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By

O. A. JONES, M.Sc., F.G.S.,

and

DOROTHY HILL, M.Sc., Ph.D.,

Department of Geology, University of Queensland.

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(PLATES VI.–XI.)

CONTENTS.

I. Summary.

In this paper the Australian Heliolitidae are described. Only three genera occur in Australia—*Heliolites, Plasmopora,* and *Propora. Heliolites parvistella,* so important in Europe, is unknown in Australia, where the commonest species is *H. daintreei,* of which the European species *H. barrandei* is shown to be a synonym.

The genera of the Heliolitidae are reviewed, and from their morphology and micro-structure it is decided that the family is best regarded as a section of the Zoantharia Madreporaria, distinct from the Rugosa, Hexacoralla and Tabulata, but of equal rank to these sections. This section we call the Heliolitida.

II. Introduction and Terminology.

The terminology used for the Heliolitidae has depended on the systematic position assigned to them by the various authors, and as this has varied considerably some confusion has arisen. We define below, terms which can be applied to them without any implications on systematic position, or misapplications of terms used in other Anthozoa.

Tabularia.—The large tubes divided transversely by tabulae; the autopores of Nicholson; the calicular tubes, sometimes calicles, of Lindström; endothekalröhren of Kiär.

Reticulum.—The common tissue, sometimes vesicular, sometimes of polyhedric tubuli, between the tabularia; the coenenchyma of Edwards and Haime and Lindström.

Tubuli.—The small tubes of the reticulum; the siphonopores of Nicholson; the coenenchymal tubes of Lindström; exothekalröhren of Kiär.

Aureola.—The ring of tubuli, always twelve in number, which surrounds the tabularium in *Plasmopora*; aureola, corona, circlet of authors.

Testae.—The overlapping domed plates of the reticulum; the dissepiments of Edwards and Haime; vesicles of Nicholson; the convex laminae or lamellae of Lindström; blasen of Kiär.

Sola.—The transverse plates in the tubuli; the dissepiments of Edwards and Haime; the tabulae of Nicholson; the tabulae of the coenenchymal tubes of Lindström; boden of Kiär.

Commutation.—The coenenchymal gemmation of Lindström and others, whereby a number of tubuli give rise to a tabularium and *vice versa*.

Carina.—A flange on the side of a septum or wall.

III. The Genera within the Heliolitidae.

The earliest Heliolitids included both thickened and unthickened genera. The thickened forms all had their vertical skeletal elements very much dilated, the trabeculae being large and easily distinguished ("baculi" of Lindström); all loculi were practically filled by the thickening. Thus *Coccoseris megastoma* (McCoy, Lindström, 1899, p. 108, pl. xii., figs. 8-11) from the Caradocian Coniston limestone of Westmoreland is like a much thickened *Heliolites* with an infilled tubular reticulum; but in *Protaraea vetusta* (Hall,* Lindström, 1899, p. 111, pl. xii., figs. 19-24), another thickened form from the Trenton of America and Arctic America and the Wesenberg beds of Estland, the reticulum is almost absent. Kiär (1903, p. 12) regarded *Coccoseris megastoma* Lindström as belonging to *Acantholithus* Lindström, 1899; it seems to us that *Coccoseris* Eichwald (1860, genotype *Lophoseris ungerni* Eichwald, Lindström, p. 107, pl. xii., figs. 3-7) is congeneric with *Acantholithus* (genotype *Heliolites asteriscus* Roemer, Lindström, 1899, p. 113, pl. xi., figs. 31-35) the only difference being in the lesser dilatation of the vertical elements in *Acantholithus*. But we think it wiser to regard *Protaraea* as a separate genus since there is no good evidence that it has a tubular reticulum.

