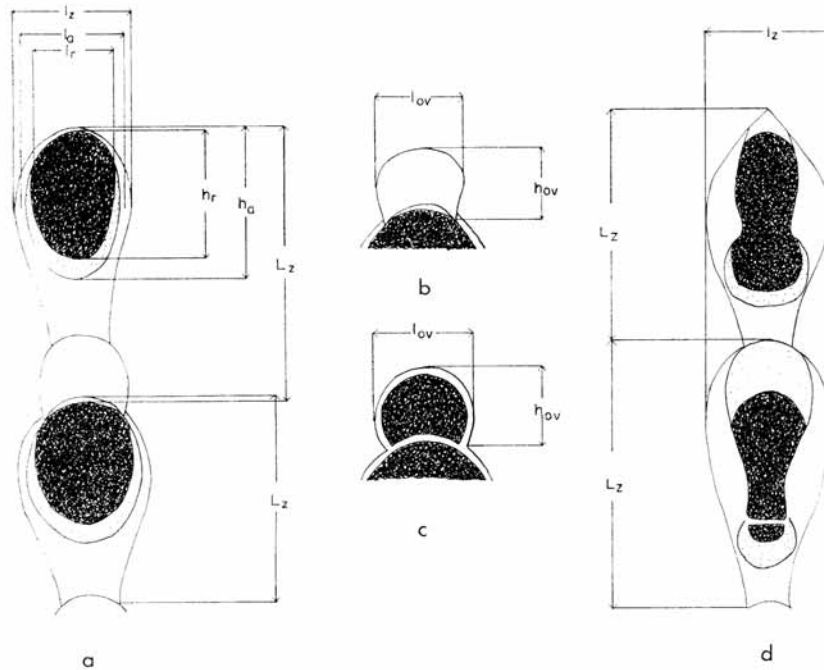
Genus *DIONELLA* gen. nov.

- 1846 *Cellepora*: von Hagenow, p. 617 [*partim*]
- 1887 *Membranipora*: Marsson, p. 58 [*partim*]
- 1906 *Membranipora*: Brydone, pp. 293, 294 [*partim*]
- 1910 *Membranipora*: Brydone, pp. 5, 76 [*partim*]
- 1910 *Cellepora*: Brydone, p. 5.
- 1914 *Membranipora*: Brydone, pp. 345-7.
- 1916 *Membranipora*: Brydone, p. 338.

[*Palaeontology*, Vol. 8, Part 3, 1965, pp. 492-517, pls. 67-71.]

- 1917 *Membranipora*: Brydone, p. 49.  
 1920 *Tegella* (*Membranipora*): Canu and Bassler, p. 166.  
 1925 *Membranipora*: Levinsen, pp. 332-3.  
 1930 *Membranipora*: Voigt, p. 421 [*partim*]; p. 434 [*?partim*]  
 1930 *Membranipora* (*Callopora*): Voigt, p. 443 [*?partim*]; p. 444 [*partim*]  
 1936 *Membranipora*: Brydone, p. 65 [*partim*]  
 1949 *Membranipora*: Voigt, pp. 16 [*partim*], 18-19.  
 1959 *Membranipora*: Voigt, p. 55.  
 1962 *Membranipora*: Voigt, p. 30 [*partim*]

*Type species.* *Cellepora trifaria* von Hagenow, 1846, p. 617. Lower Maastrichtian. Rügen, Germany.



TEXT-FIG. 1. Explanation of the abbreviations used in the measurements of: (a) autozoecia; (b) complete or (c) broken ovicells; (d) avicularia.  $L_z$  = length of the zooecium;  $l_z$  = width of zooecium;  $h_a$  = length of aperture;  $l_a$  = width of aperture;  $h_r$  = length of opesium;  $l_r$  = width of opesium;  $h_{ov}$  = length of ovicell;  $l_{ov}$  = width of ovicell.

*Diagnosis.* Membraniporacea with rounded-rhomboidal zoecia, usually budded multi-serially; zoecia with well-defined mural-rims; aperture more or less restricted by cryptocyst; gymnocyst variably developed, both proximally and laterally; mural-rim more or less spinose, with 0-12 pairs of spine-bases; dietellae present, often arranged asymmetrically; avicularia of two kinds of interzoecial, either of which may be absent, one type is small, distally rounded or acuminate, distal to the autozoecium; the other

type is solitary, elongate spatulate, and may grade into vicarious; ovicell hyperstomial, prominent.

*Remarks.* It has been found necessary to designate a new genus for those membraniporine Polyzoa which possess autozooezia with dietellae, a hyperstomial ovicell, and a single associated interzooezial avicularium at their distal margins. These avicularia are directed away from the autozooezial distal margins and their presence or absence is not influenced by the ovicell of the associated autozooezium. All of the species belonging to this genus have, until now, been placed in *Cellepora* (*sensu lato*) and *Membranipora* (*sensu lato*). There has been no previous attempt to group these species into a single taxonomic unit.

Voigt's use of *Membranipora* (*Callopora*) for some of the species [Voigt, 1930, pp. 443 ff.] is rejected, as this places such species in the subgenus *Callopora* and within the genus *Membranipora*. The group, which he regarded as comprising the genus *Membranipora*, is here considered to be the superfamily Membraniporacea. Voigt considered species placed under the subgenus *Callopora* to have zooecia with an ovicell, a spinose mural-rim and avicularia which vary in structure and position. This group is also regarded as being supra-generic.

The genus *Callopora* Gray *sensu stricto* is not available for these species, as its diagnosis requires the presence of adventitious avicularia on the autozooezial gymnocyst. Autozooezial spinosity of the mural-rim is here regarded as being, at the most, of specific importance. Also, the closely similar species *D. surculus* (Brydone) has spine-bases which are so large and numerous as to suggest cribrimorph affinities.

*Dionella* is closely similar to *Callopora sensu stricto*, however, as is seen when specimens of *D. suffragista* (Brydone) from various horizons of the Chalk are compared. A gymnocystal pore is occasionally present in this species and is reminiscent of those pores seen in *Callopora bipunctata* (Goldfuss); these are associated with adventitious avicularia in the latter species. However, the pore is not always present in *D. suffragista* and is never associated with an adventitious avicularium.

The avicularia of *Dionella* species differ from those of *Tegella* Levinsen. They are adventitious in the case of *Tegella*, and are placed on a hyperstomial ovicell. The writer disagrees with Waters (1924, p. 608), who did not consider *Tegella* to be of generic importance. Although there are several intermediate forms between these two genera, a very large proportion of specimens can be referred unambiguously to one or the other of them.

*Dionella* is similar to *Chaperia* Jullien, particularly in the shape and general structure of the zooecia, and in the presence of distal interzooezial avicularia; compare, for example, *D. trigonopora* (Marsson) with *Chaperia galeata* (Busk) figured by Canu and Bassler (1923, pl. 34, figs. 9-10). However, the presence of occlusor laminae in the zooecia of *Chaperia* species is here considered to be of at least generic diagnostic importance (Brown 1952). Brown has established the genus *Patsyella* (Brown 1948, p. 112) for species in which the occlusor laminae are vestigial or absent, but in which there are entozooezial ovicells. The zooecial structures of species referred to this genus, however, are different from those occurring in *Dionella*, but the loss of occlusor laminae in *Chaperia galeata* would render its generic diagnosis very difficult.

*Dionella* differs from *Copidozoum* Harmer by the greater consistency of occurrence,

and a different position of emplacement, of the interzoecial avicularia. The species of *Dionella* have a different autozoecial structure to those of *Ellisina* Norman, *Periporosella* Canu and Bassler, and *Parellisina* Osburn.

*Stratigraphical Distribution.* Senonian, zones of *M. cortestudinarium* to *B. mucronata*; Maastrichtian of Europe. Eocene (Middle Jacksonian) of Carolina, U.S.A.

KEY TO THE SPECIES OF *DIONELLA* GEN. NOV.

- (I) *Dionella* with well-developed cryptocyst; avicularia of two structural types, a small, acuminate, interzoecial, distal to most, or all, of the autozoecia and a large solitary, elongate spatulate, interzoecial or vicarious, which can also be distal to the autozoecia.
- (A) Mural-rim spinose, but not interrupted by the spine-bases; ovicell with distal flattening; dietellae asymmetrically arranged
    - 1. *D. trifaria* (von Hagenow)
  - (B) Mural-rim extremely spinose, interrupted by the spine-bases; ovicell distally flattened; dietellae symmetrically arranged
    - 2. *D. surculus* (Brydone)
  - (C) Mural-rim interrupted by the single pair of very large oral spine-bases; ovicell not distally flattened; dietellae impersistent; zooecia often ogival
    - 3. *D. trigonopora* (Marsson)
- (II) *Dionella* with little cryptocyst; avicularia of three structural types, a small, distally rounded or elongate-spatulate, interzoecial, distal to most of the autozoecia, and a large, solitary, spatulate vicarious; ovicell not distally flattened.
- (A) Small, distally rounded, interzoecial avicularia.
    - (1) Large vicarious avicularia present or absent; mural-rim spinose but not interrupted by the spine-bases; dietellae asymmetrically arranged
      - 4. *D. simulacrum* (Brydone)
    - (2) Large vicarious avicularia absent; dietellae symmetrically arranged.
      - (a) Mural-rim extremely spinose, slightly interrupted by the spine-bases; dietellae large
        - 5. *D. tringhamensis* (Brydone)
      - (b) Mural-rim interrupted by the single pair of very large oral spine-bases; dietellae small
        - 6. *D. flacilla* (Brydone)
  - (B) Small, elongate-spatulate, interzoecial avicularia; large vicarious avicularia absent; mural-rim spinose, slightly interrupted by the spine-bases; dietellae small, symmetrically arranged; gymnocystal pore occasionally developed
    - 7. *D. suffragista* (Brydone)

SUMMARY OF THE CHARACTERS COMMON TO ALL  
*DIONELLA* SPECIES

*Description.* Zoarium unilamellar, locally multilamellar, encrusting. Initial zoarial development either regular or irregular. Zooecial budding multiserial, generally with a regular arrangement of alternating longitudinal rows, developing from ordinary or wide

autozoecia or from vicarious avicularia when these are present; a second zooecial layer is developed over irregular patches of the zoarium, occasionally round the ancestrula.

Adult zooecia usually rounded rhomboidal, but may be irregularly so, because of an uneven substrate. Interzooecial furrows distinct. The basal wall is thin and often impersistent. Gymnocyst is smooth, variably exposed proximally and extremely so laterally. Cryptocyst descends steeply into the aperture, which is oval to irregularly so. Opesia oval, occasionally pear-shaped, or irregularly round. Mural-rim thin, usually well defined.

Ovicells hyperstomial, prominent and smooth, with a complete and differentiated ectooecium and endooecium. There is usually even distribution throughout the zoarium. Ancestrula and young zooecia like adult zooecia but smaller. The ancestrula has no associated avicularium. Regenerated zooecia: autozoecia occasionally regenerate autozoecia, singly; very occasionally forming a new zooecial layer.

When present, the large solitary avicularia occur at random throughout the zoarium. They are spatulate, with an elongate-oval aperture. Lateral constrictions infold within the proximal-central portion of the aperture. A small distal and one pair of distal-lateral dietellae are usually present. The flat palette is recessed, usually broad and can extend to the proximal-central portion of the aperture. The cryptocyst forms a flat, finely granular, narrow, U-shaped strip along the proximal quarter of the aperture. Smooth gymnocyst is commonly well developed laterally and variably so proximally.

