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BY

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By KENNETH P. OAKLEY

CONTENTS

SYNOPSIS

Studies of British and Swedish ceramoporid Polyzoa resulted in an emendation of the generic diagnosis of *Favositella,* in the recognition of two new species of this genus and of several 'formae' of the type species. The known pearl-bearing Polyzoa are referred to four species: *F. interpuncta* (Quenstedt), *F. squamata* (Lonsdale), *F. anolotichoides* sp. nov., and *F. gotlandica* sp. nov. The first three species are found in the Wenlock and Ludlow Series of Britain, the fourth in the Gotlandian formation of Sweden. In Britain the pearl-bearing *Favositella* stock ranges from the Woolhope Limestone to the Aymestry Limestone. An account is given of various morphological characters of the Ceramoporidae as exemplified by *Favositella.* It is suggested that the extra-macular zooecia were occupied by autozooids, and the mesopores by nanozooids. Evidence is adduced that maculae were the seat of reproductive processes, and it is suggested that they were sometimes converted into brood-chambers, the large macular zooecia having lodged gonozooids. The wide range of morphological facies exhibited by some species of *Favositella,* notably *F. interpuncta* (Quenstedt), is attributed to the varying effects of different environmental factors on the development of the zoarium. To express differences of this order a number of formae are established.

I. INTRODUCTION

PRELIMINARY studies of the Polyzoa of the Wenlock Limestone showed that a number of Ceramoporidae contained pearl-like phosphatic calculi which had been formed during life, sometimes around "brown bodies", and occasionally embalming the secondary embryo of a polypide (Pl. 1, fig. 1). That these phosphatic "pearls" were formed most commonly in species of the genus *Favositella* at a time when this genus was approaching extinction suggested that they represented a physiological defect to which members of this stock were prone. The structure, mineralogy, and mode of occurrence of calculi in *Favositella* have already been described in detail, and the probable biochemical factors involved in the deposition of phosphate in coelomic fluid analysed as far as possible (Oakley 1934). There remained the need to publish a systematic account of the species of *Favositella* found to contain calculi.

Professor N. Spjeldnaes (Copenhagen) informed the author (personal communication, 1951) that he had found similar but smaller phosphatic calculi in old (gerontic?) individuals of a few non-ceramoporoid Polyzoa (e.g. in an Ordovician species of the trepostome *Dianulites*, and in a Gotlandian species of the cryptostome *Ptilodictya*). He confirmed the author's observations regarding optical properties and chemical composition of polyzoan calculi and fully agreed that the deposition of phosphatic matter was probably a sign of degeneration. Professor Spjeldnaes added the interesting observation that to a vertebrate palaeontologist the phosphatic calculi of Polyzoa are practically like globular calcified cartilage.

II. SYSTEMATIC POSITION AND MORPHOLOGY OF *FAVOSITELLA*

Order CYCLOSTOMATA Busk

Suborder CERAMOPOROIDEA Bassler

Family **CERAMOPORIDAE** Ulrich

Genus ***FAVOSITELLA*** Etheridge & Foord 1884: 472

1893 *Bythotrypa* Ulrich : 324.

Type Species (by monotypy) *Favosites interpunctus* Quenstedt 1878.

The genus *Favositella* was established by Etheridge & Foord on the basis of a determination of the internal characters of *Favosites interpunctus* Quenstedt from the Wenlock Limestone of Dudley. Owing to the supposed relationships of this genus with *Favosites* it was for long regarded as a tabulate coral, but Bassler's re-investigation of topotype material (1911 : 100) showed that the type species was actually a polyzoan belonging to the generic group for which Ulrich had proposed the name *Bythotrypa*, a genus erected to include ceramoporoids with loosely constructed interzooecial tissue formed by irregular mesopores. Bassler showed that it was possible to apply Ulrich's definition of *Bythotrypa* to the type species of *Favositella* without modification. It is as follows :

> "Zoaria massive or lamellate. Zooecia forming long continuous tubes, intersected by thin diaphragms, their walls minutely crenulate and with the structure characterizing the ceramoporoids. Lunarium well defined, large, projecting above the rest of the aperture margin. Mesopores numerous, open at the surface, interiorly forming a species of vesicular tissue unusually loose and irregular in construction."

Progress in the study of ceramoporoid Polyzoa has necessitated from time to time a widening of the bases of distinction of the various genera, and *Favositella* has proved no exception to this trend. In the course of the present work further species of *Favositella* have been brought to light, and a study of these based on a large amount of material has indicated the necessity of minor modifications of the generic diagnosis. Thus the zoarium may be free or encrusting. In thin, laminate forms the mesopores are so short that there is no more than a tendency for them to form the loose vesicular tissue which characterises the genus. Relatively large, irregular pores in the zooecial walls, although not invariably present, are sufficiently common to serve as a useful guide in recognizing species. The lunarium in one newly-described species contains acanthopore-like granules.

Emended diagnosis. Zoaria massive or lamellate, encrusting or free. Zooecia forming tubes of variable length, usually long, intersected by thin diaphragms, their walls minutely crenulate and structure characteristic of ceramoporoids. Large mural pores commonly present. Lunarium well-defined, usually large and projecting above rest of apertural margin. Mesopores numerous, open at the surface, interiorly tending to production of species of vesicular tissue unusually loose and irregular in construction.

The characters of the family are well exhibited by *Favositella*. Externally the main distinguishing feature of the Ceramoporidae is the elevation of the frontal margin of the zooecial aperture into a hood-like structure known as the lunarium. When typically developed this accentuates any obliquity which the zooecial apertures may have, and gives an imbricate appearance to the celluliferous surface. The lunarium is usually crescentic in cross-section. Its position on the frontal side of the zooecium—the side on which the aperture of the zooid is situated in the living polyzoan—suggests that it may have had a protective function. It is formed of auxiliary ectocyst and originates as a lining of the frontal notch of the zooecium, which corresponds with the sinuation characteristic of the aperture of many Cheilostomes. While a reinforcement of the frontal margin of the zooecial aperture is not an uncommon feature in Polyzoa, the elevation of the thickened portion as a hood-like structure is a feature mainly characteristic of certain Palaeozoic groups. The lunarium is found with modifications in both families of the Ceramoporoidea (Ceramoporidae, Fistuliporidae) and also in one family of Cryptostomata (Cystodictyonidae). There is one Jurassic cyclostomatome, *Chilopora guernoni* Haime, in which the zooecia have raised zooecial lips indistinguishable from the lunaria of Palaeozoic ceramporoids (Haime 1854, pl. 10, fig. 5*b*).

The ectocyst in the Ceramoporoidea has a very distinctive character. In highly magnified thin-sections it exhibits a finely laminated structure and, at the same time, a clouded or minutely granulated appearance. It is thus easily distinguishable from the uniformly hyaline primary ectocyst of the Trepostomata. Whereas in the latter the ectocyst appears to consist of crystalline calcite, in the Ceramoporoidea (and probably in all Cyclostomata) it is not only minutely porous, but apparently composed of intimately connected, sub-microscopic fibres, perhaps originally embedded in a corneous ground-mass.

The fracture of a ceramoporoid zoarium is very different from that of a trepostome. On breaking a trepostome the walls of adjacent zooecia part cleanly down the middle; the fracture has thus a clean-cut appearance. On the other hand, when a ceramoporoid polyzoan, or for that matter any fossil cyclostome, is broken open, the fracture passes through and across walls without discrimination, and the broken surface appears dull and amorphous. The two styles of fracture are a reflexion of the histological differences between the two groups. In trepostomes the ectocyst is crystalline. Furthermore, the zooecial walls are duplex in origin so that a median plane of weakness exists between the ectocyst of contiguous zooecia. The amorphous style of fracture in ceramoporoids is an outcome of the intimately connected, perhaps felted, structure of the zooecial walls and the resulting absence of a median plane of weakness.

In *Favositella* the primary ectocyst is sometimes invested by auxiliary ectocyst. The secondary ectocyst lining the frontal end of the zooecial aperture, and constituting the lunarium, is distinguished from the rest of the zooecial wall by its lighter colour.

In common with those of most Ceramoporoidea the zoaria of *Favositella* exhibit an internal polymorphism. That is to say two types of 'cell' are present: zooecia, and interstitial 'cells', or mesopores. On the analogy of Recent Cyclostomata it may be assumed that the majority of the zooecia were occupied by normal polyzoan individuals, or antozooids (Borg 1926 : 188), and the mesopores by modified individuals, or heterozooids (i.e. nanozooids or kenozooids). An observation made in the course of the present work on *Favositella* tends to suggest that the mesopores were occupied by nanozooids rather than by kenozooids; that is by zooids in which there was a simplified, but nevertheless functional, polypide. I refer to the occasional presence of dahllite calculi within the mesopores of *Favositella*. Since these pearls are believed to be the indirect result of polypide-degeneration, they are unlikely to have originated in closed 'cells' occupied only by kenozooids (the extreme modification of zooid in which all functional organs have disappeared).

A striking feature of Ceramoporoidea (but one which they share with other Palaeozoic Polyzoa, notably the Trepostomata) is the grouping of the zooecia about regularly spaced centres composed of modified 'cells'. These centres are termed maculae. They consist of concentrations of mesopores, usually interspersed with, or surrounded by, zooecia larger than the average and thus falling into the category of topomorphs (Lang 1906 : 66). The maculae may be level with the general surface of the zoarium, but they are more commonly either slightly depressed or slightly raised (in which case they are known as monticules).

It would seem that the maculae were, in the first place, centres of growth. Thus the simple discoidal zoaria of *Ceramopora imbricata* Hall are made up of a central macula from which the zooecia radiate towards the growing edge (Bassler 1906 : 19). Similarly in more complex zoaria the frontal, or lunariate, ends of all zooecial apertures proximate to a macula. It is probable that in a mature zoarium the mesopore and enlarged zooecia in the maculae took on functions connected with reproductive processes. Ulrich has already suggested (1890 : 298) that the larger zooecia in or surrounding maculae served as the receptacles in which embryos were developed into the larval stage. He compares them with the genoecia of the Recent genus *Crisia*, which are merely slightly modified zooecia set aside for reproductive functions. Zooids adapted and transformed for the production of embryos have been termed gonozooids by Borg (1926 : 188). The heterozooids which are believed to have occupied the mesopores may have served a protective function.