Propora Edwards and Haime (a genus with a reticulum consisting of testae, with spinose septa, and a more or less great development of discrete trabeculae throughout the tissue) appears to be the earliest of

* According to Troedsson (1928, p. 116) following Foerste, the Richmond specimens and the Scandinavian and Baltic specimens referred to *P. vetusta* by Edwards and Haime and by Lindström are not conspecific with *P. vetusta* Hall. Foerste proposed for them the new name *P. richmondensis.* Troedsson considered it probable that the true *vetusta,* thin sections of which have never been figured, was different generically from *P. richmondensis* and suggested that it might belong to *Protrochiscolithus* Troedsson. Bassler (1915, p. 1043), however, named *Porites vetusta* Hall non Edwards and Haime quite definitely as genotype of *Protarea,* by giving a bibliographic citation. Whether this selection should be maintained as valid, as against Troedsson's suggestion that the Richmond, Scandinavian and Baltic specimens (i.e., *P. richmondensis*) should be the type of *P. vetusta,* must be left until thin sections of the Trenton topotypes of *P. vetusta* Hall are figured.

the unthickened genera. An undescribed species occurs in the Caradocian Robeston Wathen limestone of Wales.

A form from the Trenton (?) of Arctic America (Iglulik Island) was described by Teichert (1937, p. 53, pl. iv., fig. 13; pl. v., figs. 1, 2) as *Plasmopora lambei* Schuchert, but judging by his figures and description it should be placed in *Propora,* with affinities to Edwards and Haime's species *P. conferta*. Troedsson's figures (1928, pl. 33, figs. 1a, b) of *P. lambi* Schuchert from the Cape Calhoun beds (Trenton or Richmond) of Greenland show a reticulum in which more than twelve radially elongate tubuli surround a tabularium, the walls of the tubuli frequently being discontinuous vertically. These Greenland specimens seem closer to *Heliolites* than to *Propora*, and it may be that they indicate a transition between the two genera. The specimens cannot be *Plasmopora* as there are more than twelve tubuli in the aureola. Another unthickened genus, *Protrochiscolithus* Troedsson (1928, p. 116, genotype *P. kiaeri* Troedsson *id.*), occurs in the Ordovician (Trenton or Richmond) Cape Calhoun beds of Greenland. It is like the central, unthickened portion of *Trochischolithus* Kiär, defined below, from the 5a and 5b beds of Norway. *Propora nummulosa* was described by Twenhofel (1928) from the Ordovician of Anticosti. Another Ordovician record is *Heliolites depauperata* Salter and Blanford (1865) from the Central Himalayas, of which we have seen neither description nor figure.

The greatest differentiation of the Heliolitids took place around the Baltic in the stages F1 and F2 of Estland, the *Leptaena* limestone of Sweden, and 5a and 5b of Norway*, followed by a world-wide development throughout the Silurian.

The unthickened genera *Proheliolites, Heliolites* and *Plasmoporella* made their first appearance in the F beds, the *Leptaena* limestone and/or the 5a beds, only the two latter and *Propora* continuing into later beds. *Proheliolites* Lindström (1899) is an unthickened form with little reticulum and, according to Lindström's description and figures, with septal spines directed proximally. *Heliolites hirsutus* Lindström (= *Nicholsonia megastoma* Kiär, 1899 = *Propora hirsuta* Kiär, 1903) is intermediate in some respects between *Heliolites* Dana and *Propora* Lindström, with a sparse reticulum like *Proheliolites* but with septal spines directed distally. *Heliolites* is also represented by two other species, *interstinctus* (Linnaeus) from the F of Estland and *parvistella* Roemer from the *Leptaena* limestone of Sweden, the F2 beds of Estland and the 5a and 5b beds of Norway. *Plasmoporella* Kiär (1899) (= *Camptolithus* Lindström, 1899) is like *Propora* but has highly domed tabulae and testae. Numerous species of *Propora* are abundant.

Of the thickened genera, *Coccoseris* and *Protaraea* which first occurred in the Ordovician persist to the end of this group of beds, when *Protaraea*, also known from the Richmond of North America, became extinct, while *Coccoseris* persists into the Valentian.