A single interzooecial avicularium is found distal to most of the autozoecia, directed away from the autozoecial aperture. Occasionally at the distal zoarial margins, and rarely within the zoarium, several avicularia of this type may be found around a single zooecium. They are small, but exceptionally can attain autozoecial dimensions. Granular cryptocyst is a U-shaped strip of variable width and is confined to the subopercular portion of the aperture. A straight transverse-bar, or condyles, bisect the opesium. The lateral and distal walls are often well developed.

#### 1. *Dionella trifaria* (Von Hagenow)

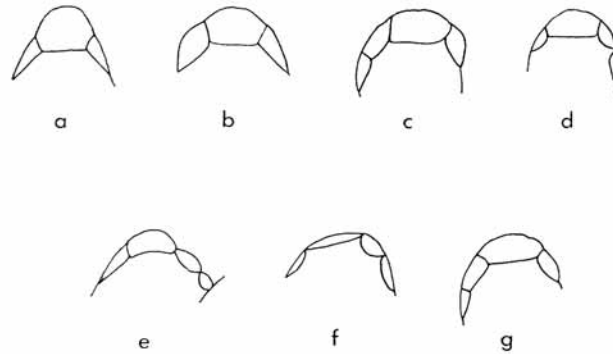
Plate 67, figs. 1-6; Plate 68, figs. 1-6

- 1846 *Cellepora trifaria* von Hagenow, p. 617, pl. 23b, fig. 40.
- 1906 *Membranipora griffithi* Brydone, p. 293, text-fig. 1.
- 1910 *Membranipora griffithi* Brydone: Brydone, p. 5.
- 1910 *Cellepora trifaria* von Hagenow: Brydone, p. 5.
- 1914 *Membranipora boletiformis* Brydone, p. 346, pl. 26, figs. 5-6.
- 1914 *Membranipora griffithi* Brydone: Brydone, p. 347, pl. 26, figs. 7-8.
- 1920 *Tegella (Membranipora) griffithi* (Brydone) Canu and Bassler, p. 166.
- 1925 *Membranipora trifaria sic* (von Hagenow) Levinsen, p. 333, pl. 3, fig. 27.
- 1929 *Membranipora bradingensis* Brydone, p. 29, pl. 9, fig. 4.
- 1929 *Membranipora retrorsa* Brydone, p. 29, pl. 9, fig. 5.
- 1930 *Membranipora griffithi* Brydone: Voigt, p. 421, pl. 10, fig. 13.
- 1949 *Membranipora griffithi* Brydone: Voigt, p. 18.
- ?1949 *Membranipora boletiformis* Brydone *subboletiformis* Voigt, p. 18, pl. 2, figs. 2-3.
- 1949 *Membranipora boletiformis* Brydone: Voigt, p. 18.
- 1959 *Membranipora trifaria* (von Hagenow): Voigt, p. 55, pl. 6, fig. 2.
- 1962 *Membranipora trifaria* (von Hagenow): Voigt, p. 30, pl. 12, fig. 3.

*Neotype* (designated by Voigt, 1959, p. 72). A zoarial fragment. Lower Maastrichtian. Rügen, East Germany. Von Hagenow Collection, Hamburg.

*Emended Diagnosis.* *Dionella* with the aperture restricted by a band of cryptocyst; mural-rim spinose, with one to four pairs of spine-bases distal and three distal-lateral dietellae present, asymmetrically arranged; avicularia either small, interzoecial, distal to each autozoecium, or large vicarious, the latter also occasionally distal interzoecial.

*Description.* Adult zooecia slightly shallow or deep. Either a large distal and one pair of distal-lateral dietellae occur, or often three asymmetrically arranged distal-lateral dietellae are present (text-fig. 2). A small distal and three or four lateral pairs of septula occur. Cryptocyst a granular or coarsely granular band, widest proximally and proximal-laterally and narrowing distal-laterally, with occasional slight distal development.



TEXT-FIG. 2. *Dionella trifaria* (von Hagenow).  $\times 40$ . The range in variation of the autozoecial dietellae of: a, B36287, figured by Brydone as *M. griffithi* Brydone; b, B36288, figured by Brydone as *M. griffithi* Brydone; c, B36108, holotype of *M. griffithi* Brydone, distal-lateral dietellae occurring asymmetrically; d, B36496, holotype of *M. bradingensis* Brydone; e, B36286, lectotype of *M. boletiformis* Brydone; f, g, B36497, holotype of *M. retrorsa* Brydone.

Mural-rim not broken up by the one to four pairs of spine-bases, which are large. The number of spine-bases on adult zooecia varies in a single zoarium; they may rarely be absent.

Ovicells with proximal-lateral grooves, and occasional distal flattening extending V-shaped proximally. Half to nearly all of the adult zooecia possess ovicells; usually there are nought to one, occasionally two, rings of adult zooecia prior to their appearance.

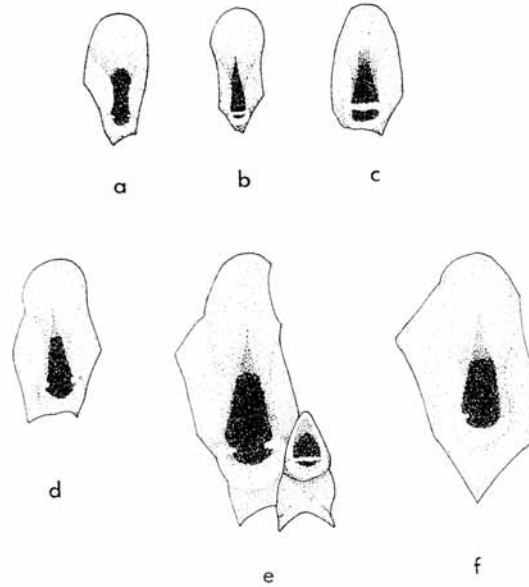
The ancestrula possesses 5 pairs of spine-bases, the primary zooecia have 4-5 pairs, the secondary zooecia 3 pairs, and the tertiary zooecia 2-3 pairs, with the reduction in pairs occurring along the proximal margins of the mural-rim.

Regenerated zooecia: vicarious avicularia occasionally regenerate from either autozoecia or other vicarious avicularia. Small interzoecial avicularia regenerated rarely from vicarious avicularia.

Avicularia are of two kinds:

(1) Vicarious, with occasional concentration at the distal zoarial margins; rarely they may be absent in a zoarium. This type can also be interzoecial, when it is found

distal to the autozoecium, ovicelled or not, and directed away from the autozoecial aperture. The aperture may be extremely laterally expanded distally; length is very variable (text-fig. 3). The flat palette variable in shape; it may have a proximal-central triangular area which is, itself, further recessed. A transverse-bar or prominent condyles are situated within the proximal-central quarter of the aperture.



TEXT-FIG. 3. *Dionella trifaria* (von Hagenow). The range in variation of the large avicularia. *a*, B36285, syntype of *M. boletiformis* Brydone. Small, interzoecial, can be found distal to an ovicelled zoecium: aperture expanded distally. *b*, B36286, lectotype of *M. boletiformis* Brydone. Opesium much restricted by lateral development of palette. *c*, B36496, holotype of *M. bradingensis* Brydone. Variation in the extent and nature of the palette seen in a single zoarium. The proximal-central portion of the palette more deeply recessed than the rest. *d*, B36288, a specimen figured by Brydone as *M. griffithi* Brydone. Large vicarious avicularium, and a small interzoecial avicularium distal to an ovicell. The distal flattening and the lateral constrictions on the ovicell also shown. *f*, B36108, holotype of *M. griffithi* Brydone. A typical vicarious avicularium.

EXPLANATION OF PLATE 67

Figs. 1-6. *Dionella trifaria* (von Hagenow). 1, [Holotype of *M. griffithi* Brydone]; incomplete zoarium with ancestrula and young zooecia. B36108. 2, Zoarial fragment showing the avicularia. B36287. 3, [Syntype of *M. boletiformis* Brydone]; incomplete zoarium with ancestrula, young zooecia and two types of interzoecial avicularia. B36285. 4, [Holotype of *M. bradingensis* Brydone]; incomplete zoarium with either of the two types of interzoecial avicularia distal to the autozoecium. B36496. 5, [Holotype of *M. retrorsa* Brydone]; incomplete zoarium with the ancestrula and young zooecia obscured by the superposition of a second zoecial layer. B36497. 6, [Lectotype of *M. boletiformis* Brydone]; ancestrula and a regular initial zoarial development. B36286.  $\times 50$ . All figures  $\times 20$  unless otherwise specified; from unretouched negatives.

(2) The single interzoecial avicularium is acuminate, with the aperture generally level with the zoarial surface. A slight, recessed palette is present and granular cryptocyst almost fills the sub-opercular portion of the aperture. Gymnocyst absent. The transverse-bar can also have a shallow V-shape. A small distal and a single distal-lateral dietella are present.

*Measurements.* (For explanation of the abbreviations, see text-fig. 1.)

	1	2	3	4
N	8	10	8	4
$L_z$	50-64/55.4	45-64/57.6	46-64/55.5	45-49/47.2
$l_z$	38-60/45.7	28-38/33.2	40-51/45.3	32-42/38.4
$h_a$	35-41/37.1	35-42/39.2	35-41/38.2	32-38/36.2
$l_a$	28-41/33.4	26-30/28.1	32-38/35.2	27-32/30.2
$h_r$	28-33/30.2	29-36/33.3	27-35/31.3	27-32/29.2
$l_r$	22-29/24.2	20-26/23.1	26-29/27.1	19-24/21.2
$h_{ov}$		16-19/17	19-20/20	
$l_{ov}$		17-19/18	19-22/20	

1 = B36286, the lectotype (here chosen) of *M. boletiformis* Brydone; 2 = B36496, the holotype of *M. bradingensis* Brydone; 3 = B36108, the holotype of *M. griffithi* Brydone; 4 = B36497, the holotype of *M. retrorsa* Brydone.

*Remarks.* *Cellepora trifaria* was clearly established by von Hagenow. The type, however, was destroyed during World War II (Voigt, 1959, p. 4). The neotype, designated by Voigt (1959, p. 72), completely corresponds to von Hagenow's species. Voigt's figure also shows regeneration of autozoecia by the small interzoecial avicularia.

*M. griffithi*, *M. boletiformis*, *M. bradingensis*, and *M. retrorsa*, all species established by Brydone, and probably *M. boletiformis* Brydone *subboletiformis* Voigt, are here regarded as synonymous with *Dionella trifaria* (von Hagenow).

All the available specimens, including Brydone's types, have been re-examined. *M. griffithi* was established by Brydone (1906, p. 293), who differentiated it from *C. trifaria* (1910, p. 5) by having 'symmetrical' vicarious avicularia, whereas he considered those of *C. trifaria* to be 'decidedly unsymmetrical'. There is no difference between the avicularia of *M. griffithi* and *C. trifaria* and the writer follows Voigt (1959, p. 55) in regarding these two species as synonymous. The 'triangular incision' of the ovicell that he mentioned (1906, p. 293) is the distal flattening referred to above.

Voigt (1930, p. 421) placed *M. griffithi* in his 'Gruppe der *Membranipora sacerdotalis* Brydone', but later (1949, p. 18) altered his opinion 'as it (*M. griffithi*) forms its own group' [translation]. He (1959, p. 55) redescribed *C. trifaria*, with *M. griffithi* as a junior synonym, and recently (1962, p. 30), in a description of Russian specimens, has noted that the specimens lacked spine-bases.