In the course of investigating the Silurian species of *Favositella* a number of observations have been made which support the idea that the maculae were, at any rate at a certain stage in astogeny, the seat of reproductive processes. It has been noted that openings in the walls of zooecia and mesopores are most frequent in the maculae, while in a few mature zoaria of *Favositella interpuncta* the maculae are found to have been converted into moderately deep, stellate, or circular pits, open at the surface. These were first described by Quenstedt (1878 : 10, pl. 143, fig. 9*y* ; ' *Sterngruben* ') who seems to have regarded them as either pathological or due to damage during the life of the organism. It appears, however, that they have originated through the coalescence of the mesopores and zooecia in the maculae by the breaking-down, or resorption, of their walls. These pits (Pl. 3, fig. 6 ; Pl. 9, fig. 6) are so strikingly similar to the ' brood-chambers ' observed in certain Recent Heteroporidae (Borg 1933 : 267, pl. 2, figs. 1, 4) that they may have served the same function. It is not improbable, on the analogy of Recent forms, that in the breeding season the walls of the mesopores and large zooecia in the maculae were partially resorbed, and that the developing embryos were discharged into the central space so formed, there to undergo larval development. However, further work on this aspect of the Ceramoporidae is required before this interpretation can be credited with any degree of certainty.

III. DESCRIPTION OF PEARL-BEARING SPECIES

Favositella interpuncta (Quenstedt)

(Pl. 1, figs. 1–6 ; Pl. 2, figs. 1–3, 6, 7 ; Pl. 3, figs. 4–6 ; Pl. 4, figs. 1–6 ; Pl. 6, figs. 1–5 ; Pl. 7, figs. 1, 2 ; Pl. 8, figs. 1, 3, 4 ; Pl. 9, figs. 6, 7)

1851 *Chaetetes Bowerbanki* (partim) Edwards & Haime : 272.
1855 *Monticulipora? Bowerbanki* (partim) Edwards & Haime : 268, pl. 63, figs. 1*b*, *c* (non fig. 1*a*).
1873 *Monticulipora* sp. 5 (partim) Salter : 109.
1873 *Monticulipora* sp. 6 (partim) Salter : 109.
1878 *Favosites interpunctus* Quenstedt : 10, pl. 143, fig. 9.
1879 *Favosites fibrosus* Sollas : 510 (vide pl. 24, figs. 12, 17–20).
1884 *Favositella interpuncta* (Quenstedt) Etheridge & Foord : 473, pl. 16, figs. 1, 1*a–f*.
1911 *Favositella interpuncta* (Quenstedt) ; Bassler : 101, text-fig. 35.

The specimen figured by Edwards & Haime (1855) as an immature form of their *Chaetetes* (*Monticulipora?*) *bowerbanki* has been found on examination to be identical with the polyzoan described below as *Favositella interpuncta* forma *texturata*. As this specimen (now preserved in the Sedgwick Museum, Cambridge : A4024) is one of the syntypes of *Chaetetes* (*Monticulipora?*) *bowerbanki*, that name must be included in the synonymy of *Favositella interpuncta*. However, it is clear that Edwards & Haime mainly based their diagnosis of *C. bowerbanki* on specimens such as the other syntype figured by them (1855 : pl. 63, fig. 1*a*). Since this specimen is a coral referable to the genus *Favosites*, it is convenient to restrict the name *bowerbanki* to forms agreeing with the anthozoan syntype, and to reject it as a name for the polyzoan on the grounds of its being a homonym.

LECTOTYPE (here chosen). Specimen from the Wenlock Limestone of Dudley figured by Quenstedt (1878 : pl. 143, fig. 9). Preserved in the Museum of the Institute of Geology and Palaeontology at Tübingen, Germany. This is almost certainly the type since it is the only specimen preserved in the Quenstedt Collection.

DESCRIPTION (Pl. 2, figs. 1, 6; Pl. 8, figs. 1, 4). Free, roughly campanulate zoarium with spreading margins. Total height 31 mm.; maximum diameter 47 mm. Actual thickness averages 7 mm., but locally this is exceeded owing to the superposition of two or more layers of zooecia. The deeply concave inferior surface is covered by a thin, coarsely wrinkled epitheca or epizoarial membrane; where this is worn the nearly prostrate bases of the zooecia tend to show through (Pl. 2, fig. 6). The celluliferous surface is moderately smooth. Over the greater part of the surface the zooecial tubes have relatively thick walls and in outline are mainly rounded polygons (Pl. 8, fig. 1). There are 4 to 5 of these zooecial openings in an interval of 2 mm. The lunaria are represented by inconspicuous slightly raised thickenings of the frontal angle. In one area of the zoarial surface (Pl. 8, fig. 4) the zooecia are thin-walled and more quadrangular in outline, while the lunaria are thin, hood-like structures occupying the frontal fourth of the zooecial margin.

Open mesopores are moderately frequent; the majority are small and circular, and occur mainly at the angles of junction of the zooecia. They are more abundant in some areas than in others.

Maculae are well developed and arranged roughly quincuncially; the average distance separating their centres is 5 mm. They show no tendency to become monticules. Two types, or phases, can be recognized amongst the maculae. The first type, which occurs in areas where the zooecial walls are thick and the lunaria inconspicuous, is characterized by an abundance of small circular mesopores scattered amongst zooecia which are slightly larger than average. There is a tendency for the walls of the zooecia and mesopores to break down in the centre of such maculae, resulting in the formation of the stellate pits noted by Quenstedt, and now regarded as brood-chambers (p. 7). The second type of macula is associated with the other surface phase, characterized by thin-walled zooecia and conspicuously developed hood-like lunaria. Such maculae consist of a ring of large zooecia, with overarching, lunarial hoods, enclosing an irregularly-shaped area occupied by a cluster of large, thin-walled mesopores which seem to form a species of open vesicular tissue. The exposed surfaces of the adjacent lunarial hoods are marked by a series of fine lines which converge upwards and appear to be continuations of the walls of the mesopores on which the lunaria impinge.

Internal characters may be deduced from topotypes (see p. 10).

VARIATION IN EXTERNAL CHARACTERS. Examination of a large number of specimens of *F. interpuncta* has shown that the external variation in this species is very great, and it is found convenient to recognize a number of formae (see p. 13).

Forma *typica* (Pl. 1, figs. 4–6; Pl. 2, figs. 2, 3; Pl. 3, fig. 6; Pl. 4, figs. 1, 5; Pl. 6, figs. 3–5, Pl. 9, fig. 6). Zoaria tumular, with well-defined circular or elongate-oval outlines. Commonly such zoaria commenced their growth on some bulbous foreign body, such as a large gastropod shell, but eventually extended beyond it, so that when fully developed their margins were free epithecated expansions (Pl. 1, fig. 4). As observed by Etheridge & Foord, the form of the shell or other foreign body to which this species became attached frequently determined the external form assumed by the zoarium. This is illustrated by a specimen in the Holcroft Collection at Birmingham University (Pl. 1, figs. 4, 5). This polyzoan commenced growth on the side of a large *Loxonema*, with the result that the zoarium is broader and higher at one end than at the other and has the general form of a drumlin. Some campanulate, or tumular zoaria appear to have commenced growth on a knot of hardened mud on the sea-floor. In such specimens the base is deeply concave.

While the total height of these tumular zoaria may be as much as 50 mm., the zoarial thickness rarely exceeds 7 mm., either on account of the space occupied by the 'host' or by reason of their actual concavity (see Pl. 2, fig. 2). Where the zoarial thickness exceeds about 7 mm. there has usually been reduplication of the zooecial layers.

In forma *typica*, zoaria range in size from small bun-shaped colonies measuring 30 mm. in diameter and 12 mm. in height (e.g. B.M. N.H., D.33918) to large tumular masses 90 mm. in length, 60 mm. in width and 30 mm., or more, in height.

The zooecial apertures are relatively thick-walled and present the form of rounded polygons. Lunaria are inconspicuous, usually little more than blunt processes. Thin-walled quadrangular zooecia, with prominent cowl-like lunaria, are only present when there has been new growth. This type of surface is regarded as constituting a distinct forma (see last paragraph below).

Mesopores are small and scattered, and have the appearance of pin-pricks in the thickened angles of junction of the zooecial walls. Typically the maculae are inconspicuous (cf. first type in lectotype), but in some zoaria they are raised into low monticules (Pl. 1, fig. 6). Occasionally the zooecia and mesopores in the maculae have become confluent through break-down of the walls, thus giving rise to conspicuous pits which in all probability served as brood-chambers (see p. 7 and Pl. 3, fig. 6; Pl. 9, fig. 6).

Forma *brevipora* (Pl. 2, fig. 7; Pl. 4, figs. 2, 6; Pl. 6, figs. 1, 2; Pl. 9, fig. 7). This forma is typically exhibited by thin zoaria encrusting the surface of smooth-shelled brachiopods such as *Meristina tumida* (Dalman), and more rarely tumid gastropods such as *Poleumita globosa* (Schlotheim). The thickness of the zoarium is normally 2–3 mm.; the surface is remarkably smooth and maculae are inconspicuous. The zooecial walls are thickened distally with the result that the apertures are sub-polygonal or rounded. Small circular mesopores, occurring at the zooecial angles, are relatively abundant, particularly in the maculae. A local tendency to linear arrangement of the zooecia is occasionally noticeable.

Forma *texturata* (Pl. 3, fig. 5; Pl. 4, fig. 4; Pl. 7, fig. 2; Pl. 8, fig. 3). This facies is also typically expressed when the whole zoarium is a thin encrusting sheet, as on smooth-shelled brachiopods such as *Meristina tumida* (Dalman), or *Gypidula galeata* (Dalman). Over the whole surface the zooecial apertures are arranged in a regular lace-like pattern, a dominant feature of which is the occurrence of sharply defined star-like maculae in quincunx. Each macula consists of an irregular ring of five or six large zooecia with prominent, usually finely ribbed, lunarial hoods which face away from a slightly depressed area of thin-walled, angular mesopores. The bases of the lunarial hoods of the large zooecia occupy about a third of the whole circumference of the zooecial aperture.

The zooecia outside the maculae are thin-walled and mainly quadrangular. They are slightly larger than in the forma *typica*, there being $3\frac{1}{2}$ to 4 in an interval of 2 mm. They have small but prominent lunaria, the frontal or external surface of which is rounded and sometimes marked by fine ribs converging upwards. Mesopores are almost entirely confined to the maculae.

All zooecia are oriented with respect to some macula. The intersection of the zones of propagation of the several maculae has resulted in the surface being divided up into variously shaped sectors, within each of which the lunarial hoods have the same direction, and across the boundaries of which the orientation of the zooecia changes. Within each sector of constant orientation the zooecia consequently have a very characteristic appearance (rather like that of a net pulled from various centres) which is markedly different from that of the forma *typica*. Nevertheless, the fact that areas of new growth in typical zoaria closely approximate to the *texturata* condition (see p. 13, and Pl. 8, fig. 4), is proof that this form is largely transitory.