* The exact position of the boundary between the Ordovician and Silurian in the Baltic countries and North America is still under discussion, and the stage F of Estland, the *Leptaena* limestone of Sweden, the 5a and 5b beds of Norway and the Richmond of North America are placed by some in the Bala, by others in the Valentian. The position of the G1, G2, and H beds and the boundary between the Valentian and the Wenlock are also in doubt in the Baltic States. (See Troedsson, 1928, p. 181; O. T. Jones, 1928, p. 513; Ruger, 1934, p. 12; Reed, 1935, p. 371; Lamont, 1935, p. 303; Troedsson, 1936, p. 497).

Trochiscolithus (Kiär, 1903, genotype *Coccoseris micraster* Lindström, 1899 = *Palaeopora inordinata* (Lonsdale), Kiär, 1899), a genus sometimes massive, sometimes ramose, shows little thickening in the earlier portions of the colonies but much thickening elsewhere and has sparsely perforate walls and septa (see Kiär, 1903, pp. 13-29, figs. 1, 2 on p. 15; figs. 3, 4 on p. 17; figs. 5, 6 on p. 19; fig. 7 on p. 21). It is confined to this group of beds. The perforation of its walls was denied by Lindström, 1903, but is in our opinion definite and of the type seen in perforate Hexacorals, and not like the mural pores of *Favosites*. *Diploepora* Quenstedt which first occurred in these beds also is thin walled in the early stages, which closely resemble *Propora*, and thick in the later, but it is not perforate; it continued into the Ludlovian. *Palaeoporites* Kiär (1899, genotype *P. estonicus* Kiär, *id.*, p. 18) which is confined to this group of beds is highly perforate and thickened throughout; judging by Kiär's figures the trabeculae are rhabdacanthine and combine at the axis of the tabularium to form an axial structure, while the reticulum consists of tubuli with highly perforate walls.

The unthickened genus *Plasmopora* Ed. and H. (genotype *P. petaliformis* Ed. and H.) makes its first appearance with *P. stella* Lindström in G1 of Estland. It is like *Heliolites*, but the septa are continuations of the walls of the twelve tubuli around the tubularia, and the tubuli walls are usually discontinuous vertically. *Propora conferta* occurs in G1, G2, and H of Estland. Stratum *a* (*Arachnophyllum* bed) which is at or near the top of the Valentian in Gotland, contains *Coccoseris asteriscus* (highest record of this genus), and several species of *Propora*, *Plasmopora* and *Heliolites*, while *Cosmiolithus* Lindström (1899, which is like *Heliolites* but has tubuli of two sizes in the reticulum) makes its first appearance here. In Norway *Heliolites intricatus* Kiär and *Propora intercedens* Kiär occur in stage 6. *Plasmoporella* is figured (Yoh, 1932, p. 69) from the Valentian of China.

In Lindström's beds b-d of Gotland (= Wenlock of England) species of *Heliolites*, *Plasmopora*, *Propora*, and *Diploepora* are abundant, *Cosmiolithus* makes its last appearance and *Pycnolithus* Lindström (1899, genotype *P. bifidus* Lindström) occurs. This genus, founded upon one detached specimen from the shore near Visby but probably from b or c, has radially elongated tubuli with much thickened walls and bifid septa. In the Niagaran of America the genera *Heliolites*, *Plasmopora* and *Propora* are common and *Plasmoporella* Kiär (= *Camptolithus* Lindström) makes its final appearance. In beds e-h of Gotland (= Ludlow) species of *Heliolites* and *Plasmopora* occur, and *Propora* and *Diploepora* have their last occurrences. In Norway *Propora intercedens* occurs in stage 9. *Plasmopora* and *Propora* both occur in the Gotlandian of Korea (Shimizu, Ozaki, and Obata, 1934) and *Heliolites* in the Silurian of China (Grabau, 1925), and Indo-China (Mansuy, 1920). In Spiti, India, *Propora* occurs (Reed, 1912).