Brydone considered *M. boletiformis* to be 'ancestral to *M. griffithi*'. In the R. M. Brydone Collection, the maximum number of specimens of *M. boletiformis* and *M. griffithi* are from the *Gonioteuthis quadrata* and the *Belemnella lanceolata* zones respectively. However, the earliest specimens of *M. griffithi* come from the *G. quadrata* zone, and some of these were found in the same quarry as one-third of all of the specimens of *M. boletiformis* collected from that zone. Examination of all of the specimens of these two Brydone species shows that they differ only in the nature and position of the large, spatulate avicularium. These are vicarious in *M. griffithi* and their apertures are



only slightly expanded distally; and are vicarious or interzoecial in *M. boletiformis*, often distal to an autozoecium, and their apertures are expanded distally. However, there are many intermediate forms of both characters and the variation in shape and position of avicularia in this species is a systematic unit of great subjectivity and is not sufficiently important to warrant continued separation of these two species. Also Voigt (1962, p. 30) states 'on both zoaria [of *M. trifaria*], there are no larger avicularia, but these are not always developed: they are also absent on some Rügen examples' [translation].

Voigt (1949, p. 18) established *M. boletiformis* Brydone *subboletiformis*, which he diagnosed as having a greater number of apertural spines than the Brydone species, and also by having 'larger zooecia'. These 'larger zooecia' have the same measurements as the lectotype of *M. boletiformis* (B36286). Also the number of spine-bases is not excessive for this species, particularly for the young zooecia, and subspecific discrimination is not considered justifiable.

Brydone considered *M. boletiformis* to be ancestral or an early form of *M. griffithi*, differing 'only by a general slimness and narrowness, and by the small avicularia' having a different shape. As the species occurs in the *Bellefinitella mucronata* zone, it is not stratigraphically distinct from *M. griffithi*. The autozoecial and apertural width is smaller than *M. griffithi*, but is not so great as to be of statistical significance and to be used as a systematic discriminant. The final difference, a lack of acumination of the small avicularium, is not considered to be of sufficient systematic importance to warrant the continued separation of these two species. Thus this species is a synonym of *D. trifaria* (von Hagenow).

*M. retrorsa* was established by Brydone on the basis of a unique specimen, which is a small incomplete zoarium of fourteen zooecia. There is one possible vicarious avicularium present, and the mural-rim bears fairly large spine-bases which are typical of *D. trifaria*. The 'rounded' avicularia are considered to be a result of weathering, and so *M. retrorsa* is synonymous with *D. trifaria*.

*D. trifaria*, therefore, is a species with a relatively wider range of morphological variation, especially in the nature and the position of the avicularia of both types, than has been previously stated, and includes the four species, and probably the one subspecies, discussed above. *D. trifaria* is distinguished from *D. simulacrum* (Brydone) by its greater development of cryptocyst, the structures on the ovicell, and in the slight differences in both types of avicularia. *D. trifaria* is distinguished from *D. tringhamensis* (Brydone) by its mural-rim which is not indented by the spine-bases, by a slightly different type of avicularium; and by a different arrangement and number of the die-

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EXPLANATION OF PLATE 68

Figs. 1-6. *Dionella trifaria* (von Hagenow). 1, [Holotype of *M. retrorsa* Brydone]; ancestrula and initial regular zoarial development obscured by overgrowth of a second zooecial layer. B36497. 2, [Holotype of *M. griffithi* Brydone]; ovicelled autozoecia with associated distal interzoecial avicularia; subvicarious avicularium with the proximal-central portion of the palette more deeply recessed. B36108. 3, Distal margin of a zoarium. B36287. 4, [Lectotype of *M. boletiformis* Brydone]; ovicelled autozoecia and two types of interzoecial avicularia. B36286. 5, Distal margin of a zoarium with clusters of avicularia. B70237. 6, Regeneration of an avicularium by an autozoecium. B36288.

All figures  $\times 50$ ; from unretouched negatives.

tellae. *D. trifaria* is distinguished from *D. trigonopora* (Marsson) by a different type of autozoecium, spine-base structure, and a slightly different type of avicularium. These species, however, are all characterized by having an interzoecial avicularium distal to most, or all, autozoecia. Many other specimens from the R. M. Brydone Collection have been assigned to *D. trifaria*, as here revised.

*Stratigraphical Distribution.* Senonian, zones of *M. cortestudinarium* to *B. mucronata*; Maastrichtian, including the zone of *Belemnella lanceolata* of Europe.

*Specimens.* B36108. Holotype of *M. griffithi* Brydone. Incomplete zoarium. Maastrichtian, zone of *B. lanceolata*. Trimingham, Norfolk. B36285. Syntype of *M. boletiformis* Brydone. Incomplete zoarium. Senonian, zone of *G. quadrata*. Locality 1086 of Brydone (1912, p. 100). B36286. Lectotype (here chosen) of *M. boletiformis* Brydone. Incomplete zoarium. Senonian, zone of *G. quadrata*. Cliff at Seaford, Sussex. B36287-8. Two incomplete zoaria, figured by Brydone as *M. griffithi* (1914, pl. 26, figs. 5-6). Horizon and locality as for B36108. B36496. Holotype (by original configuration) of *M. bradingensis* Brydone. Incomplete zoarium. Senonian, lower part of the zone of *B. mucronata*. Near Brading, Isle of Wight. B36497. Holotype (by monotypy) of *M. retrorsa* Brydone. Zoarial fragment. Horizon and locality as for B36108.

Other specimens. England: from numerous localities in south-east and east England, ranging from Dorset and the Isle of Wight to Norfolk. Sedgwick Museum: (a) zone of *B. lanceolata*—B60522-4, B69557-612, B84569. (b) zone of *B. mucronata*—B63603-17, B70264-8, B85348-56, B85372-3, B85597-601, B65611-27, B85646. (c) zone of *G. quadrata*—B70225-33, B70235-63, B82289-91, B85567-96, B85603, B85605, B85607-10. (d) zone of *O. pilula*: subzone of *E. scutata* var. *cincta*—B70208-24, B85556-66; subzone of *E. scutata* var. *depressula*—B70177-207, B82286-8, B85538-55. (e) zone and subzone of *M. testudinarium*—B70175-6, B72299-300, B85519-37. (f) zone of *M. coranguinum*—B69908, B85518. France: Fecamp. Zone of *M. cortestudinarium*—F16111.

## 2. *Dionella surculus* (Brydone)

Plate 69, figs. 3, 5

1929 *Membranipora surculus* Brydone, p. 29, pl. 9, figs. 6-9.

1949 *Membranipora surculus* Brydone: Voigt, p. 19.

*Lectotype* (here chosen), SM, B36499. An incomplete zoarium, with the ancestrula obscured by a second zoecial layer. Maastrichtian, zone of *B. lanceolata*. Trimingham, Norfolk.

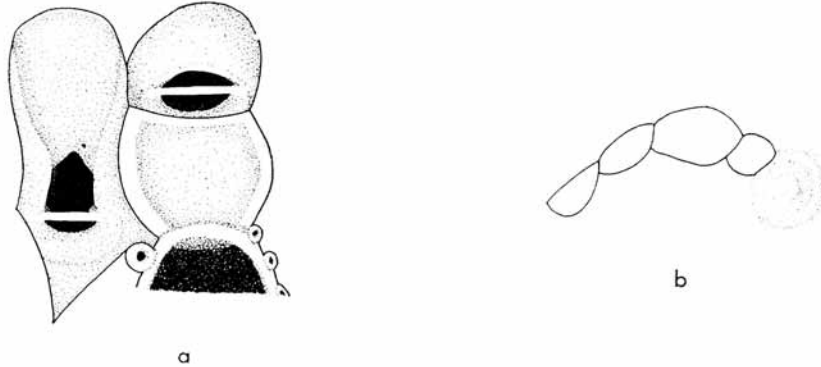
*Emended Diagnosis.* *Dionella* with the aperture restricted by a band of cryptocyst; mural-rim extremely spinose with ten to eleven pairs of spine-bases, crenulated; distal and two pairs distal-lateral dietellae present; avicularia of two types of interzoecial, solitary, spatulate, occurring at random, and single, acuminate, distal to each autozoecium.

*Description.* Adult zoecia of average depth. A distal and two pairs of distal-lateral dietellae occur, usually large. A small distal, and two lateral pair of septula are present. Gymnocyst can be extensively developed. Cryptocyst a coarse-granular band, variable in width, widest proximally and proximal-laterally, narrowing distal-laterally to a granular lining of the inner part of the mural-rim, also slight distal development. Mural-rim broken up by the ten to eleven pairs of large spine-bases; the number of spine-bases varies within a single zoarium. Where the stumps of spines are seen, they are found to be laterally fused and to curve over the aperture.

Ovicells with deep proximal-lateral grooves and a flattened triangular area on the distal dorsal surface (text-fig. 4). Nearly all of the adult zoecia possess ovicells; usually there is either nought or one ring of adult zoecia prior to their appearance.

The ancestrula possesses six pairs of spine-bases, the primary zooecia have seven to eight pairs, with the increase in numbers along the proximal portion of the mural rim. The ancestrula is usually obscured by overgrowth of a later zooecial development.

Regenerated zooecia: both the large, solitary, and the small, interzooecial avicularia commonly regenerate from autozooecia, and the small avicularium very rarely regenerates from the large, solitary type.



TEXT-FIG. 4. *Dionella surculus* (Brydone).  $\times 150$ . a, B36499, lectotype, showing two types of avicularia and distal portion of an autozooecium, with a broken ovicell. b, B36498, syntype, with a large echinoid boss interfering with the autozooecial diatellae arrangement.

Avicularia are of two kinds.

(1) Interzooecial, solitary, with some tendency towards a concentration at the zoarial distal margins and to be formed by a regeneration from an autozooecium. The aperture is expanded distally. A transverse-bar is situated within the proximal-terminal quarter of the aperture. Smooth gymnocyst is slightly developed both proximally and laterally (text-fig. 4).

(2) The small interzooecial avicularia are in the case of a few young zooecia, directed distal-laterally away from the aperture. They are acuminate, with the aperture raised

#### EXPLANATION OF PLATE 69

Fig. 1. *Dionella flacilla* (Brydone). Holotype: zoarial fragment with typical adult autozooecia and an enlarged interzooecial avicularium. B36319.  $\times 40$ .

Figs. 2, 4, 6. *Dionella trigonopora* (Marsson). 2, Neotype; zoarial fragment with calcified autozooecia and a kenozooecium, which terminates the preceding longitudinal zooecial row. F16071.  $\times 20$ .

4. [Lectotype of *M. crateroides* Brydone]; ancestrular region, the ancestrula without an associated interzooecial avicularium. B36333.  $\times 40$ . 6, [Syntype of *M. crateroides* Brydone]; a typical elongate spatulate interzooecial avicularium; to the left of it is an enlarged acuminate type of avicularium, which has regenerated from an autozooecium. B36332.  $\times 80$ .

Figs. 3, 5. *Dionella surculus* (Brydone). 3, Lectotype; zoarial fragment with an avicularium regenerated from an autozooecium. B36499.  $\times 40$ . 5, Lectotype; autozooecium and both types of avicularium; the distal wall of the broken ovicell is concave. B36499.  $\times 120$ .

All figures from unretouched negatives.

distally and sunken proximally, with respect to the zoarial surface; there is practically no palette. Gymnocyst is rarely seen due to the sunken nature of the proximal region of the avicularium. The septula are occasionally externally visible. A small distal, and one pair distal-lateral, dietellae are present.