Forma *irregularis* (Pl. 4, fig. 3 ; Pl. 7, fig. 1). Zoaria forming irregular crusts on the surface of gastropods, corals and brachiopods. The zoarium usually has a very uneven surface, and varies in thickness from 2 mm. to 10 mm. The character of the surface shows an irregular transition from that of forma *typica* to that of forma *texturata*. The two types of surface-character are so intimately mixed that the zoaria have a distinctive appearance. Maculae are unevenly distributed, and very variable in structure, although the type associated with the pure *texturata* condition predominates. There are on the average 4 zooecial apertures in 2 mm.

Forma *intermedia* (Pl. 3, fig. 4) only differs from *irregularis* in mode of origin of the zooecial irregularity (see p. 14).

Description of internal characters. These have been studied in topotype material.

Forma *typica* (Pl. 4, figs. 1, 5 ; Pl. 6, figs. 3–5). In tangential sections (Pl. 4, figs. 1, 5) the majority of the zooecia appear as irregularly rounded polygons with an average diameter of 0·4 mm. Such zooecia have an indistinct lunarium occupying a notch in the frontal margin. The zooecial walls in the mature zone of a typical zoarium are relatively thick (*circa* 0·05 mm.), and are formed of coarsely lamellar, crypto-fibrous tissue. The lunaria are formed of more pellucid tissue. Sporadic breaks can be observed in the zooecial walls and indicate the occurrence of large mural pores. Mesopores appear as rounded or oval spaces 0·1 mm. to 0·2 mm. in diameter, and occur at the angles of junction of the zooecial walls. They are noticeably more abundant in the maculae.

The occurrence of areas in which the zooecia show linear arrangement, sub-ovate, quadrangular, or subtriangular outlines, and more distinct, pointed lunaria, indicates that the section has passed into an immature zone in which there is an approach to the *texturata* condition.

In deeper transverse sections through the mature region the zooecia and mesopores have thinner walls and appear more angular in outline ; irregularly pentagonal and sub-triangular outlines predominate amongst the zooecia. In macular areas the zooecia show elongate outlines with a longer axis measuring as much as 0·6 mm. Breaks in the walls are relatively common and lead occasionally to meandrine zooecial spaces. The lunaria are inconspicuous, each being represented by a small triangular patch of light-coloured tissue in the frontal angle of the zooecium.

Transverse sections through the sub-ephebic levels show rather quadrangular zooecia arranged in diagonal rows, recalling the *texturata* condition fully described below.

Vertical sections through typical zoaria (Pl. 1, fig. 3 ; Pl. 6, figs. 3–5) show one to three layers of zooecia varying in thickness from 3 mm. to 12 mm. Each layer has a thin basal lamina. In free expansions the basal lamina of the lowest zooecial layer is coated by a thin, corrugated epithecal membrane. The zooecial tubes arise obliquely from the basal lamina (Pl. 6, fig. 3), but after a short distance become more or less vertical. In the mature zone mesopores are locally intercalated between the zooecia.

The walls of the zooecia are irregularly crenulate ; in sufficiently thin sections it is possible to detect small, and often rather oblique, mural pores. When a vertical section cuts a zooecial wall tangentially the ectocyst is seen to have a transversely laminated structure. The zooecial walls sometimes show oblique, upwardly directed, spine-like processes jutting into the zooecial cavity (Pl. 6, fig. 3). It is unlikely that these are comparable with the spines observed in certain trepostomes (Cumings & Galloway 1915 : 358) ; they more probably represent incipient mesopores. Thin diaphragms occur at intervals throughout the zooecial tubes ; they are slightly convexo-concave in the upward sense, and are separated by an interval generally varying from one to two tube-diameters.

Mesopores tend to be loosely vesicular in character. Their walls contract and expand in an irregular manner so as to produce a roughly moniliform effect (Pl. 1, fig. 3 ; Pl. 6, fig. 5). In some cases the mesopores are cut up into vesicles by oblique or transverse projections of the wall, similar to those already noted in the zooecia. Thin diaphragms occur sporadically in the mesopores. The walls of the mesopores in fully mature zoaria are thickened near the surface.

Forma *brevipora* (Pl. 4, figs. 2, 6 ; Pl. 6, figs. 1, 2). Tangential sections of zoaria in this condition do not differ materially from those of forma *typica*. Mesopores are variable in size and frequency. The zooecia present mainly sub-polygonal, rounded or oval outlines with an average diameter of 0·4 mm. ; lunaria are indistinct.

Vertical sections show that the zooecia become erect after an abbreviated oblique phase. The essential differences from forma *typica* are : (i) the shortness of the mature zone ; and (ii) the simplicity of the mesopores, which are formed by a bifurcation of the zooecial wall, as in forma *texturata*.

Forma *texturata* (Pl. 4, fig. 4 ; Pl. 7, fig. 2). Tangential sections bring out the marked linear arrangement of the zooecia within circumscribed sectors. The zooecia are predominantly quadrangular in outline, although some may show oval or rounded pentagonal cross-sections. They are thinner walled (average thickness, 0·035 mm.) than in forma *typica*, and vary in diameter from 0·4 mm. to 0·5 mm. The lunaria of all zooecia are sharply defined, and usually sagittate in outline (Pl. 4, fig. 4). Small rounded mesopores occur, but are almost entirely confined to the maculae.

Vertical sections (Pl. 7, fig. 2) are indistinguishable from those through the proximal region of forma *typica*. They bring out the shortness and obliquity of the zooecia typical of this form. Lunaria are difficult to distinguish in vertical sections, but are clearly direct prolongations of the frontal walls of the zooecia, lined internally with auxiliary ectocyst. Mesopores are shallow and thin-walled. Each is formed by the bifurcation of a ' septum ' from the upward-facing, or basal surface of a zooecial wall, usually at a distance of 0·5 mm. to 1·0 mm. above the basal lamina. There is no epitheca ; the so-called basal lamina has no separate existence but is merely the common basal wall of the prostrate portions of the zooecia. Diaphragms are usually present.

The zooecia vary in height from 1 mm. to 3 mm. The superposition of several layers of zooecia in the *texturata* condition is rare. Consequently the average thickness of zoaria which are wholly in this condition is 2 mm.

Forma *irregularis* (Pl. 4, fig. 3 ; Pl. 7, fig. 1). Tangential sections show areas with regularly aligned, quadrangular zooecia, with distinct sagittate lunaria, which pass abruptly, or by mixture, into areas where the zooecia have rounded polygonal outlines and indistinct lunaria. Vertical sections show that this forma is associated with the irregular and local reduplication of zooecial layers ; thick layers show the characters of forma *typica*, thin layers those of forma *texturata* (cf. Pl. 7, fig. 1).

Stratigraphical distribution. The earliest known example of the species is a specimen from the Lower Wenlock Shales at Buildwas, preserved in the Foord Collection at the British Museum (Natural History) (D.36318). It is in the *brevipora* condition, and forms an incrustation on a shell of *Meristina tumida* (Dalman). Similar specimens occur in the Upper Wenlock Shales at Walsall.

The species occurs in greatest abundance in the Wenlock Limestone, particularly in Staffordshire and at Rumney, near Cardiff. In common with other Ceramoporidae it is rare in the Wenlock Limestone of Shropshire. There is a single record of the species in the Wenlock Limestone of the Woolhope area in Herefordshire (Gardiner 1927 : 323).

Twenty-five per cent of all the Polyzoa recovered from the thin representative of the Wenlock Limestone exposed in the Ty Mawr Lane at Rumney proved to belong to this species[1]. The zoaria from this locality are all small. Most of them seem to belong to the typical forma, but the intractable ferruginous matrix with which they are encrusted makes an examination of surface features a matter of difficulty. In some specimens mesopores are very sparse (Pl. 6, fig. 4).

The great majority of the specimens of *F. interpuncta* preserved in old collections

[1] Many of the specimens of *Favositella interpuncta* from Rumney are remarkably rich in pearls. There can be no doubt that the pearl-bearing specimens erroneously described by Sollas as *Favosites fibrosus* actually belong to this species.

appear to have come from the shaly beds of the Wenlock Limestone at Wren's Nest and Castle Hill, Dudley, Staffordshire. Recent collecting has shown that the horizon at which they occur in greatest abundance is in the upper part of the Middle Nodular Beds. All the described formae appear to be represented at this level. The only specimen recovered from the Lower Limestone is one in the *brevipora* condition from the basement beds at Walsall. One specimen of forma *irregularis* from Dudley, preserved in the Sedgwick Museum (A5943), has a matrix which suggests derivation from the passage beds between the Upper Limestone and the Lower Ludlow.

A small fragmentary specimen of *Favositella* from the Aymestry Limestone of Shucknall Hill, Woolhope, Herefordshire, in the Geological Survey & Museum (57956) appears to represent a variant of this species.

REMARKS. So great is the diversity of form exhibited by *Favositella interpuncta* that some sort of subdivision of the species would seem to be desirable. An examination of an extensive series of specimens from the Wenlock beds has indicated, however, that the observed variation is continuous and not of a mutational order. The diversity of form is partly explained by the fact that different stages of astogeny are quite distinct in appearance, and partly by the marked effects on the development of this polyzoan produced by different environments.

It was therefore proposed by the author (1938) that the only way of expressing the main structural facies exhibited by the species was by applying *formal* as distinct from *varietal*, names to the several forms. The differences which the form-names indicate may be in one case developmental, in another due to the effect of a special environment, and so on. However, in the present state of our knowledge of these Polyzoa it is possible to make only very tentative correlations of this sort.

The forma *typica* seems to represent the normal form assumed by a zoarium which developed to full maturity (?gerontic stage) under constantly favourable conditions.

The forma *brevipora* is apparently the condition of zoaria which attained maturity under constant, but unfavourable conditions. In tubular Polyzoa it would seem that the length of the zooecia is not a reflexion of the rate of deposition of sediment as it is in corals, but depends mainly on the frequency of polypide-regeneration ; this in its turn being correlated with such factors as temperature, salinity and food-supply.

The forma *texturata* is the one which provides the most interesting problem. Zoaria showing this forma are so different in aspect from the typical zoaria that they were for long considered as belonging to a distinct species. In fact, judging by the evidence of museum labels, they have been generally regarded, even by palaeontologists familiar with typical *Favositella interpuncta*, as representing a species of *Ceramopora*.

The recognition of the zoaria in question as a forma of *Favositella interpuncta* resulted from the discovery that they showed features almost identical with those of a small portion of the celluliferous surface of the type-zoarium of that species. A close examination of the holotype and other typical specimens of *F. interpuncta* has shown, in fact, that wherever a new layer of zooecia has commenced to develop on the surface of a mature zoarium (i.e., wherever there has been local rejuvenation), the area of new growth shows the characters which comprise the *texturata* condition.