The variety of forms is greatly reduced in the Devonian though at certain localities particular species are very common. No Heliolitid is known later than the Givetian. *Heliolites* occurs throughout the Lower and Middle Devonian of Europe and is rare in the Devonian of America and Asia, while *Plasmopora* has been recorded from the Middle Devonian of the Carnic Alps, and Australia. *Paeckelmannopora* Weissermel (1939, p. 94, pl. 11, figs. 3-5) from the Gedinnian near Istanbul resembles *Plasmopora* in having tabularia with tabulae, and tubuli with discontinuous walls and sola, but differs in that the tabularia have twelve longitudinal corrugations which Weissermel considers represent the septa, although no lamellae or spines are present; further the tubuli around each tabularium number more than twelve.

IV. The Microstructure of the Vertical Skeletal Elements.

(*a*) *The Trabeculae.*—The vertical skeletal elements are trabeculate throughout the family. Monacanths and rhabdacanths (Hill, 1936, p. 197) occur, though the latter are uncommon, being found only in *Plasmoporella papillatus* (Rominger), in *Palaeoporites* Kiär, and sporadically in individuals of several species of *Propora,* viz., *tubulata, conferta, speciosa,* and *bacillifera.* In the Heliolitida rhabdacanths are not associated with lamellar sclerenchyme as they are in the Rugosa. The walls and septa of *Heliolites* are of thin monacanths very closely packed except in the septa of *daintreei* and *porosus* where their axial parts are free spines. The inclination of the monacanths varies in the different species. In *interstinctus* they are inclined at an angle of 40° from the vertical; in the septa of *porosus* they make an angle of about 45°; in *daintreei* and its variety *spongodes* the septal spines are curved, and in the wall the monacanths are inclined at 30° from the vertical; in *parvistella* and its variety *intricatus,* and possibly in *fasciatus* the monacanths seem from Lindström's figures to be vertical in both septa and walls; in *liljevalli* it would appear that the monacanths in the walls are vertical but those of the septa are inclined at 30° from the vertical; in *repletus* the inclination is 20°. In *Cosmiolithus ornatus* the monacanths in the septa are inclined at 30°.

In *Plasmopora* also the septa and walls both consist of thin monacanths, whose inclination from the vertical is greater in the septa than in the reticulum. In this genus any monacanth may be extended laterally to form a carina, usually on one side only of a septum, occasionally on both sides; but the carinae* may be localised on the septa, in the aureola, or in the reticulum, and are yardarm or xyloid. In some species of *Plasmopora* the walls are vertically continuous as in *Heliolites,* but in many they are discontinuous and the monacanths are short and, while still arranged in vertical series, become normal to the curvature of the testae rather than keep their original inclination in the walls. These monacanths, normal to the testae, are the "aculae" of Lindström. The monacanths are of the order of 0·05 to 0·1 mm.

In *Propora* and *Plasmoporella* there are no continuous walls in the reticulum and the vertical skeletal elements consist of free trabeculae which are usually monacanths and are normal to the testae, are usually profuse and seldom in vertical series, and have a wide range in diameter and length. Lindström referred to the trabeculae under three names—"baculi," with radiating fibrous structure, a diameter of about 0·15 to

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* Carinae may be parallel to the trabeculae or parallel to the growing edge of the septum. When parallel to the trabeculae they may be opposite—yardarm, e.g. *Heliophyllum* (see Hill, 1935, text figs. 15H, I.) or sub-opposite—xyloid, e.g. *Xylodes* (see Smith and Tremberth, 1929, pl. viii., figs. 3, 4) as seen in transverse section. When parallel to the distal edge of the septum they are cymatoid, e.g. *Cymatelasma* (see Hill and Butler, 1936, p. 522, text fig. 4). Yardarm and xyloid carinae are each formed by extensions of the fibres of one trabecula; cymatoid carinae on the other hand consist of a series of trabeculae. Xyloid and cymatoid carinae both make the septa appear zig-zag in transverse section.