*Measurements.* (For explanation of the abbreviations used, see text-fig. 1.)

	1	2		1	2
N	10	10	N	10	10
$L_z$	49-57/51/2	46-55/51/2	$h_r$	26-31/29/1	29-33/31/1
$l_z$	32-41/36/3	37-45/39/3	$l_r$	18-20/19/1	18-24/22/2
$h_a$	32-38/35/3	37-38/38/0	$h_{ov}$	17-19/18	18-22/19
$l_a$	23-29/26/2	26-31/28/2	$l_{ov}$	18-20/19	19-22/20

1 = B36498, the syntype of *D. surculus* (Brydone); 2 = B36499, the lectotype of *D. surculus* (Brydone).

*Remarks.* The syntype and specimens B69420-9 have been re-examined.

Brydone (1929, p. 29) considered *M. surculus* to have a 'very distinct place of its own in the group of *M. griffithi*'. *D. surculus* is differentiated from all other members of this group in the increased number and size of the spine-bases. These form an unbroken crenulation of the lateral gymnocyst, which is a characteristic cribrimorph arrangement. However, no case of complete solid spines, overarched the aperture, has been found. Also, *D. surculus* is similar to *D. trifaria* (von Hagenow), particularly in the slight structural variation of the large interzoecial avicularia; and so *D. surculus* is retained in the group as Brydone suggested.

Voigt (1949, p. 18) considered *M. boletiformis* Brydone *subboletiformis* to be intermediate to *M. boletiformis* Brydone and to *M. surculus*. Although the spine-base occurrence in *D. trifaria* (von Hagenow) is very variable, they are inconspicuous and do not crenulate the autozoecial mural-rim. Hence *D. trifaria* (von Hagenow) and *D. surculus* are retained as separate species.

*Stratigraphical Distribution.* Senonian, zone of *B. mucronata* and Maastrichtian, zone of *B. lanceolata*.

*Specimens.* B36499. Lectotype—see above. B36498. Syntype of *M. surculus* Brydone. Incomplete zoarium. Horizon and locality as for the lectotype. Other specimens: (a) zone of *Belemnella lanceolata*—B69420-9; (b) zone of *Belemnella mucronata*—B85714-16.

### 3. *Dionella trigonopora* (Marsson)

Plate 69, figs. 2, 4, 6

- 1887 *Membranipora trigonopora* Marsson, p. 58, pl. 5, fig. 16.  
 1910 *Membranipora trigonopora* Marsson: Brydone, p. 76.  
 1917 *Membranipora crateroides* Brydone, p. 49, pl. 3, figs. 1-2.  
 1925 *Membranipora trigonopora* Marsson: Levinsen, p. 332, pl. 3, fig. 26.  
 1929 *Membranipora trigonopora* Marsson: Brydone, p. 25.  
 1930 *Membranipora (Callopora) trigonopora* Marsson: Voigt, p. 444, pl. 9, fig. 6.  
 1936 *Membranipora trigonopora* Marsson: Brydone, p. 61.  
 1936 *Membranipora crateroides* Brydone: Brydone, p. 65.  
 ?1949 *Membranipora flammula* Voigt, p. 16, pl. 3, figs. 2-3.  
 1963 *Membranipora trigonopora* Marsson: Veenstra, p. 101, pl. 2, fig. 6.

*Neotype* (here designated), SM, F16071. A zoarial fragment. Lower Maastrichtian, zone of *Belemnella lanceolata*. Rügen, East Germany.

*Emended Diagnosis.* *Dionella* with deep zooecia; aperture restricted by a broad band of cryptocyst; mural-rim spinose with two to three pairs of spine-bases the oral spine-base pair being very large; one pair small, impersistent, distal-lateral dietellae; avicularia of two kinds of interzooecial, either of which may be absent, and vicarious: small, acuminate, distal to the autozooecium, and elongate spatulate, solitary, occurring at random throughout the zoarium, including distally to an autozooecium.

*Description.* Zoarium occasionally now unattached. Adult zooecia wide and deep, occasionally ogival in shape. One pair of small, impersistent, distal-lateral dietellae present (text-fig. 5). A distal and two lateral pair of septula occur. The basal wall is thin and continuous, often with a central depressed area. Gymnocyst very slightly developed proximally only. Cryptocyst a coarsely granular, variably developed band, widest proximally and proximal-laterally, narrowing distal-laterally, but with good distal development. The distal part of the cryptocyst bears two small pits. Opesia oval to very irregularly rounded-rectangular. One pair of very large oral spine-bases occurs at the distal-lateral termination of the mural-rim, and there is one, occasionally two, pair of very small apertural spine-bases.

Ovicells occur on about one-tenth of the adult zooecia, with patchy distribution throughout the zoarium; usually there are one to three rings of adult zooecia prior to their appearance.

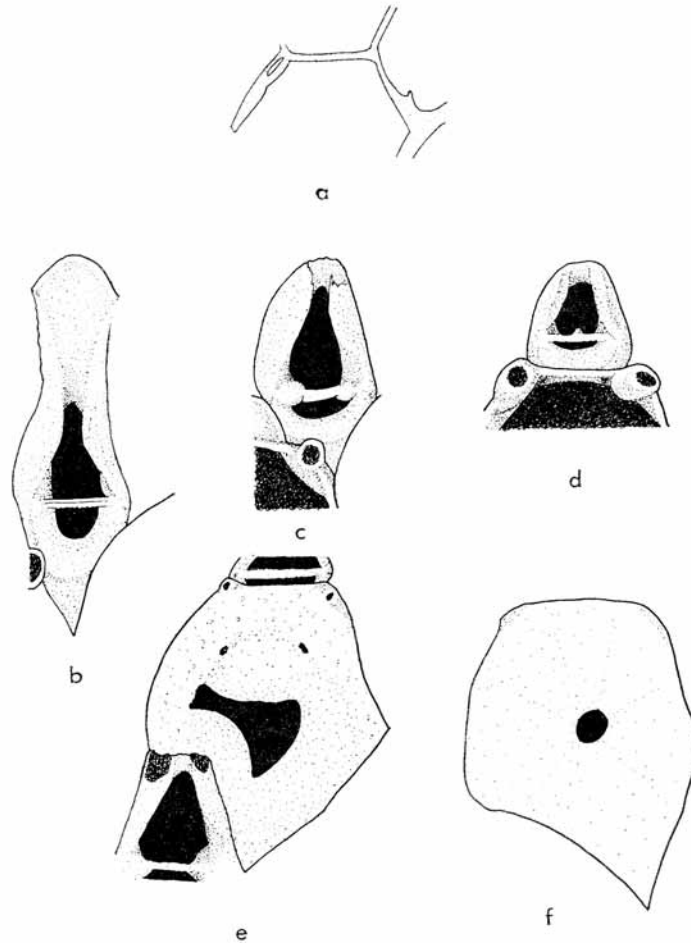
Ancestrula and young zooecia rounded-rhomboidal in shape and possess little cryptocyst. The oral pair of spine-bases is not dominant before the tertiary, or even the quaternary, ring of zooecia. The ancestrula possesses five pairs of spine-bases, all of equal size; the primary zooecia have four pairs, with the oral and the oral-apertural pairs larger than the others; the secondary zooecia have a persistent, large or small pair of oral spine-bases, an impersistent, large or small, oral-apertural pair, and one or two, impersistent, small apertural pair, thus the secondary zooecia possess one to three pairs of spine-bases; the tertiary zooecia have the same spine-base arrangement as those on the adult zooecia, with only an occasional absence of dominance of the oral pair. Occasionally the central primary zooecium also has no associated avicularium.

Regenerated zooecia: vicarious avicularia commonly regenerate from normal, or calcified, autozooecia, either singly or repeatedly. Calcified zooecia: occasionally the autozooecial aperture is partially or completely closed by coarsely granular secondary calcareous tissue (text-fig. 5). Kenozooecia occasionally present; are of the simple type, with granular cryptocyst and a circular opesium.

Avicularia are of two kinds:

(1) Vicarious or interzooecial, solitary. When interzooecial, they occur singly, distal to an autozooecium. Their size is very variable, the largest being those that regenerate from autozooecia. Dietellae are absent. A transverse-bar of variable structure, or prominent condyles are situated within the proximal-terminal quarter of the aperture (fig. 5). Gymnocyst is practically absent.

(2) When the autozooecium is ovicelled, the small interzooecial avicularium is absent; occasionally none of the zooecia possess this type. It is directed distally away from the aperture, not tangential to it, as with the first type of avicularium occurring in this



TEXT-FIG. 5. *Dionella trigonopora* (Marrson). *a*, F16071, neotype, showing impersistent nature of the autozooeal dietellae.  $\times 100$ . *b*, B36332, lectotype of *M. crateroides* Brydone, showing the large characteristic interzooeal avicularium.  $\times 60$ . *c, d*, F16071,  $\times 60$ : *c*, large interzooeal avicularium with broken distal part of the aperture; *d*, small interzooeal avicularium with a small boss in the centre of the transverse-bar, found at the distal end of the autozooeum, which has very large oral spine-bases. *e, f*, F16071,  $\times 70$ : *e*, autozooeum calcified from the base of the cryptoecyst; *f*, autozooeum calcified from the inner edges of the mural-rim.

position. They are acuminate, with the distal half of the aperture raised above the zoarial surface, and the proximal half sunk below it. A slight, recessed palette is present. Gymno-cyst is absent (fig. 5). Dietellae are absent.

Measurements. (For an explanation of the abbreviations, see text-fig. 1.)

	1	2	3		1	2	3
N	7	10	10	N	7	10	10
$L_z$	57-81/71/10	67-90/77/7	67-80/73/6	$h_r$	35-54/45/7	40-55/49/5	40-53/47/4
$l_z$	52-67/62/5	67-80/70/4	65-90/74/9	$l_r$	30-46/40/5	37-43/40/1	37-57/45/7
$h_a$	51-74/61/7	57-70/63/4	50-73/60/6	$h_{ov}$		38-40/39	
$l_a$	40-60/54/6	50-70/58/5	50-73/60/7	$l_{ov}$		40-41/40	

1 = F16071, the neotype of *D. trigonopora* (Marsson); 2 = B36332, the lectotype of *M. crateroides* Brydone; 3 = B36333, the syntype of *M. crateroides* Brydone.

*Remarks.* *M. trigonopora* was established by Marsson and subsequently revised by Levinsen. Marsson's collection of Rügen Chalk Polyzoa, including the type specimens of *D. trigonopora*, was destroyed during World War II (Voigt, 1949, p. 6; 1959, p. 7). The neotype, here designated, completely corresponds with the description and figure of Marsson.

*M. crateroides* Brydone and probably *M. flammula* Voigt are here regarded as being synonymous with *D. trigonopora* (Marsson).

Marsson considered *D. trigonopora* to be a species with deep zooecia, raised mural-rims, and triangular or quadrilateral opesia. He ended his description: 'a triangular avicularium is found above the opesium, which may be absent. On the anterior part of the mural-rim is a pair of pores' [translation]; his 'pores' are here regarded as being spine-bases. Levinsen (1925, p. 332) said that the gymnocyst was weakly developed due to the projection of the older (proximal) zooecia on to it. He also noted the presence of the rare large avicularia that could attain autozooecial length and half the width. His specimens were 'free, lamellar plates with irregularly arranged zooecia'. Voigt (1930, p. 444) placed *M. trigonopora* in his group of *Membranipora* (*Callopora*).