In other words this condition is essentially that of the neanic or sub-ephebic phases of development in *Favositella interpuncta*. Nevertheless there are reasons for regarding this condition as constituting in some cases a distinct forma.

Complete zoaria consisting of a single layer of zooecia in the *texturata* condition are of common occurrence, particularly on smooth-shelled brachiopods. The well-defined maculae which they exhibit suggest that the zoaria were fertile. The probable explanation of these forms is that they represent zoaria whose development was arrested at the sub-ephebic stage owing to certain environmental conditions.

The forma *texturata* preserves, to some extent, features of more primitive Ceramoporoid genera such as *Crepipora*; for example, the restriction of mesopores to the maculae.

Zoaria in which there has been a tendency for new layers of zooecia to develop at irregular intervals, and over small, limited areas, have a very irregular aspect which contrasts markedly with that of both forma *typica* and forma *texturata*. For such zoaria the term forma *irregularis* was proposed in 1938.

The irregular rejuvenation of the zoarial surface which tended to the production of this forma, was most probably connected with the variable character of the micro-environment. The extent to which environmental factors may have controlled growth-form in *Favositella*, may be gauged by the fact that 12 out of 13 specimens of *F. interpuncta* recovered from a single exposure in the Wenlock Limestone proved to belong to the same forma. The bed from which they came was largely composed of current-drifted shells and corals which had been accumulated in an area adjacent to a coral reef (' ball-stone ').

After further work on *Favositella interpuncta* the author found it desirable to recognize another forma, amongst the forms grouped as forma *irregularis*. The additional forma, called *intermedia*, is illustrated by Pl. 3, fig. 4. It differs from forma *irregularis* in so far as the irregularity of the surface is not due to patchy rejuvenation, but to unequal development of individual zooecia.

Favositella squamata (Lonsdale)

(Pl. 2, fig. 4 ; Pl. 3, fig. 2 ; Pl. 5, figs. 1, 3 ; Pl. 7, fig. 5 ; Pl. 8, fig. 2 ; Pl. 9, figs. 4, 5)

1839 *Discopora squamata* Lonsdale : 679, pl. 15, figs. 23, 23*a*.
1873 *Monticulipora* sp. 4 (partim) Salter : 109.
1890 *Crepipora squamata* (Lonsdale) Ulrich : 471.

LECTOTYPE (here chosen). Specimen marked *a* on slab of shelly flagstone from Wenlock Limestone, Sedgeley, figured by Lonsdale (1839, pl. 15, figs. 23, 23*a*). Geological Society Coll. 6596, Geological Survey & Museum. It is probable that Lonsdale's diagonsis of the species was wholly based on this specimen.

DESCRIPTION (Pl. 9, fig. 5). Fragment of flat laminate zoarium, 1·5 mm. thick, apparently encrusting the valve of a brachiopod. The fragment is 8 mm. long and 5 mm. wide. The surface is rather worn. The zooecia are sub-erect and contiguous. Outside the raised area the zooecial apertures are thin-walled, mainly rhomboidal and arranged in intersecting, diagonal rows ; 4 to $4\frac{1}{2}$ apertures occur in an interval of

2 mm. In the subtriangular frontal half of the zooecium the apertural margin is elevated as a well-defined lunarium. The raised part of the zoarial surface is clearly a macula ; it is distinguished by the relatively large size of the zooecia and by the occurrence of numerous irregular mesopores. Mesopores have not been observed outside the macula.

External characters. Based on study of topotype material (see Pl. 2, fig. 4 ; Pl. 3, fig. 2 ; Pl. 8, fig. 2 ; Pl. 9, figs. 4, 5). Zoaria form thin encrusting sheets, generally on flat surfaces such as are provided by the valves of strophomenid brachiopods. The margins of the zoarium sometimes extend beyond the encrusted object. Free marginal expansions formed in this way have developed a coarsely wrinkled basal epitheca (Pl. 2, fig. 4). The surface of the zoarium is sometimes irregularly monticulose, but the raised areas do not invariably coincide with maculae.

The zooecial apertures are subtriangular, oval or rhomboidal. In the frontal half of the zooecium the apertural margin is raised into a prominent and rather angulated lunarium, the apex of which is often slightly overarching particularly in the maculae. The external angle of the lunarium may be acute or rounded ; in the latter case it is marked by several strong rugae or ribs which converge towards the apex. There are from 4 to 5 zooecial apertures in an interval of 2 mm. Maculae are well-marked and sometimes form low monticules ; they are superficially similar to those in *F. interpuncta* forma *texturata*, but usually show a more confused structure. The large zooecia in typical maculae have abnormally high, pointed lunarial hoods.

Mesopores are mainly small and rounded, although larger, more angular ones occur in some of the maculae. Outside the maculae, mesopores are, for the most part, only of sporadic occurrence. A notable feature of the species is the occurrence of certain circumscribed areas, distinct from normal maculae, in which minute thick-walled mesopores are so abundant that they surround the zooecial apertures. In these areas which are of irregular distribution and usually larger than the maculae, the zooecial apertures are oval or sub-pyriform, and have low, inconspicuous lunaria (Pl. 8, fig. 2).

Internal characters. Based on study of topotype material. Tangential sections (Pl. 5, fig. 3) show fairly regularly aligned, thin-walled zooecia, varying in outline from rhomboidal to sub-polygonal or sub-pyriform, and with an average diameter of 0·4 mm. The frontal end of the zooecial aperture is deeply arcuate, and lined with the lighter coloured tissue of the lunarium, which varies in form from a wide crescent to a small triangle, depending on the level at which the section has been cut. The zooecial walls are composed of the finely laminated and minutely granular tissue characteristic of the genus ; they have an average thickness of 0·028 mm. Rounded or oval mesopores, ranging in diameter from 0·08 mm. to 0·1 mm., are seen in localized areas.

In transverse sections through the sub-distal or proximal region (Pl. 5, fig. 1), the zooecia present irregularly polygonal outlines. The zooecial walls are very tenuous and tend to be somewhat flexuous. Small sub-polygonal mesopores occur mainly in the maculae. In the macular areas frequent breaks can be observed in the zooecial walls.

Vertical sections (Pl. 7, fig. 5): in typical zoaria there are from one to four layers of zooecia. The layers vary in thickness from 1 mm. to 4 mm. The zooecial tubes arise from a thin, basal lamina, which, in the case of the lowest zooecial layers in free-growing parts of a zoarium, is usually covered by a thin epitheca. The zooecial tubes normally become almost vertical after a short prostrate phase, although in some specimens they maintain an oblique course. In the peripheral region the zooecial walls become thickened and sometimes irregularly crenulate; short and rather thick-walled mesopores are rarely more than 0·2 mm. deep. In the peripheral zone, the walls of the mesopores and the zooecia commonly develop a ragged or loosely constructed appearance, owing to the occurrence of irregular mural pores. Diaphragms are infrequent, or absent.

Occurrence. The species has been recorded only from the Wenlock Limestone of Dudley and Sedgeley. It occurs mainly in the upper part of the Middle Nodular Beds (for example at Wren's Nest), and is much rarer than *F. interpuncta*.

Remarks. This species is easily confused with *F. interpuncta* forma *texturata*. In both the lunaria are prominent, and in both the zoarial surface tends to be divided into sharply defined sectors within which the zooecia have a constant orientation with respect to some macula. However, *F. squamata* differs from *F. interpuncta* forma *texturata* in the following respects: (i) the zooecial apertures are on the average slightly smaller and narrower; (ii) the lunaria tend to be longer and more arcuate; (iii) the maculae show a more confused structure; (iv) there are circumscribed areas, apart from normal maculae, in which mesopores are abundant; (v) the zooecial tubes are longer and more erect. The character mentioned under (iv) is an example of topomorphism.

There is no doubt that specimens of *F. squamata* showing the characters described above are normal, fully mature zoaria; whereas the superficially similar specimens of *F. interpuncta* forma *texturata* are evidently immature, or stunted zoaria.

Favositella anolotichoides sp. nov.

(Pl. 3, figs. 1, 3; Pl. 5, figs. 2, 5; Pl. 7, figs. 3, 4; Pl. 9, fig. 3)

1873 *Monticulipora* sp. 6 (partim) Salter: 109.
1934 *Ceramoporella* sp., Oakley: 314, pl. 14, figs. 15, 18.

Holotype (Pl. 3, fig. 3; Pl. 5, figs. 2, 5; Pl. 7, figs. 3, 4; Pl. 9, fig. 3). Brit. Mus. (Nat. Hist,), D.33926, Wenlock Limestone, upper part of Middle Nodular Beds; exposure by lime-kiln on SW side of Wren's Nest, Dudley, Staffs. The holotype is an oval, encrusting zoarium, 4–5 mm. thick, originally 40 mm. long and 27 mm. wide, attached to the surface of an '*Orthoceras*' shell.

Paratypes. Brit. Mus. (Nat. Hist.), 8 specimens from the type locality (D.36324, D.36326–36332), and 5 others (PD.4613, D.36319, D.36325, D.36333–34); Sedgwick Museum, Cambridge, 2 specimens (A5964, A5899); National Museum of Wales, 1 specimen (G.591).

Horizon and locality. The species is common in the upper part of the Middle Nodular Beds of the Wenlock Limestone at Wren's Nest, Dudley. It has also been recorded from the Wenlock Limestone of Ty Mawr Lane, Rumney, near Cardiff; and from the middle beds of the Wenlock Limestone in the Coate's Farm Quarry, Presthope Road, near Much Wenlock, Shropshire.

Description. *External characters.* Zoaria form moderately thick encrusting sheets on cephalopod shells, corals, stromatoporoids, and more rarely on brachiopod shells. Where the zoarium extends beyond the encrusted body, the basal surface becomes enveloped by a thin, wrinkled epitheca. The surface of the zoarium is usually somewhat uneven, but there are no definite macular elevations or depressions. The zooecia are relatively thick-walled and radiate from macular centres spaced at intervals of about 5 mm. Each has a thin, horse-shoe shaped lunarium, the edges of which bear minute, acanthopore-like granules. The zooecial apertures vary in outline; they tend to be roughly elongate-oval or sub-pyriform, but a slight constriction of the walls at the ends of the lunarial loop gives the apertures the form of a key-hole. Locally the apertures become meandrine owing to the coalescence of some of the zooecia.