0·2 mm. and a length of from 0·16 to more than 3 mm; "bacilli," in which he could observe no structure, with a similar diameter and length; and "aculae," very short and with a diameter of about 0·05 to 0·1 mm. in which he described no structure. In the septa the trabeculae are usually monacanths, and they are inclined as in *Plasmopora* and *Heliolites.*

Throughout the family Heliolitidae, thickened tissue consists of dilated monacanths, with the single exception *of Palaeoporites,* in which rhabdacanths are dilated. Both Lindström (1899, p. 104) and Kiär (1903, p. 37) considered that thickened genera arose from thin ones. It is difficult for us to form an opinion as we have not had the opportunity of examining specimens of some of the genera, but their view is contrary to our observations on other corals, in which in general, thickened forms give rise to unthickened.

Lindström and Kiär both consider that in *Proheliolites* the septal trabeculae are directed downwards at an angle of about 45° from the horizontal—a condition without a known parallel in the whole of the Anthozoa.

(*b*) *Discontinuity of the Vertical Elements.*—Whereas in *Heliolites* the walls in the reticulum are continuous both vertically and horizontally, in *Plasmopora* discontinuity occurs, such that segments of the walls stand on testae, each segment containing more than one monacanth. In transverse section these segments, combined with cut edges of testae, frequently give an appearance of complete tubuli. It is possible that a somewhat similar discontinuity seen in the tubuli walls in *Heliolites hirsutus* and in *Proheliolites dubius* may be connected in some way with the rapid change of the tubuli into tabularia and *vice versa*. As explained above the absence of walls in the reticulum of *Propora* is due to the complete and sometimes distant separation, one from another, of the individual trabeculae.

Perforation exactly similar to the perforation of the vertical skeletal elements in the perforate Hexacoralla and Rugosa, occurs in the Heliolitida, profusely in *Palaeoporites,* and rather rarely in *Trochiscolithus* and *Protrochiscolithus.*

V. Increase.

As in all compound coralla, the protocorallites of Heliolitid colonies must have arisen from planulae, after sexual reproduction. Lindström (1899, pp. 19-23, 45-47) distinguished three methods of asexual reproduction. His "coenenchymal" gemmation is well illustrated by his figures (1899, pl. i., figs. 21, 32, 33; pl. ii., fig. 37; pl. iii., fig. 27) and by those of Sardeson (1896, figs. 7-9), which show that tabularia may originate from a number of tubuli by the disappearance of the walls, and that also tabularia may be replaced by tubuli by the growth of dividing walls. This type of increase we propose to call commutation*; it possibly corresponds to differentiation and dedifferentiation in the soft parts, and may occur in Hexacorals such as *Turbinaria* (unpublished work by Edgar Riek, of the University of Queensland); a somewhat similar process takes place in the Alcyonarian *Heliopora* where a number of small "pores" give rise to a large "pore." Lindström's "intracalicinal" gemmation does not seem clear to us from his description and figures, and his "epithecal" gemmation may well be a special case of "coenenchymal gemmation."

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* Commuto—to interchange.

Multiplication of the tubuli takes place by the growth of new divisional walls; a solitary carina may arise on any wall and by continued growth bisect the tubulus. This multiplication is similar to "fission" in *Chaetetes* and is quite different from the mode of increase in the Favositidae, which is intermural and at the angles. The growth of young corallites in *Favosites* is well illustrated in Jones (1936, text-figs. i.-xii.).

VI. Systematic Position of the Family.

(*a*) *Historical*.—The Heliolitidae have been classed at various times as Hydrozoa, Alcyonaria, Tabulata, Rugosa, Hexacoralla, a separate section of the Madreporaria, Tubocoralla, and as part of a new sub-class of Anthozoa, the Schizocoralla.