Brydone (1929, p. 25; 1936, p. 61) established a (sub) group of *M. trigonopora* containing several species which he had established. There is, however, no similarity between these species, and the (sub) group is here rejected.

Brydone (1917, p. 49), in his original description of *M. crateroides*, said that this species was distinguishable from *M. trigonopora* Marsson by its subvicarious avicularia and perhaps its ovicells, as none were recorded for Marsson's species. Notwithstanding Brydone's later comments on the merging of these two species (1936, p. 65), the writer agrees with Voigt (1930, p. 444) and considers *M. crateroides* to be a synonym of *D. trigonopora*.

Voigt (1949, p. 16) established *M. flammula*, 'distinguished by having zooecia with a completely open area, two pairs of apertural spines and subvicarious avicularia of medium size, approximately spatulate in shape. Dietellae absent. . . . Ovicells small, hyperstomial. . . . Occurs only in the "quadratenkalk" of Lägerdorf' [translation]. An examination of his figures, however, indicates the presence of a thin band of cryptocyst and the autozooecia are identical with those of the type specimens of *M. crateroides* Brydone. Only in the absence of the distal interzooecial avicularium does *M. flammula* differ from *D. trigonopora*. This type of avicularium does not always occur within a zoarium and within a population it is probable that a few zoaria may lack them. Hence *M. flammula* is a probable synonym of *D. trigonopora*.

*D. trigonopora* is, therefore, a species with a wider range of morphological variation.

especially in the position of the avicularia, than has been previously stated, and comprises the two species, and probably a third, discussed above.

*D. trigonopora* is distinguished from all other members of the *D. simulacrum* group in having a different type of autozoecium and distal, interzoecial avicularium; and, with the exception of *D. flacilla* (Brydone), also in a different spine-base arrangement.

*Stratigraphical distribution.* Senonian, zones of *G. quadrata* to *B. mucronata* in England. The type specimen, from Rügen, Germany, was labelled 'mucronata zone' but is probably Maastrichtian, zone of *B. lanceolata*.

*Specimens.* F16071. Neotype—see above. B36332. Lectotype (here chosen) of *M. crateroides* Brydone. Incomplete zoarium. Senonian, zone of *B. mucronata*. Weybourne, Norfolk. B36333. Syntype of *M. crateroides* Brydone. Incomplete zoarium. Senonian, zone of *B. mucronata*. Whitlingham, Norfolk. Other specimens. England. (a) B68422, B68424–8. Horizon and locality as for B36332. (b) Zone of *G. quadrata*—B70234.

#### 4. *Dionella simulacrum* (Brydone)

Plate 70, figs. 1–6

- 1914 *Membranipora simulacrum* Brydone, p. 345, pl. 26, figs. 1–21.  
 1916 *Membranipora feronia* Brydone, p. 338, pl. 14, fig. 4.  
 ?1920 *Tegella nicklesi* Canu and Bassler, p. 167, pl. 30, figs. 9–10.  
 1930 non *Membranipora simulacrum* Brydone: Voigt, p. 421, pl. 10, fig. 12.  
 ?1930 non *Membranipora (Callopora) feronia* Brydone: Voigt, p. 443, pl. 10, fig. 1.  
 1949 non *Membranipora simulacrum* Brydone: Voigt, p. 18.

*Lectotype* (here chosen), SM, B36281. An incomplete zoarium. Senonian, zone of *Micraster corangium*. Gravesend, Kent.

*Emended Diagnosis.* *Dionella* with the opesium occupying almost all of the aperture, there being little cryptocyst; mural-rim spinose, with one to four pairs of spine-base; large distal and three distal-lateral dietellae present, asymmetrically arranged; avicularia of one or two types, a single interzoecial distal to each autozoecium, and a large vicarious.

*Description.* Adult zooecia slightly shallow or deep. A large distal and three asymmetrically arranged distal-lateral dietellae occur (text-fig. 6). A small distal and three to four lateral pairs of septula occur. Cryptocyst a thin granular band on the proximal and proximal-lateral margins of the mural-rim, tapering distally to a granulation of the wall, the spine-base occurrence on the adult zooecia being variable within a single zoarium. Half to nearly all of the adult zooecia possess ovicells; usually there are nought to one, occasionally two, rings on adult zooecia prior to their appearance.

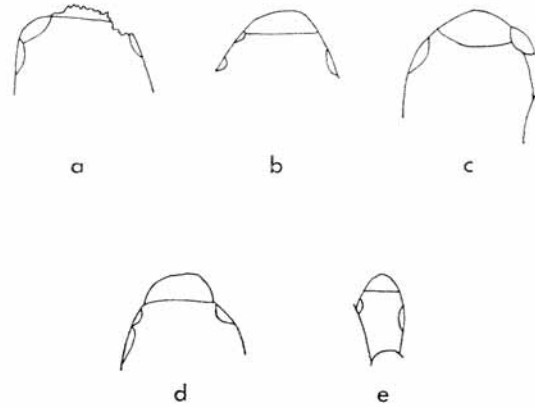
The ancestrula possess 5 pairs of spine-bases, the primary zooecia have 4–5 pairs, the secondary zooecia, 3 pairs and the tertiary zooecia 2–3 pairs, with the reduction in number occurring along the proximal region of the mural-rim.

Avicularia of two kinds:

(1) Vicarious, solitary, not present in all zoaria considered to belong to this species (text-fig. 7), usually a crescentic band, confined to the distal half of the aperture; rarely it is more extensive, occupying the whole of the distal half of the aperture. Prominent condyles occur within the proximal quarter of the aperture (text-fig. 7). The small



inter-zoecial avicularia are distally round, with the aperture either level with the zoarial surface or with the distal half raised. There is no true palette, but the granular cryptocyst, which may almost fill the sub-opercular region of the aperture, continues into the opercular region and thins out distal-laterally. Gymnocyst is absent. A small distal and a single distal-lateral dietella are present.



TEXT-FIG. 6. *Dionella simulacrum* (Brydone).  $\times 40$ . *a-d*, the range in variation of the autozoecial dietellae: *a*, B36281, lectotype, with a broken distal dietella and asymmetrical distal-lateral dietellae; *b, c*, B36282, syntype; *d*, B36318, holotype of *M. feronia* Brydone. *e*, B26282, the dietella arrangement of a distal inter-zoecial avicularium.

Measurements. (For an explanation of the abbreviations, see text-fig. 1.)

	1	2	3		1	2	3
<i>N</i>	10	8	10	<i>N</i>	10	8	10
$L_z$	64-87/76/6	68-81/72/5	67-84/73/7	$h_r$	43-59/51/4	47-57/51/3	53-67/57/4
$l_z$	38-45/42/2	40-50/44/3	39-60/49/6	$l_r$	28-36/32/2	28-37/31/3	30-42/36/4
$h_a$	46-61/56/3	51-61/54/3	57-70/61/5	$h_{ov}$		17-20/19	16-19/18
$l_a$	33-41/38/2	33-42/37/2	33-47/41/4	$l_{ov}$		19-22/20	18-23/21

1 = B36318, the holotype of *Membranipora feronia* Brydone; 2 = B36281, the lectotype of *D. simulacrum* (Brydone); 3 = B36282, the syntype of *D. simulacrum* (Brydone).

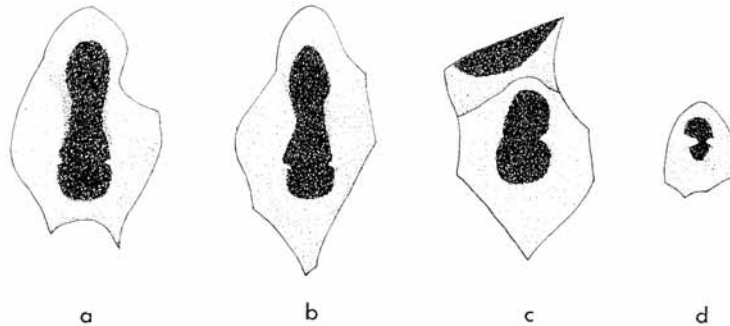
#### EXPLANATION OF PLATE 70

Figs. 1-6. *Dionella simulacrum* (Brydone). 1, Lectotype; incomplete zoarium showing the ancestrula and young zooecia. B36281.  $\times 20$ . 2, [Holotype of *M. feronia* Brydone]; incomplete zoarium, including an enlarged interzoecial avicularium. B36318.  $\times 20$ . 3, Autozoecium and both types of avicularia present. B85477.  $\times 50$ . 4, Syntype; showing autozoecial and interzoecial avicularian dietellae. B36282.  $\times 20$ . 5, Lectotype; autozoecia with, and without, associated distal interzoecial avicularia; the subvicarious avicularium present has a slightly distally expanded aperture. B69885.  $\times 50$ .

All figures from unretouched negatives.

*Remarks.* The types and all available specimens, identified by Brydone as *M. simulacrum* and *M. feronia*, have been re-examined. *M. feronia* Brydone and probably *T. nicklesi* Canu and Bassler are synonymous with *D. simulacrum* Brydone.

Brydone established *M. simulacrum* as a species with 'slender side-walls' and with both adventitious and vicarious avicularia. Referring to the adventitious type, he said that 'this type seems to separate the species from the *M. griffithi* line and ally it to *M. triminghamensis*'. He considered that vicarious avicularia 'occur very capriciously'.



TEXT-FIG. 7. *Dionella simulacrum* (Brydone).  $\times 50$ . Vicarious and interzoecial avicularia of: a, B36281, lectotype, vicarious avicularium with a crescentic palette; b, B36282, syntype; c, B36318, holotype of *M. feronia* Brydone, vicarious avicularium with a typical sub-opercular region of the aperture, but with the opercular region truncated and reminiscent of the small interzoecial avicularia; d, B36281, typical small interzoecial avicularium, occurring distally to the autozooecium.

Finally he stated that he had found specimens only in the *Micraster coranguinum* zone of Kent and Hampshire, and once in the *Uintacrinus* band of Hampshire. Voigt (1930, p. 421) identified a specimen from the 'Quadraten oder Mukronatenkreide bei Misburg', although he (1949, p. 18) later doubted this identification, but was unable to prove it as the specimen had been destroyed. It is not possible to decide the systematic position of the specimen from his figure (1930, pl. 10, fig. 12).

There are several specimens in the collection of *Membranipora feronia* labelled by Brydone, but he only positively identified the holotype. He defined the species as having very slender zooecia with a tapering front-wall; ovicells not numerous and avicularia much like those of '*Membranipora fascelis* Brydone 'even to the occasional vicarious specimen'. He considered it to be 'rare in the zones of *A. quadratus* (restricted) and *B. mucronata* in Hampshire', and that it 'closely resembles *Reptoflustrella ovalis* d'Orbigny (1852, p. 571, pl. 731, figs. 17-18)'. The avicularia, however, bear little, if any, resemblance to those of '*M. fascelis*', whilst the presence of an occasional enlarged avicularium of an otherwise small type is a character met with throughout the membraniporphs. No specimens have been recorded from any zone higher than *Goniot euthis quadrata* and there is no resemblance to *R. ovalis* d'Orbigny. The autozoecia are identical with those typical of *D. simulacrum* and the absence of true vicarious avicularia is not of sufficient systematic importance to warrant the continued separation of these species.

Voigt (1930, p. 443) identified a specimen as *M. (Callopora) feronia* Brydone from the 'Mammillatensenon Ifo/Schonen'; his figure, however, shows a form without the characteristic distal interzoecial avicularia, but with occasional scattered interzoecial avicularia, and with a slightly different type of autozoecium, there being a greater development of both gymnocyst and cryptocyst. These differences are too great for this specimen to be identified as *M. feronia*.