Internal characters. In tangential sections (Pl. 5, figs. 2, 5) the majority of the zooecia present slightly 'waisted', oval outlines, with an average major axis of 0·45 mm. and an average minor axis of 0·27 mm. The outlines of some zooecia appear geniculate owing to a slight declination of the axis of the lunarium relative to the axis of the anterior part of the aperture. As seen in section, the lunarium is a narrow band of light-coloured tissue, varying in form from a semi-circle to a three-quarter circle, and constituting the frontal third of the zooecial wall. In sections of well-preserved specimens it is possible to see 9–12 acanthopore-like granules, or tubules, within the lunarium (Pl. 5, fig. 2). These appear as pellucid spots with an average diameter of 0·02 mm. They are rather irregularly placed and their margins occasionally project into the zooecial cavity. The zooecial walls vary considerably in thickness; the frontal wall, formed by the lunarium, has an average thickness of 0·025 mm., but elsewhere the walls may attain a thickness of as much as 0·05 mm. Sub-polygonal mesopores, varying in diameter from 0·1 mm. to 0·3 mm., are abundant and practically surround the zooecia. Gaps in the walls of both mesopores and zooecia are common and lead locally to meandrine outlines.

Vertical sections (Pl. 7, figs. 3, 4) usually reveal a single layer of zooecia; more rarely there are two superimposed layers. The thickness of a zooecial layer varies from 2 mm. to 5 mm. The zooecial tubes arise from a thin basal lamina which is epithecated in the case of free-growing expansions. The zooecia pass through a brief prostrate phase and then rise vertically; they have irregularly crenulate walls in which occasional breaks may be observed. The walls are thickened throughout the mature zone by auxiliary ectocyst. Thin diaphragms, concave upwards, occur fairly frequently, but without any regular spacing, the intervals separating them varying from one to three tube-diameters. Mesopores are intercalated between the zooecia at the point where they become vertical, and persist throughout the mature zone. They are loosely moniliform, or in some cases definitely vesicular in character

(Pl. 7, fig. 4). Diaphragms similar to those in the zooecia are usually seen in some of the mesopores. The walls of the mesopores, like those of the zooecia, are locally broken by numerous gaps, a tendency particularly marked in macular centres.

The wall-tissue is less laminar and more granulated than in the two preceding species.

Remarks. This species provides an interesting problem in systematics. It differs from all previously described species of *Favositella* in the isolation of its zooecia by mesopore tissue and in the presence of acanthopore-like granules in its lunaria. In the first of these characters, as in its habit, it recalls species of *Ceramoporella*. On the other hand, the lunarial structures as seen in tangential sections are reminiscent of the tubules found in the lunaria of the Ordovician genus *Anolotichia*. However, in *Anolotichia* the maximum number of tubules in a lunarium appears to be seven, whereas in the present form there are often as many as twelve. Furthermore, in vertical section there is no indication that the tubules in this species have either the extension or the tabulated structure characteristic of those in *Anolotichia*. They can scarcely be regarded as tubules at all, and seem to have much more in common with the granules found in the walls of certain species of *Ceramoporella* (e.g. *C. granulosa* Ulrich 1890 : 466). This fact, considered in conjunction with the abundance of the mesopores, at first suggested that the correct reference of this polyzoan was to *Ceramoporella*. More detailed investigation showed, however, that the zooecial walls are frequently perforated by irregular pores—a feature, which has never been observed in species of *Ceramoporella*. Moreover, in many specimens the mesopores are found to exhibit the loose, vesicular character generally associated with those of *Favositella*. These and more general considerations finally left no doubt in the author's mind that this polyzoan was, in fact, like the commoner pearl-bearing forms, a species of *Favositella*, but one with a superficial resemblance to *Anolotichia* on the one hand, and to *Ceramoporella* on the other.

Although there is no doubt that this polyzoan agrees more closely with *Favositella* than with any other known genus of Ceramoporidae, the fact that it differs from all previously described species of that genus in having acanthopore-like granules in the frontal wall of the zooecium might have been taken as sufficient reason for regarding it as the type of a new genus or sub-genus. It is considered, however, that the wiser course is to include it in *Favositella*, at any rate until there is more proof that such acanthopore-like granules are of phylogenetic significance. The sporadic appearance of these or similar structures in isolated species of distantly related stocks suggests that they are of no more than specific importance. For example, acanthopore-like granules can be detected in the zooecial walls of *Crepipora lunatifera* Bassler (1911 : 88, fig. 27*d*), but have not been observed in other species of that genus. Again, analogous granules occur in the zooecial walls of some species of *Ceramoporella* (e.g. *C. granulosa* Ulrich 1890 : 466), but not in others. Tabulated lunarial tubules fall into a different category, since they are only found in species with a number of important characters in common, and their presence is therefore justifiably taken to indicate membership of a single generic group, to which the name *Anolotichia* has been given.

Favositella gotlandica sp. nov.

(Pl. 2, fig. 5; Pl. 5, figs. 4, 6; Pl. 9, figs. 1, 2)

HOLOTYPE. Brit. Mus. (Nat. Hist.), D. 33919; and D.33923 (thin-section); Upper Silurian (Gotlandian), Mülde-margelsten (=Lower Ludlow), Mülde Tile-factory, near Fröjel, Gotland. It consists of an encrustation on a shell of *Meristina tumida* (Dalman).

DESCRIPTION. Zoarium thin and encrusting; surface slightly uneven. Zooecial apertures regularly aligned, thin-walled and sharply rhomboidal in outline, with small, sharply elevated lunaria. On the average there are 4 zooecia in 2 mm. The zooecial tubes are sub-erect and contiguous. Small mesopores, having the appearance of punctations, occur sporadically at wall-intersections. Maculae, although sometimes slightly raised, are relatively inconspicuous; they are mainly recognizable by the local abundance of mesopores.

In sections the zooecial walls are remarkable for their uniform thinness throughout. Their average thickness is 0·02 mm. (compared with 0·05 mm. in the mature zone of *F. interpuncta* forma *typica*; 0·035 mm. in the forma *texturata* of that species; and 0·028 mm. in *F. squamata*).

In tangential section the zooecia show rhomboidal outlines with an average major axis of 0·6 mm., and an average minor one of 0·35 mm. in length. The frontal end of the zooecium is narrowly rounded and lined by an extremely narrow, crescentic lunarium which can only be observed in sections which pass very close to the surface. Mesopores are initially quadrangular, but their lumen has usually become rounded through the growth of auxiliary ectocyst.

The vertical section shows a single zooecial layer with an average thickness of 0·7 mm. The zooecial tubes curve obliquely upwards after a brief prostrate stage. The actual apertures are sub-direct. Mesopores are simple, short, and widen upwards. Small gaps in the zooecial walls can be observed in parts of the zoarium, and indicate the presence of mural openings. Diaphragms have not been observed.

REMARKS. This species is closely related to *F. squamata* (Lonsdale) from the Wenlock Limestone, the two resembling one another in the rhomboidal form of the zooecial apertures and in the comparative thinness of the zooecial walls. The present species is mainly distinguished from *F. squamata* by the smallness of its lunaria, by the more regular shape of the zooecial apertures, and by the curving obliquity of its zooecial tubes as seen in vertical section.

The horizon from which the holotype was collected is in Lindström's Division *c* of the Gotlandian formation; that is the Mülde-margelsten, which has been correlated by Hede (1921 : 87) with the Lower Ludlow beds of this country.

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PLATE 1

FIG. 1. Section of spherule with nucelus resembling polyzoan 'secondary embryo' (cf. Borg 1926 : pl. 14, 90). Taken from section of ***Favositella interpuncta*** (Quenstedt). ×420. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33702.

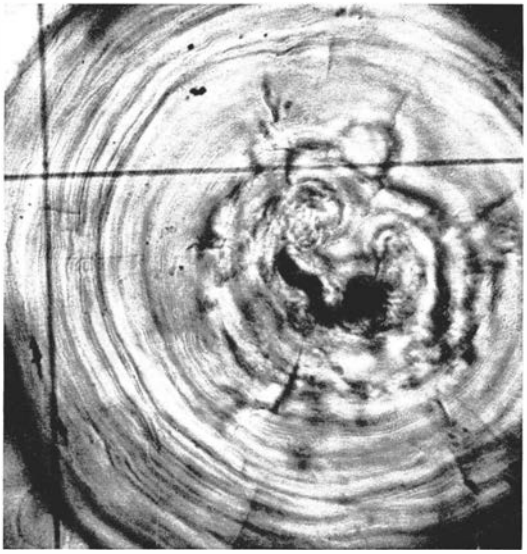
FIG. 2. Group of polyzoan pearls. × 50 (approx.). Extracted from specimen of ***Favositella interpuncta*** (Quenstedt) from Wenlock Limestone; Rumney. Brit. Mus. (N.H.) D.36473.

FIG. 3. ***Favositella interpuncta*** (Quenstedt). Vertical section showing typical position of pearl-like spherules within a zooecium. ×60. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33702.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Inferior aspect of Fig. 5, showing shell of *Loxonema* over which the polyzoan has grown.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Lateral aspect of 'drumlinoid' zoarium. ×1. Wenlock Limestone; Dudley. Holcroft Coll. 370, Geol. Dept., Birmingham University.

FIG. 6. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Lateral aspect of tumular zoarium with conical elevation, showing monticulose maculae; originally figured by Etheridge & Foord (1884, pl. 17, fig. 1). ×1. Wenlock Limestone; Dudley (erroneously catalogued as from Benthall Edge). Brit. Mus. (N.H.) R.1186.



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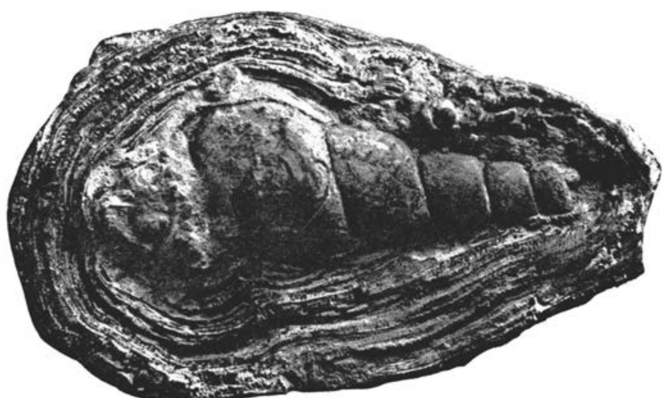

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PLATE 2

FIG. 1. ***Favositella interpuncta*** (Quenstedt). Lectotype. Lateral aspect. ×2. Wenlock Limestone; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Vertical section through 'drumlinoid' zoarium showing hollow base. ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33701.

FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Large tumular zoarium. ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.36340.

FIG. 4. ***Favositella squamata*** (Lonsdale). Inferior surface of zoarium showing epithecated marginal expansion. ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33711.