Linnaeus (*fide* Lindström, 1899, p. 38) made the first mention of a Heliolitid in literature, when (in 1745, p. 30) he referred a Gotlandian species to *Millepora*; but later (1767, p. 1276) he separated this species from *Millepora*, which has since been accepted as a Hydrozoan, and placed it with the corals, under the name *Madrepora interstincta*. Goldfuss (126, p. 64) likewise considered an Eifelian species to be a coral, *Astraea porosa*. Blainville (1830, p. 357) put this Devonian species in a new genus *Heliopora*, with *H. coerulea* of recent seas. Lonsdale (1839, p. 686) referred a number of Silurian species to *Porites* Lamarck. Dana (1848, p. 541) regarded the Palaeozoic and recent species of Blainville's *Heliopora* as distinct genera, and proposed *Heliolites* with type *Astraea porosa* Goldfuss for the Palaeozoic forms. About the same time McCoy recognised differences between the Palaeozoic and recent *Porites*, and proposed *Palaeopora* for the Palaeozoic species (1849, p. 129, no species mentioned; 1850, p. 276, only species mentioned, *Palaeopora subtilis**).

D'Orbigny also noted the differences between the Palaeozoic and recent forms and proposed for the former, first *Lonsdalia* (*fide* Lindström, 1899, p. 38) and later, probably because *Lonsdaleia* was pre-occupied, *Geoporites* (1850, p. 49). However, the priority of Dana's genus was quickly recognised and Edwards and Haime, in their classification of the Coelenterata (1850, p. lviii.) included Dana's genus in their new sub-order Zoantharia tabulata—corals in which the entire lumen is occupied by a tabularium, and in which the septa are rudimentary, and do not show a pinnate arrangement.

In 1876 Moseley recognised the Alcyonarian affinities of *Heliopora*, with which *Heliolites* has usually been compared. *Heliopora*, like the other Alcyonaria, has eight tentacles and eight mesenteries, the muscles being on the sulcar side of the mesenteries. Nevertheless, the skeleton of *Heliopora* is fibrous and trabecular as in the Madreporaria, not spicular like the rest of the Alcyonaria. Moseley regarded *Heliopora* as a dimorphic Alcyonarian, suggesting that the small tubules were modified zooids, siphonozooids, and the larger, autozooids. He accepted the affinity of the Heliolitidae with *Heliopora*, and concluded that all the Tabulata of Edwards and Haime were Alcyonaria; consequently, that the Heliolitidae were dimorphic. Nicholson (1875, p. 248) had previously expressed the view that *Heliolites* was dimorphic, and following Moseley's work, he placed this genus in the Alcyonaria (1879, p. 25).

* It is, however, doubtful if this species, which must be taken as the genotype of *Palaeopora*, is a Heliolitid.

These observations caused a flood of speculation on the possible Alcyonarian affinities of *Heliolites* and even of other genera of Edwards and Haime's Tabulata. Sardeson (1896) and Zittel (1900) followed Nicholson in placing *Heliolites* in the Alcyonaria. But Bourne (1895), after detailed studies on *Heliopora* concluded that neither was dimorphic, but that the coenenchymal tubules of *Heliopora* were part of a complex system of solenia. Nevertheless, he retained them in the Alcyonaria. Romer (1883, p. 500), Neumayr (1889, p. 326), Weissermel (1937, p. 93), and Wentzel (1895) considered the Heliolitidae to have no relation to the Helioporidae, leaving them as an isolated family of the Tabulata.