An examination of the figures and descriptions of *Tegella nicklesi*, established by Canu and Bassler, indicates that this species is probably synonymous with *D. simulacrum*. Examination of all specimens assigned to *D. simulacrum* shows that the large vicarious avicularia are absent in specimens from zones higher than *Micraster coranguinum*.

*Stratigraphical Distribution.* Senonian, zones of *M. coranguinum* to *G. quadrata* in England. Probably Eocene (Middle Jacksonian) of Carolina, U.S.A.

*Specimens.* Lectotype—see above. B36282: Syntype of *D. simulacrum* (Brydone). Incomplete zoarium. Horizon and locality as for the lectotype. B36318: Holotype (by monotypy) of *M. feronia* Brydone. Incomplete zoarium. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Locality 914 of Brydone (1912, p. 90). Other specimens. England, from numerous localities in the south-east. (a) Zone of *G. quadrata*—B36592-4, B72358, B81962-4, B85602, B85604, B85606. (b) Zone of *O. pilula*: subzone of *E. scutata* var. *cineta*—B36591; subzone of *E. scutata* var. *depressula*—B85632. (c) Zone of *M. testudinarius*: subzone of *M. testudinarius*—B36590; subzone of *U. socialis*—B69886-9. (d) Zone of *M. coranguinum*—B69863-85, B85477, B85629-31.

#### 5. *Dionella trimminghamensis* (Brydone)

Plate 71, figs. 1-3

- 1906 *Membranipora trimminghamensis* Brydone, p. 294, text-fig. 2.  
 1910 *Membranipora trimminghamensis* Brydone: Brydone, p. 5.  
 1910 *Membranipora trimminghamensis* (nom. emend.) Brydone: Brydone, p. 5, pl. 3, figs. 7-8.  
 1914 *Membranipora trimminghamensis* Brydone: Brydone, p. 345.  
 1920 *Tegella (Membranipora) trimminghamensis* (Brydone) Canu and Bassler, p. 166.

*Holotype.* SM, B36109. An incomplete zoarium. Maastrichtian, zone of *Belemnella lanceolata*. Trimmingham, Norfolk.

*Emended Diagnosis.* A multiserial, or pleuriserial *Dionella*; aperture restricted by a band of cryptocyst; mural-rim spinose, with seven to ten pairs of spine-bases; distal and one, or two, pair distal-lateral dietellae present; avicularia interzoecial, distal to each autozoecium, aperture distally round.

*Description.* Zoarium rarely pleuriserial. Adult zooecia of average depth, occasionally slightly deep. A distal and two to four distal-lateral dietellae occur, which may be large or

#### EXPLANATION OF PLATE 71

Figs. 1-3. *Dionella trimminghamensis* (Brydone). 1, Holotype; initial stages of the development of a large zoarium; the incoming of ovicells is shown, as is a 'ring' of small, interzoecial avicularia. B36109.  $\times 20$ . 2, The distal margin of a zoarium having pleuriserial growth. B69455.  $\times 20$ . 3, Holotype; typical adult autozoecia and avicularia. B36109.  $\times 40$ .  
 Figs. 4-6. *Dionella suffragista* (Brydone). 4, Lectotype; the ancestrular region of the zoarium with irregular initial zoarial development. B36284.  $\times 40$ . 5, Lectotype; the zoarial distal margin. B36284.  $\times 40$ . 6, Adult autozoecium with a large gymnocystal pore. B69937.  $\times 80$ .  
 All figures from unretouched negatives.

small (text-fig. 8), and may be symmetrically or asymmetrically arranged. A small distal and one, generally two, lateral pairs of septula are present. Cryptocyst a granular band, variable in width, widest proximally and proximal-laterally, narrowing distal-laterally to a granular lining of the inner part of the mural-rim, with slight distal development. Mural-rim variably defined, often slightly broken up by the large seven to ten pairs of spine-bases, the number of spine-bases varies within a single zoarium. Where the stumps of the spines are seen, they are found to be distinct and not laterally fused, and curve over the aperture.

Ovicells with prominent proximal-lateral grooves and occasional, slight distal flattening. Nearly all of the adult zooecia possess ovicells; usually there is nought or one ring of adult zooecia prior to their appearance. The ancestrula possesses 6 pairs spine-bases, the primary zooecia have 6–9 pairs, the secondary zooecia 7 pairs with an increase in numbers along the proximal region of the mural-rim. The central primary zooecium also usually lacks an associated avicularium.

Regenerated zooecia: the small interzoecial avicularia very rarely regenerate from autozooecia or from other such avicularia.

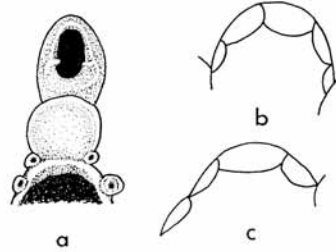
Avicularia of one kind only: small, interzoecial. They are distally and sunken proximally, with respect to the zoarial surface. A small recessed palette is usually present. Variable development of proximal and proximal-lateral gymnocyst occurs, and may be extensive (text-fig. 8). A small distal and one pair distal lateral dietellae are present.

*Measurements.* (For an explanation of the abbreviations, see text-fig. 1.) B36109, the holotype of *D. tringhamensis* (Brydone).

	N	12		N	12
$L_z$	57–83/68/8		$h_r$	35–41/38/2	
$l_z$	38–57/48/6		$l_r$	24–31/28/2	
$h_a$	42–47/44/2		$h_{ov}$	19–20/19	
$l_a$	28–37/34/2		$l_{ov}$	19–20/20	

*Remarks.* The holotype and all available specimens identified by Brydone as *M. tringhamensis* have been re-examined.

*M. tringhamensis* was established by Brydone (1906, p. 294), who noted that it could 'be constructed from . . . [*M. griffithi*] by rounding and smoothing all sharp angles and corners'. Later (1910, p. 5) he discussed the differences between these two species and *Cellepora trifaria* von Hagenow, considering *M. tringhamensis* to be the species possessing 'no large avicularia'. He also said (1914, p. 346) that the 'accessory type' of avicularia separated *M. simulacrum* from the *M. griffithi* line and allied it to *M. tringhamensis*. The writer agrees with Brydone in there being a morphological break between *D. trifaria* (von Hagenow) on the one hand, and *D. tringhamensis* and *D. simulacrum* on the other. The two latter species are similar in their zooecial shape, but *D. tringhamensis* has a greater development of lateral gymnocyst and an increased spinous nature of



TEXT-FIG. 8. *Dionella tringhamensis* (Brydone) B36109, holotype.  $\times 60$ . a, General view of the distal end of an autozooecium, with a broken ovicell. b, c, dietella variation in a single zoarium.

the mural-rim. These two characters are of sufficient systematic importance to warrant the separation of these two species.

*Stratigraphical Distribution.* Maastrichtian, zone of *Belemnella lanceolata*.

*Specimens.* B36109. Holotype—see above. Other specimens. B50826, B69455–79, B69481–3. Horizon and locality as for the holotype.

#### 6. *Dionella flacilla* (Brydone)

Plate 69, fig. 1

1916 *Membranipora flacilla* Brydone, p. 338, pl. 14, fig. 5.

?1930 *Membranipora (Callopora)* aff. *flacilla* Brydone: Voigt, p. 443, pl. 9, fig. 3.

*Holotype* (by monotypy), SM, B36319. A zoarial fragment. The only specimen. Senonian, zone of *Belemnitella mucronata*. Weybourne, Norfolk.



TEXT-FIG 9. *a*, *Dionella flacilla* (Brydone), B36319, holotype, non-ovicelled autozooeceum with very large oral spine-bases, and a distal interzooeceal avicularium.  $\times 70$ . *b*, *c*, *D. suffragista* (Brydone). B36284, lectotype.  $\times 70$ . *b*, Distal interzooeceal avicularium surrounded by the proximal autozooeceal gymnocyst; *c*, autozooeceal dietellae.

*Emended Diagnosis.* *Dionella* with slightly shallow zooecia; opesium occupying almost all of the aperture, there being little cryptocyst; mural-rim with only one pair of very large oral spine-bases; one pair small, distal-lateral dietellae; avicularia interzooeceal, distal to most of the autozooeceia, with distally rounded aperture.

*Description.* Adult zooecia wide and shallow. One pair of small impersistent distal-lateral dietellae present. A distal and three lateral pair of septula occur. Cryptocyst a thin granular band on the proximal and proximal-lateral margins of the mural-rim, tapering distally to a granulation of the wall. One pair of oral spine-bases only occurs, very large with a diameter of 0.08 mm. (text-fig. 9).

Ovicells apparently globular, prominent, and overlapping on to the distally adjacent zooecium; seen only in the broken state. One-third of the adult zooecia possess them, with irregular distribution throughout the zoarium.

Ancestrula and young zooecia not seen.

Avicularia of one kind only: small, interzooeceal; they are absent if the autozooeceum is ovicelled and occasionally if not. Rarely at the distal margins a second such avicularium, distal-lateral in position, is associated with the autozooeceum. Distally

round, with the aperture either level with the zoarial surface or with the distal half raised. A small recessed palette is present. Variable development of smooth, proximal, and proximal-lateral gymnocyst occurs, usually not extensive (text-fig. 9). Dietellae absent.

*Measurements.* (For an explanation of the abbreviations, see text-fig. 1). B36319 the holotype of *D. flacilla* (Brydone).

	N	10		N	10
$L_z$	77	97/86/6	$h_r$	59	70/63/3
$l_z$	53	67/58/4	$l_e$	39	50/42/4
$h_a$	63	77/68/4	$h_{ov}$	19	26/22
$l_{in}$	45	57/49/4	$l_{ov}$	22	24/23

*Remarks.* The only known specimen of *D. flacilla*, the holotype, has been re-examined. Brydone slightly under-estimated the dimensions of the aperture, and so the difference between these measurements and those of the specimen referred by Voigt (1930, p. 443) to this species is even greater and Voigt's identification remains uncertain.

*D. flacilla* Brydone differs from *D. simulacrum* Brydone only in the absence of a vicarious avicularium and in the presence of the very large pair of oral spine-bases. These spine-bases are of sufficient importance to warrant the continued separation of these two species.

*Stratigraphical Distribution.* Senonian, zone of *B. mucronata*.

*Specimen.* B36319. Holotype—see above.

#### 7. *Dionella suffragista* (Brydone)

Plate 71, figs. 4-6

1914 *Membranipora suffragista* Brydone, p. 346, pl. 26, figs. 3-4.

?1920 *Tegella aculeata* Canu and Bassler, p. 166, pl. 30, fig. 11.

?1930 *Membranipora suffragista* Brydone: Voigt, p. 434, pl. 6, figs. 13-14.

*Lectotype.* (Here chosen), SM, B36284. An incomplete zoarium. Senonian, zone of *Micraster coranguinum*. Gravesend, Kent.

*Emended Diagnosis.* *Dionella* with the aperture restricted by a thin band of cryptocyst; mural-rim spinose, with 8 pairs of spine-bases; distal and one pair distal-lateral dietellae present; avicularia interzoecial, distal to each autozoecium, elongate, spatulate; autozoecial gymnocystal pore and associated secondary calcareous tissue may occur.