FIG. 5. ***Favositella gotlandica*** sp. nov. Holotype, zoarium encrusting shell of *Meristina tumida* (Dal.). ×1. Mülde-margelsten; nr. Fröjel, Gotland. Brit. Mus. (N.H.) D.33919.

FIG. 6. ***Favositella interpuncta*** (Quenstedt). Lectotype. Inferior surface showing corrugated epitheca. ×2. Wenlock Limestone; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

FIG. 7. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Zoarium encrusting shell of *Meristina tumida* (Dalman). ×3/2. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.

PLATE 2

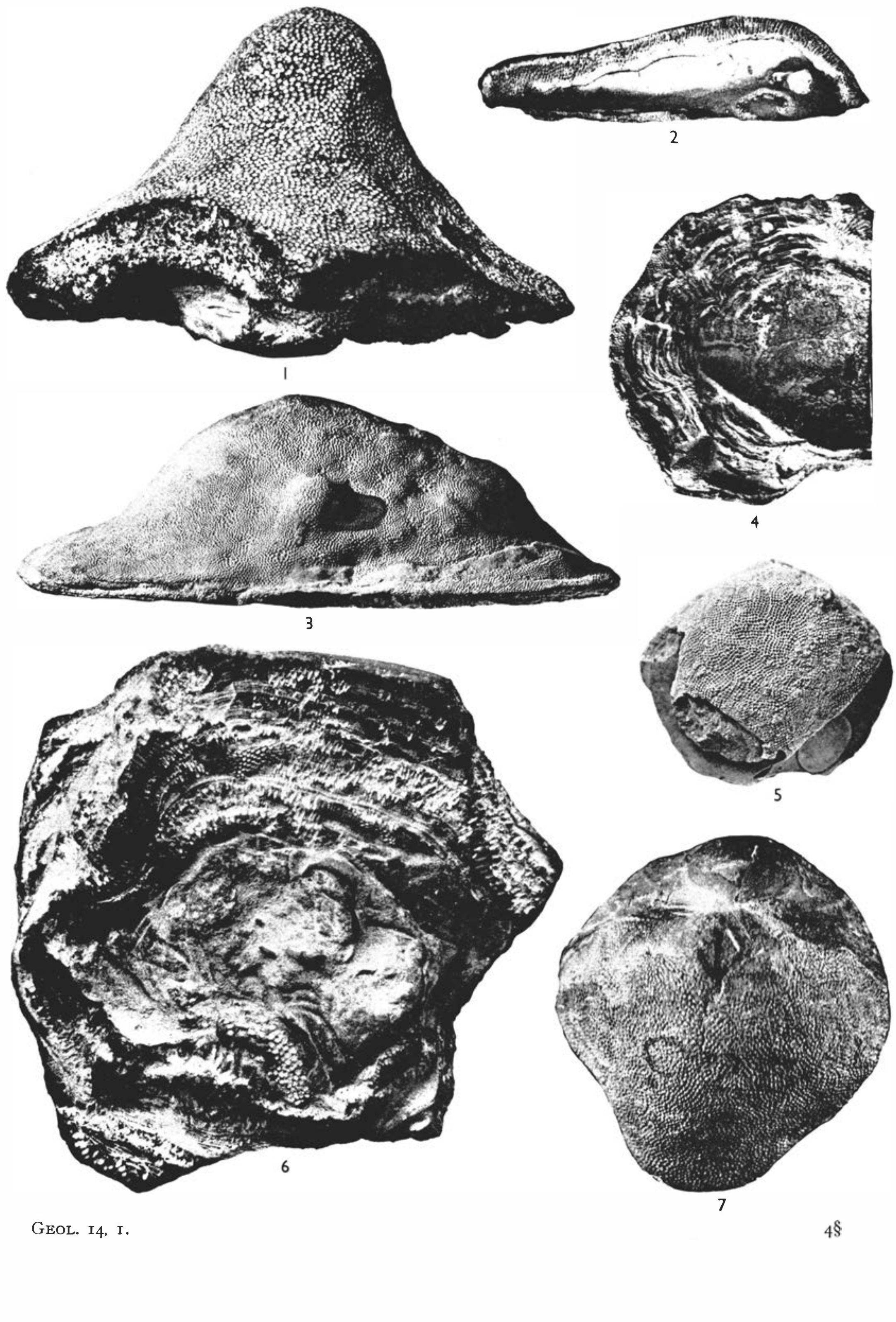

PLATE 3

FIG. 1. ***Favositella anoloticho ides*** sp. nov. Paratype $\times 4 \cdot 5$. Wenlock Limestone; Coate's Farm Quarry, Much Wenlock. Brit. Mus. (N.H.) D.36325.

FIG. 2. ***Favositella squamata*** (Lonsdale). Celluliferous surface of zoarium. $\times 2$. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) R.2592.

FIG. 3. ***Favositella anolotichoides*** sp. nov. Holotype. $\times 2$. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926*a*.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***intermedia***. Zoarium encrusting ramose coral. $\times 1 \cdot 5$. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.36339.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Zoarium encrusting shell of *Meristina tumida* (Dalman.). $\times 1$. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33715.

FIG. 6. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Tumular zoarium with several hollow maculae. $\times 2$. Wenlock Limestone; Dudley. Holcroft Coll. 570, Geol. Dept., Birmingham University.

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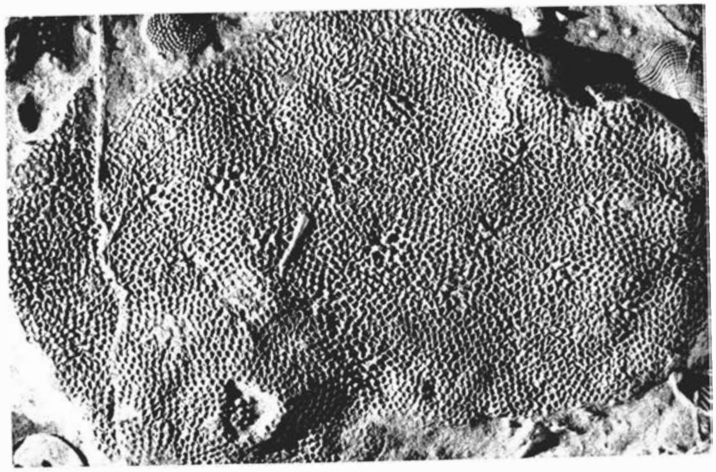

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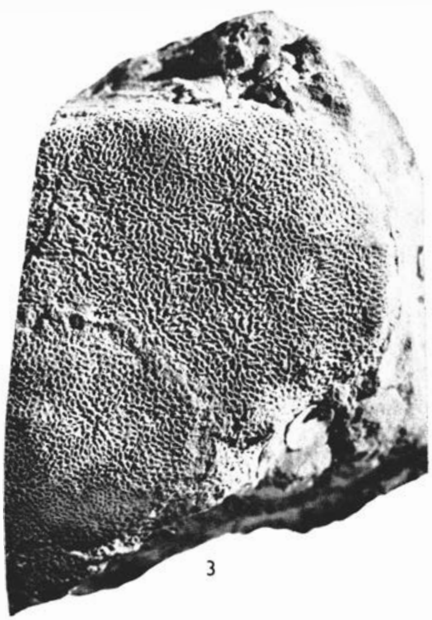

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PLATE 4

FIG. 1. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Tangential section. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33697.

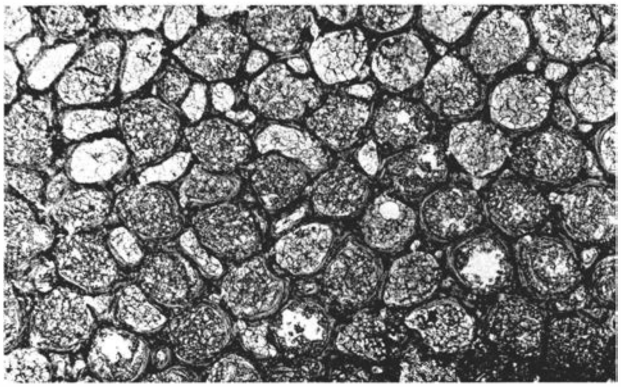
FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Tangential section. ×22. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.

FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***irregularis***. Tangential section showing transition from immature zone, with diagonal rows of quadrangular zooecia showing sagittate lunaria, to mature zone with rounded-polygonal zooecia of the typical forma. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33720.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Tangential section showing sagittate lunaria. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33672.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Tangential section passing through macular area in which numerous mural openings are evident. ×22. Wenlock Limestone; Ty Mawr Lane, Rumney. Brit. Mus. (N.H.) D.33686.

FIG. 6. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Tangential section. ×22. Wenlock Limestone, Basement beds of Lower Limestone; Daw End railway-cutting, Walsall. Brit. Mus. (N.H.) D.36337.



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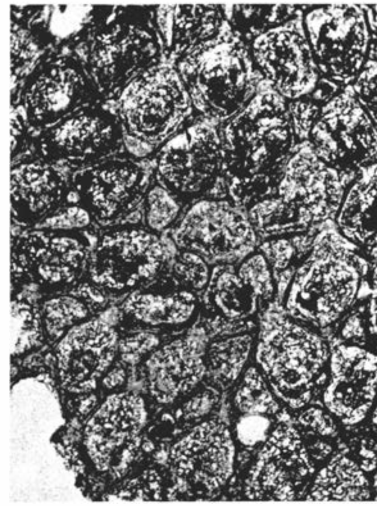

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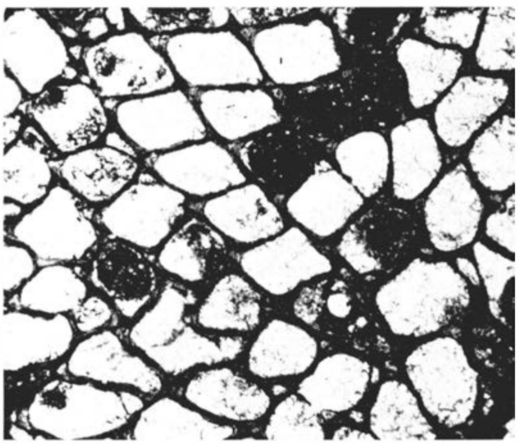

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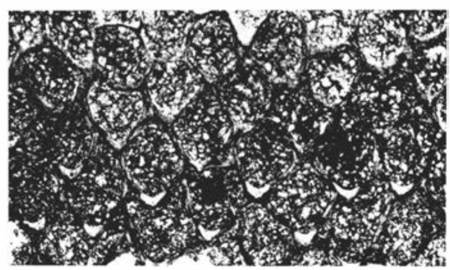