*Description.* Adult zooecia of average depth, occasionally slightly deep. A distal and one, very rarely two, pairs of distal-lateral dietellae are present, variable in size and position (text-fig. 10). A small distal and one, generally two, lateral pairs of septula occur. A gymnocystal pore occasionally present with associated secondary calcareous tissue. Cryptocyst a thin granular band, variable in width, widest proximally and proximal-laterally, narrowing distal-laterally to a granular lining of the inner part of the mural-rim, with very slight distal development. Often slightly broken up by the eight pairs of large spine-bases.

Ovicells with slight proximal-lateral grooves and occasional, very slight, distal flattening. Nearly all of the adult zooecia possess ovicells; usually there are nought or one, occasionally up to three, rings of adult zooecia prior to their appearance. The

ancestrula possesses 6 pairs of spine-bases, the primary zooecia have 5–7 pairs, the secondary zooecia 7–9 pairs, with the increase in number occurring along the proximal region of the mural-rim.

Avicularia of one kind only; small, interzooecial. They are spatulate, with the aperture often slightly raised distally above the zoarial surface. The distal end of the aperture is prolonged into an elongate, narrow finger, that encroaches on to the gymnocyst of the distally adjacent zooecium, as far as its mural-rim. Variable development of proximal gymnocyst occurs (text-fig. 10). A small distal and one pair of distal-lateral dietellae are present.

Other heterozooecia: in conjunction with the gymnocystal pore, there is often developed a rim of calcareous tissue on the proximal gymnocyst of the autozooecium, which is very reminiscent of the base of an eroded heterozooecium.

*Measurements.* (For an explanation of the abbreviations, see text-fig. 1.)

	1		2			1		2	
	10		10		<i>N</i>	10		10	
<i>L<sub>z</sub></i>	55–66/59/4	56–67/61/4	<i>h<sub>r</sub></i>	37–43/40/2	37–43/40/2				
<i>l<sub>z</sub></i>	33–38/36/1	35–46/40/4	<i>l<sub>r</sub></i>	23–27/24/1	24–31/27/2				
<i>h<sub>a</sub></i>	43–47/46/1	42–49/45/2	<i>h<sub>ov</sub></i>	15–19/17	17–19/18				
<i>l<sub>a</sub></i>	28–32/30/1	29–36/32/3	<i>l<sub>ov</sub></i>	17–19/18	18–20/19				

1 = B36283, the syntype of *D. suffragista* (Brydone); 2 = B36284, the lectotype of *D. suffragista* (Brydone).

*Remarks.* Brydone (1914, p. 346) established *Membranipora suffragista* as a species that 'might by its spines be ancestral to *M. trininghamensis*, but by its avicularia it is probably ancestral to *M. griffithi*'. Voigt (1930, p. 434) placed *M. suffragista* into his division that possessed 'a complete ring of spines around the area' and 'which belongs to *Callopora*' [translation]. He recorded specimens from the 'Granulatensenon' of Germany and the 'Mammillatensenon' of Sweden, but in neither of his figures can the diagnostic feature of this species, the spatulate nature of the avicularium, be recognized; moreover, the specimens have been destroyed, and so his identifications are only tentatively accepted.

The re-examination of the syntypes and all available specimens has shown that the spatulate nature of the interzooecial avicularium is very constant. The avicularium is quite distinct from that possessed by *D. trininghamensis* (Brydone) and *D. trifaria* (von Hagenow). The autozooecia of the types of *D. suffragista* and *D. simulacrum* (Brydone) are, however, very similar, apart from the greater spinosity of the former species. A gymnocystal pore and associated secondary calcareous tissue have also been found in many specimens. The pore and tissue are absent in specimens from the Zone of *M. coranguinum*, present in a few specimens from the Zone of *Marsupites*: subzone of *Uintacrinus*, whereas all of the specimens from the subzone of *Marsupites* have them; finally, of the two specimens coming from the Zone of *O. pilula*: subzone of *E. scutata* var. *depressula*, only one has the pore and tissue. From the material examined, it is not possible to say whether this structure is an eroded heterozooecium, such as is found in specimens of *Callopora bipunctata* (Goldfuss); but if so, then there is a transition between *Dionella* and *Callopora* Gray.

*Tegella aculeata*, established by Canu and Bassler, is regarded as being a probable

synonym of *D. suffragista*. The only difference is the occurrence of fewer spine-bases spinosity and this character probably does not warrant the continued separation of these two species. However, no specimens have so far been recorded from deposits between the Senonian Zone of *G. quadrata* for *D. suffragista* and the Eocene (Middle Jacksonian) for *T. aculeata*, but this is not considered to be sufficient reason for the continued separation of these two species.

*Stratigraphical Distribution.* Senonian, zones of *M. coranguinum* to *O. pilula*: subzone of *E. scutata* var. *depressula* in England, and the zones of *Marsupites* and *G. quadrata* in Europe. Eocene (Middle Jacksonian) of Carolina, U.S.A.

*Specimens.* B36284. Lectotype—see above. B36283. Syntype of *D. suffragista* (Brydone). Incomplete zoarium. Horizon and locality as for the lectotype. Other specimens. From numerous localities in east and south-east England, ranging from the Isle of Wight to Suffolk. Sedgwick Museum: (a) Zone of *O. pilula*: subzone of *E. scutata* var. *depressula*—B69949–50. (b) Zone of *M. testudinarius*: subzone of *M. testudinarius*—B69936–48, B85642–5; subzone of *U. socialis*—B69933–5, B85641. (c) Zone of *M. coranguinum*—B69890–907, B69909–32, B85633–40.

#### EVOLUTION

Evolution has little, if any, apparent direction in this genus, and the major factor affecting the zoarial development is the environment. The present revision has resulted in the merging of several species and the plexus of evolution within the genus is now shown to be much more complex. It seems as if there were two main evolutionary developments, the first being the initial early Senonian one, and the second one being late Senonian (Zone of *B. mucronata*).

*D. trifaria* is the earliest occurring species, being first recorded in the Zone of *M. cortestudinarium*, and has the longest range, being present throughout the Senonian and the Maastrichtian; it is also represented by a large number of specimens, particularly in the Zones of *Belemnitella mucronata* and *Belemnella lanceolata*. It is probably ancestral to *D. surculus*, which is introduced in the Zone of *B. mucronata*, and to *D. trigonopora*, first introduced in the Zone of *G. quadrata*. *D. surculus* differs from *D. trifaria* by its increased spinosity of the mural-rim, whilst *D. trigonopora* possesses a reduced but greatly enlarged spinosity and the distal portion of its ovicell is not flattened.

*D. simulacrum* is first found in beds of the Zone of *M. coranguinum* and differs from *D. trifaria* both in the structure of the autozoecia and of the ovicell. It is probable that these two species possessed a common ancestor rather than *D. simulacrum* being evolved from *D. trifaria*.

*D. suffragista*, also first found in the Zone of *M. coranguinum*, possibly evolved from an early member of the *D. simulacrum* lineage, by an alteration in the structural type of the distal interzoecial avicularium; by the Subzone of *U. socialis* it had also developed a gymnocystal pore, and a specimen of this type has been recorded from the Eocene of the U.S.A.

*D. flacilla* is confined to the Zone of *B. mucronata* and it may have evolved from *D. simulacrum* by a reduction in the autozoecial spinosity, together with the development of a pair of very large oral spines and a reduction in the size of the dietellae.

*D. trininghamensis* is confined to the beds of Maastrichtian age; its ancestry is uncertain for, although it may have evolved from *D. simulacrum* by an increase in spinosity



and proximal-lateral gymnocyst development, no specimens of either of these two species have been found from the Zone of *B. mucronata*. *D. flacilla* is not considered to be a possible intermediate form. However, *Tegella nicklesi* Canu and Bassler, which is probably synonymous with *D. simulacrum*, is an Eocene form, and so *D. simulacrum* may continue into the Tertiary. Hence, the possibility that *D. triminghamensis* is derived from *D. simulacrum* is not excluded.

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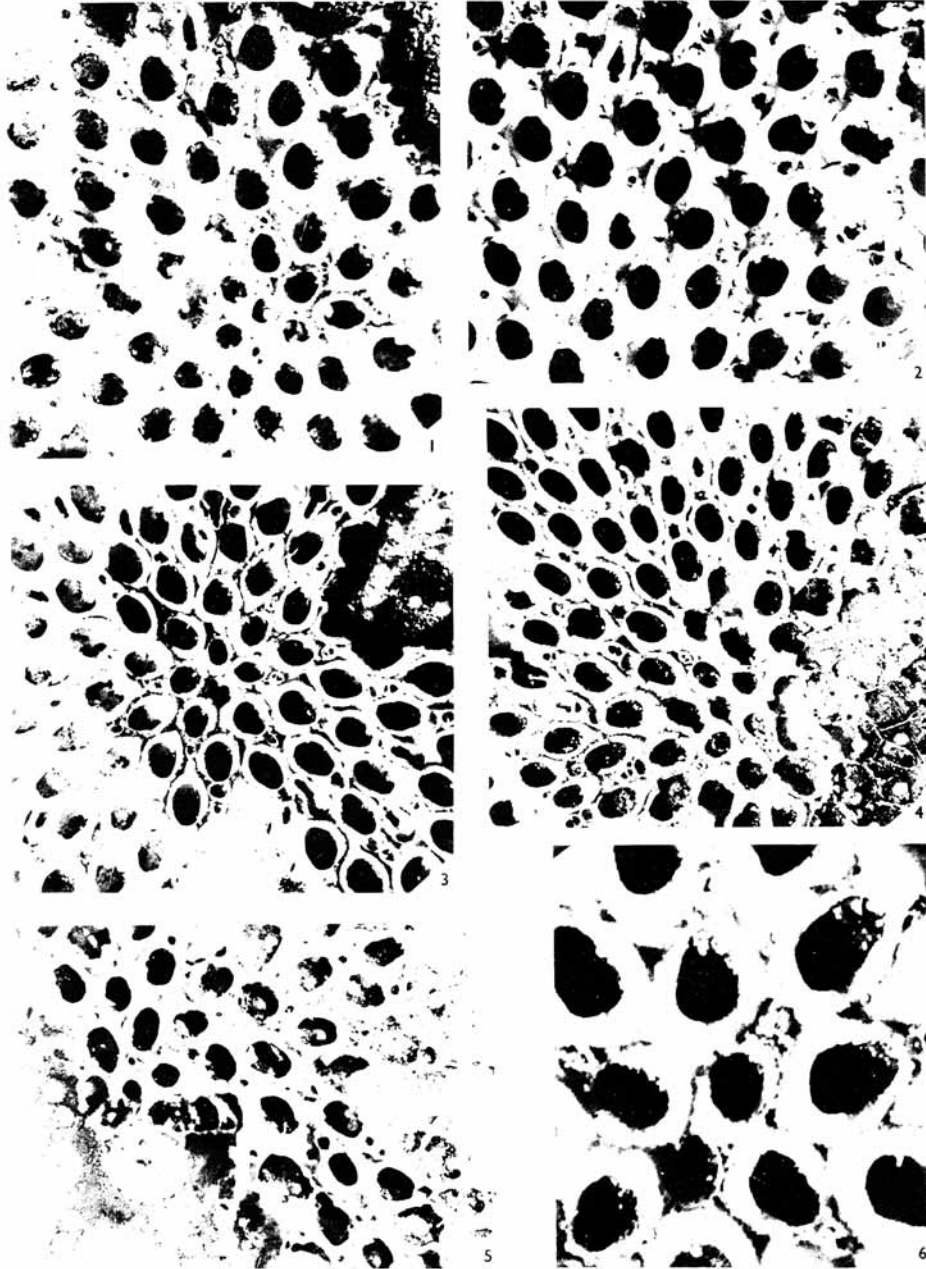
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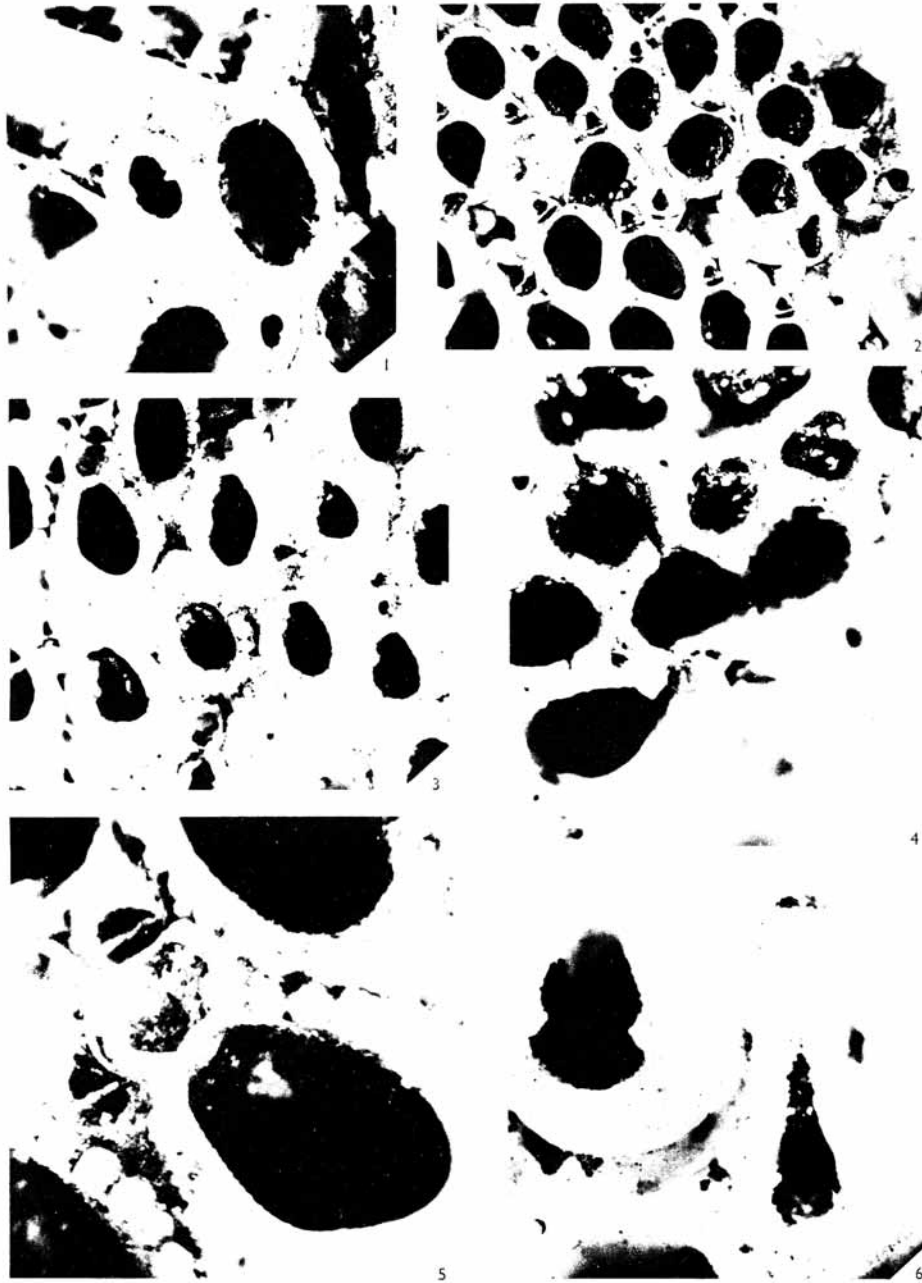
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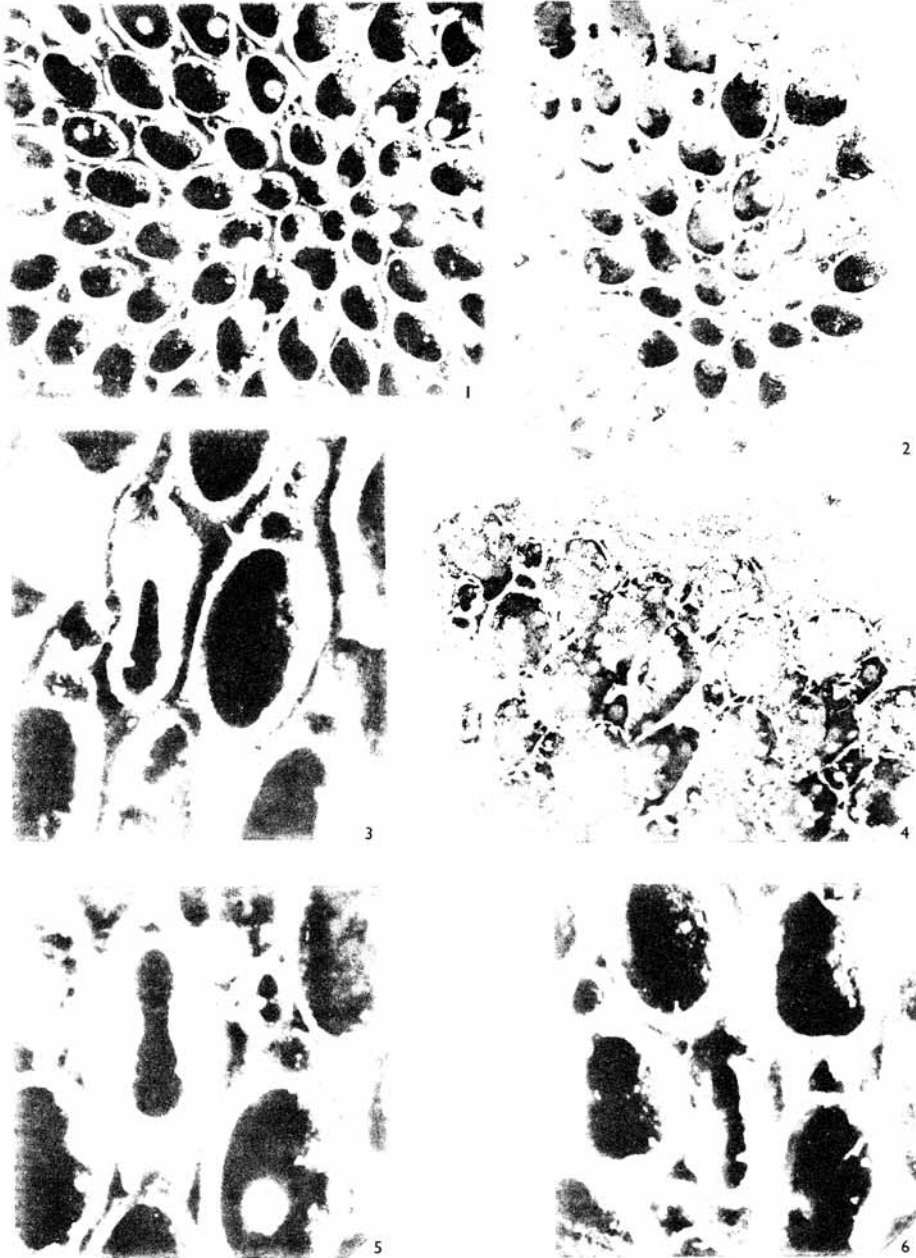
MEDD, Cretaceous membraniform Polyzoa



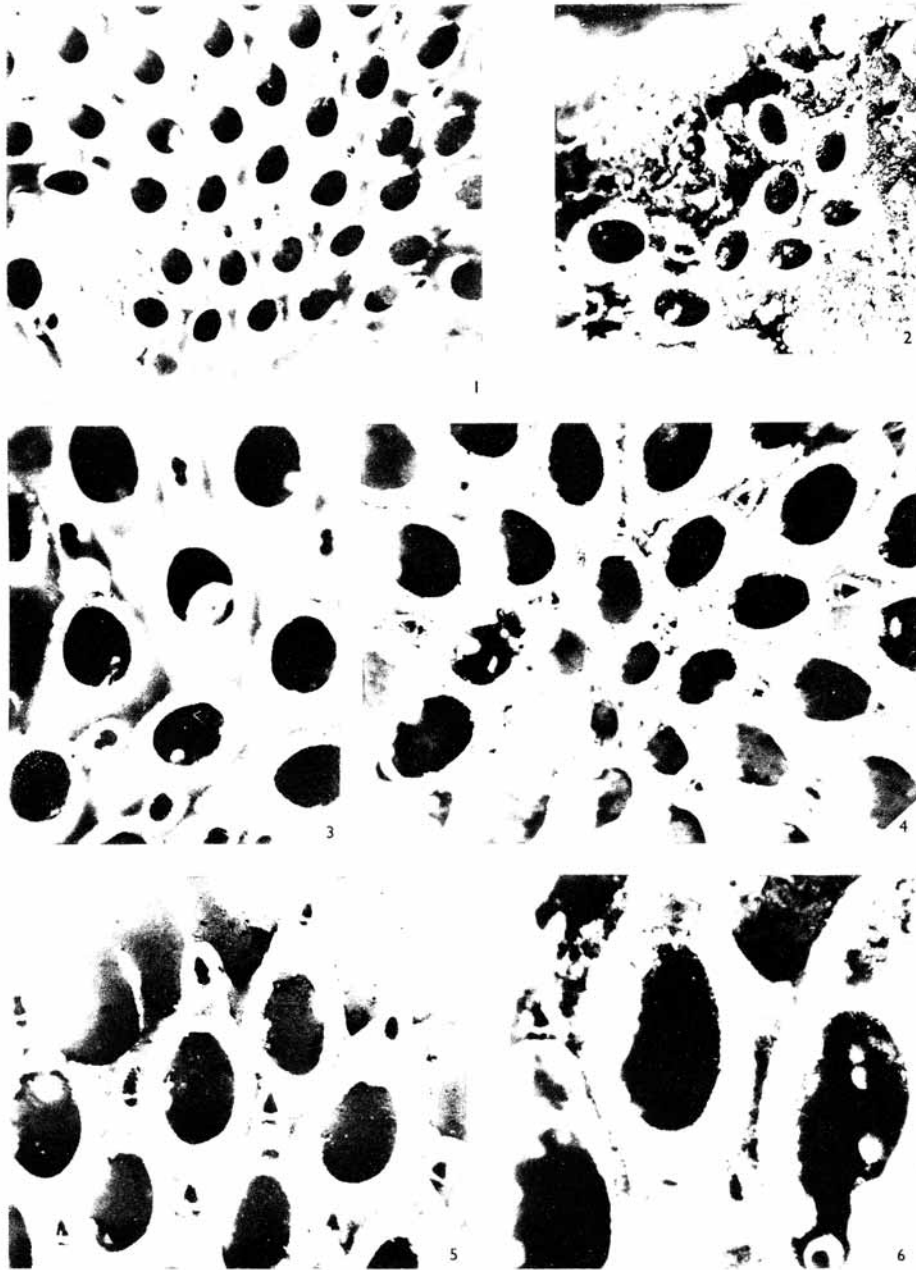
MEDD, Cretaceous membraniform Polyzoa



MEDD, Cretaceous membraniform Polyzoa



MEDD, Cretaceous membranimorph Polyzoa



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