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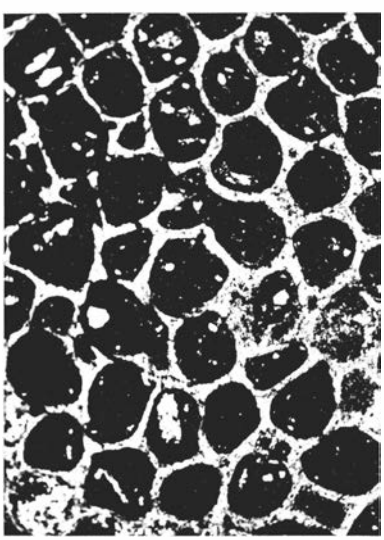

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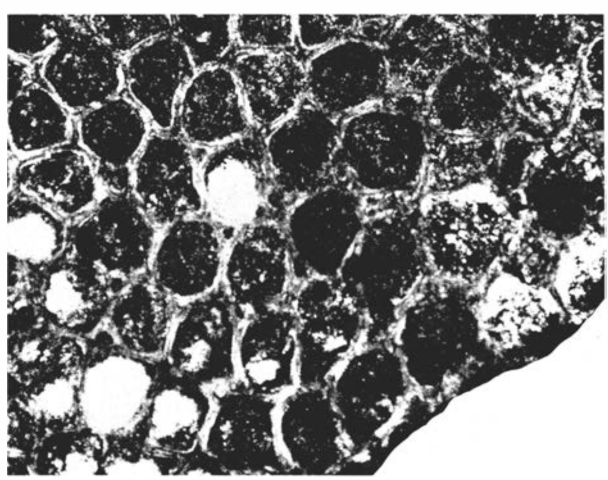

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PLATE 5

FIG. 1. ***Favositella squamata*** (Lonsdale). Transverse section through sub-ephebic level of zoarium. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33718.

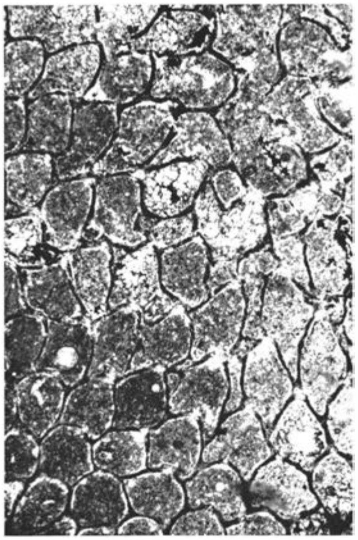
FIG. 2. ***Favositella anolotichoides*** sp. nov. Thin tangential section of holotype, showing acanthopore-like granules in lunarium. ×40. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926*c*.

FIG. 3. ***Favositella squamata*** (Lonsdale). Tangential section showing arcuate form of lunaria. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33714.

FIG. 4. ***Favositella gotlandica*** sp. nov. Sagittal section of holotype, showing narrow lunarium (l) and obliquely curving zooecia. ×22. Upper Silurian (Gotlandian); nr. Fröjel, Gotland. Brit. Mus. (N.H.) D.33923.

FIG. 5. ***Favositella anolotichoides*** sp. nov. Tangential section of holotype. ×30. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926.

FIG. 6. ***Favositella gotlandica*** sp. nov. Transverse section of holotype, showing dahllite pearls within the zooecia. ×30. Upper Silurian (Gotlandian); nr. Fröjel, Gotland. Brit. Mus. (N.H.) D.33923.



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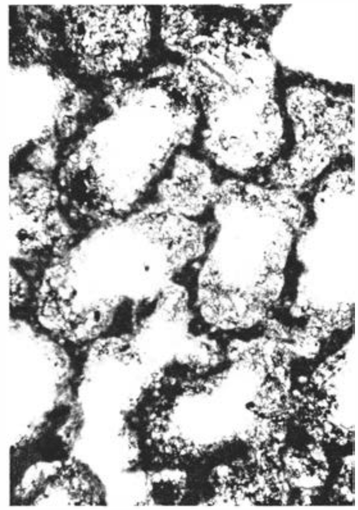

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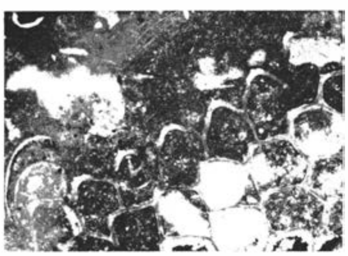

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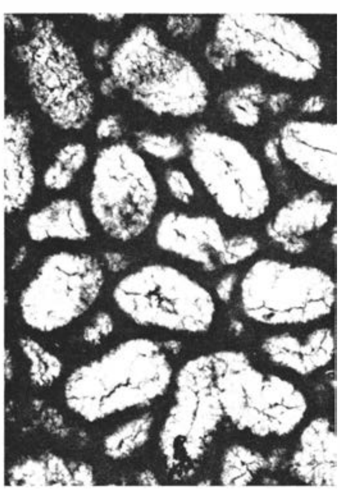

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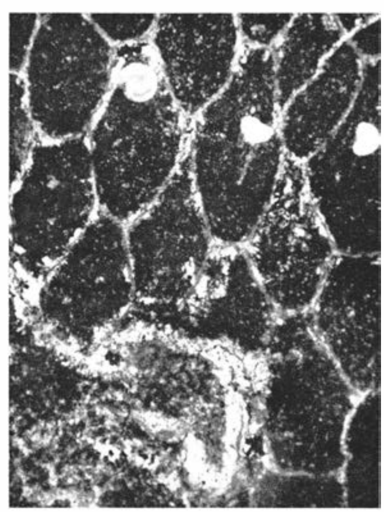

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PLATE 6

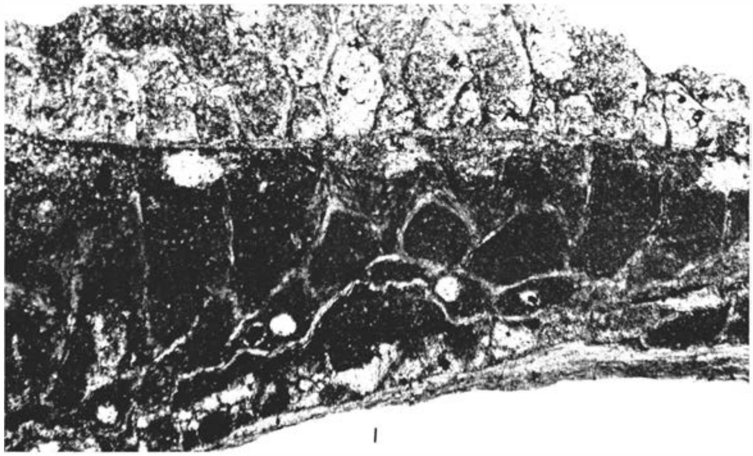
FIG. 1. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Vertical section showing two superimposed layers of zooecia. ×22. Wenlock Limestone, Basement beds of Lower Limestone; Daw End railway-cutting, Walsall. Brit. Mus. (N.H.) D.36338.

FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Vertical section showing two layers of zooecia. ×22. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.

FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Vertical section cutting prostrate bases of zooecia longitudinally. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33689.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***typica***? Vertical section showing contiguous zooecia with crenulate walls; a pearl is visible on bottom right of mid-line. The upper surface of the section is on the left. ×22. Wenlock Limestone; Ty Mawr Lane, Rumney. Brit. Mus. (N.H.) D.33696.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Vertical section through mature zone. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33696.



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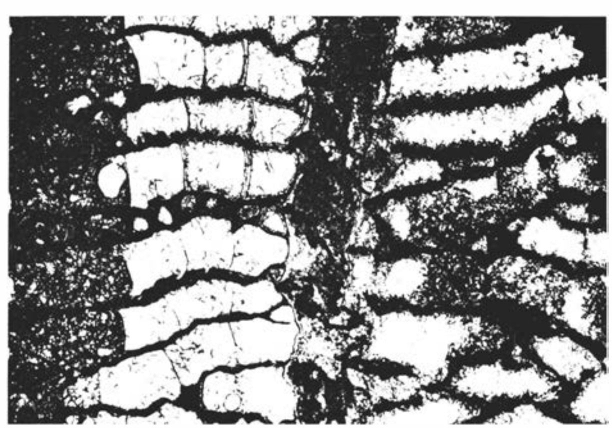

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PLATE 7

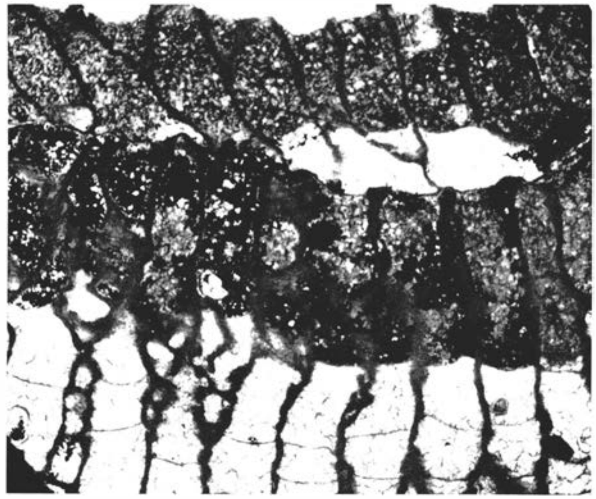
FIG. 1. ***Favositella interpuncta*** (Quenstedt) forma ***irregularis***. Vertical section of zoarium showing local rejuvenation of zoarial surface: layer of zooecia in ***texturata*** condition (cf. Pl. 7, fig. 2) overlying normally matured zooecia. ×20. Wenlock Limestone; Dudley. Sedgwick Museum, Cambridge. A5891*d*.

FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Vertical section. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33670.

FIG. 3. ***Favositella anolotichoides*** sp. nov. Vertical section of holotype, showing characteristic mesopores. ×30. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926*d*.

FIG. 4. ***Favositella anolotichoides*** sp. nov. Vertical section of holotype, showing unusually vesicular mesopores. ×22. Brit. Mus. (N.H.) D.33926*b*.

FIG. 5. ***Favositella squamata*** (Lonsdale). Vertical section through double-layered zoarium; in the lower layer the prostrate portions of the zooecia are cut longitudinally, in the upper, transversely. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33712.



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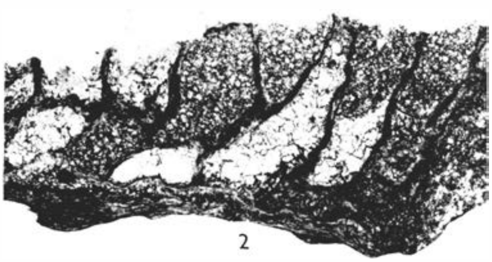

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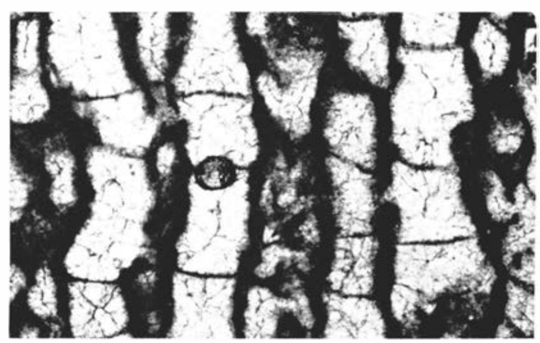

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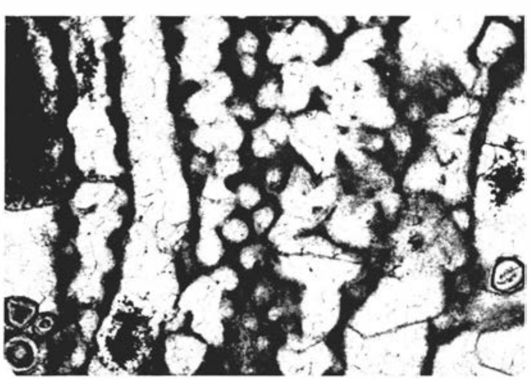

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PLATE 8

FIG. 1. ***Favositella interpuncta*** (Quenstedt). Lectotype. Typical portion of celluliferous surface showing rounded thick-walled zooecial apertures; hollow stellate macula in centre. ×10. Wenlock Limestone; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

FIG. 2. ***Favositella squamata*** (Lonsdale). Celluliferous surface of a typical zoarium; area with abundant mesopores and repressed lunaria in top right-hand corner. ×8. Wenlock Limestone; Dudley. Holcroft Coll. 517, Geol. Dept., Birmingham University.

FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Celluliferous surface. ×10. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33670.

FIG. 4. ***Favositella interpuncta*** (Quenstedt). Lectotype. Rejuvenated portion of celluliferous surface showing thin-walled, quadrangular zooecia with thin, hood-like lunaria; a macula is visible at the centre. ×10. Wenlock Limestone; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

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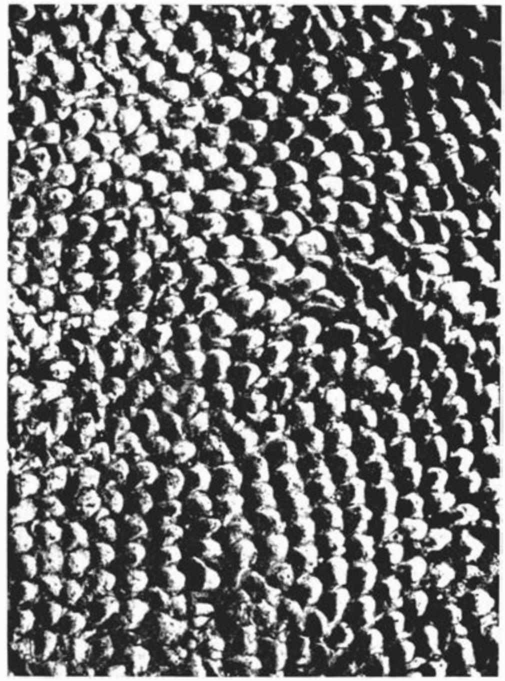

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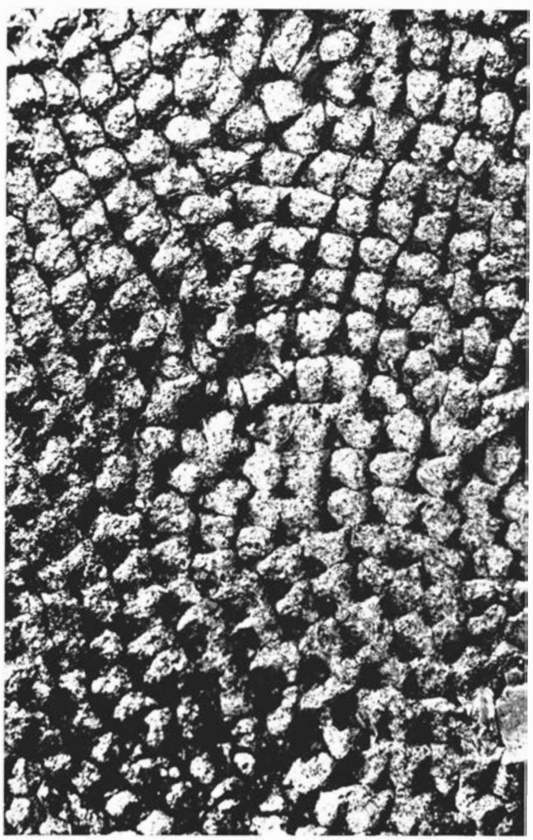

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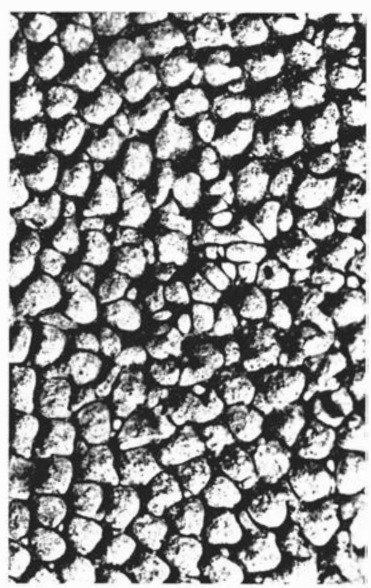

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PLATE 9

FIG. 1. ***Favositella gotlandica*** sp. nov. Celluliferous surface of holotype. ×6. Upper Silurian (Gotlandian) ; nr. Fröjel, Gotland. Brit. Mus. (N.H.) D. 33919.

FIG. 2. ***Favositella gotlandica*** sp. nov. Ditto. ×6.

FIG. 3. ***Favositella anolotichoides*** sp. nov. Celluliferous surface of holotype. ×5. Wenlock Limestone, Middle Nodular Beds ; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926.

FIG. 4. ***Favositella squamata*** (Lonsdale). Celluliferous surface. ×6. Wenlock Limestone; Dudley. Holcroft Coll. 182, Geol. Dept., Birmingham University.

FIG. 5. ***Favositella squamata*** (Lonsdale). Celluliferous surface of lectotype. ×4. Wenlock Limestone; Dudley. Geol. Soc. Coll. 6596, Geol. Surv. Mus.

FIG. 6. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Portion of surface of Pl. 3, fig. 6, enlarged to show hollow maculae (cf. brood-chambers in *Neofungella* ; Borg 1933 ; pl. 2 fig. 4). Wenlock Limestone ; Dudley. Holcroft Coll. 570, Geol. Dept., Birmingham University.

FIG. 7. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Celluliferous surface of zoarium (on reverse aspect of specimen illustrated in Pl. 2, fig. 7). ×4. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.

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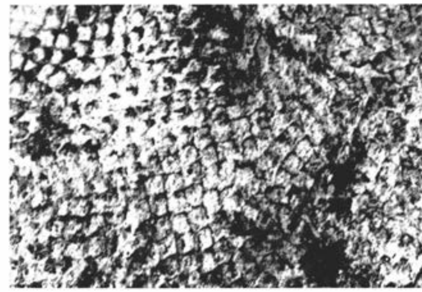

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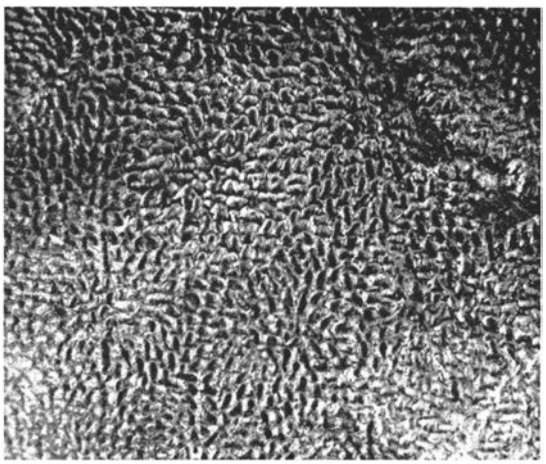

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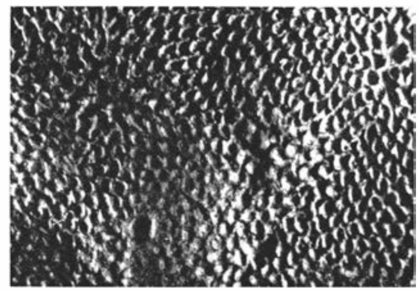

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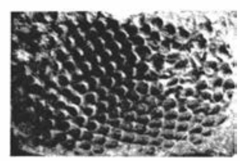

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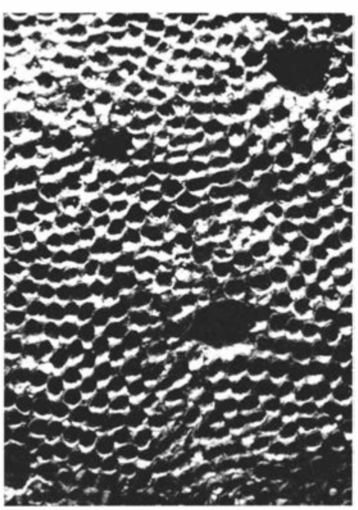

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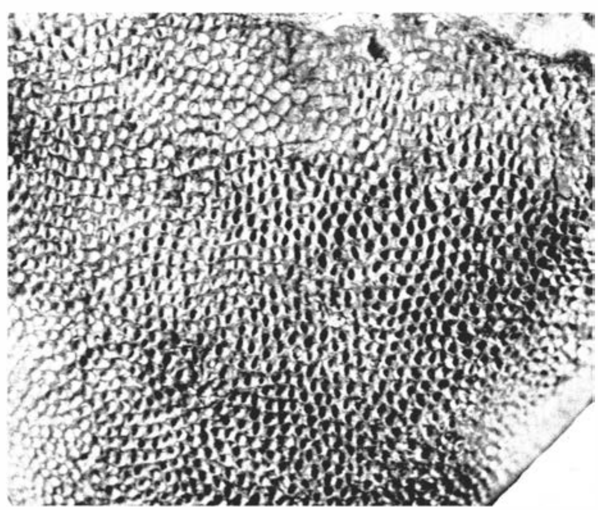

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