Lindström (1876, 1899a, 1899b) and Kiär (1899, 1903) have made outstanding studies on *Heliolites* and its allies. Lindström in 1876 (p. 15) placed *Heliopora* in the Alcyonaria but argued against any affinity between *Heliolites* and *Heliopora*. He created a special family for the former together with *Plasmopora* (including *Propora*), *Lyellia, Calapoecia, Thecostegites Halysites,* and *Thecia.* In 1899 he removed *Calapoecia, Thecostegites, Halysites,* and *Thecia* from the Heliolitidae and made two sub-families of the latter—the Heliolitidae with the genera *Heliolites, Cosmiolithus, Proheliolites, Plasmopora, Propora, Camptolithus, Diploepora* and *Pycnolithus,* and the Coccoseridae with the genera *Coccoseris, Protaraea,* and *Acantholithus.* He reiterated that he saw no affinity to *Heliopora* and no affinity with any other Palaeozoic corals. He did not discuss the possible affinity to the Hexacoralla. Kiär (1899, p. 49) considered the similarity of *Heliolites to Heliopora* to be homeomorphic only, and placed the Heliolitidae as a family of his Zoantharia Madreporaria (in which he appeared to include only Rugosa, Hexacoralla, and Heliolitidae). He thought them distinct from the "isolated group of the Tabulata." He gave a different grouping of the genera into sub-families.

Some authors—e.g. Gerth (1908)—have pointed out the morphological similarity between the Heliolitidae and many of the Hexacorals (especially *Seriatopora, Stylophora and Pocillopora*), and have regarded the former as the ancestors of the latter. The genera which Gerth studied were those grouped as the Madreporaria Tubocoralla by Steinman (1907). Zittel (1900) placed the Heliolitidae in the Alcyonaria. Woods (1926) considered that the systematic position of the "Tabulate Corals," in which he placed the Heliolitidae, was not yet satisfactorily established. Okulitch (1936) recently united the Heliolitidae with the Tetradidae and Chaetetidae in a new subclass, the Schizocoralla, the diagnostic characteristics being given as (1) increase by fission and (2) absence of true septa. But, in the Heliolitidae, only the tubuli of the reticulum increase by fission and true septa are present. Weissermel (1937, p. 93), in a review of Okulitch's work, criticised his grouping of families and summarised the evidence for regarding the Heliolitidae as Tabulata, which he considered a valid group.

(*b*) *Comparison with Other Groups.*—The elucidation of the affinities of the Heliolitidae is rendered all the more difficult as their soft parts are quite unknown, whereas three of the groups to which they have been referred are classified on soft parts almost entirely; further the relationship of the hard parts to the soft parts in groups where both are known is not always made clear by writers. Again, structural similarities in forms of such widely separated ages as Devonian and Present are very likely to be due to homeomorphy, not to generic affinity, when no clear links are known

(1) *Alcyonaria.*—

The Alcyonaria are Actinozoa with eight mesenteries and eight pinnate tentacles; the stomodaeum has a single siphonoglyph (ciliated groove); the skeleton is internal, consisting of spicules in the mesoglaea, occasionally supplemented by an external skeleton; the longitudinal muscles are on the ventral faces of the mesenteries (Potts, p. 180, in Borradaile and Potts, 1935).

The Alcyonarian with which *Heliolites* has been frequently compared is *Heliopora* Blainville (Plate XI., fig. 6). Its soft parts leave no doubt that it is Alcyonarian; but, were the skeleton alone known, it would almost certainly be placed with the Madreporaria, being trabeculate like that of the Madreporaria, not spicular as in other Alcyonaria. Each trabecula consists of fibres directed upwards and outwards. Both skeletons consist of two sizes of vertical tubules, both of which are divided by horizontal plates. A detailed comparison, however, immediately brings out important differences. In *Heliopora* one to five vertical trabeculae occur massed together to form a pillar at the point where more than two tubules meet, and the walls between the tubules consist of continuations of fibres from the pillars at the corners. There is never a trabecula in the wall between two tubules, they are always massed at the point of junction of three or more.* The "pseudosepta" of the tubes consist of several vertical trabeculae, so closely placed in series that their fibres cannot be differentiated. In *Heliolites* the wall between two tubuli does not differ in structure from the wall at the point of junction of more than two tubuli; the walls consist everywhere of trabeculae, curved, inclined, or rarely vertical, the fibres of the trabeculae radiating obliquely upwards and outwards. The septa have a similar structure to the walls, being built up of a number of curved or inclined trabeculae. Thus in *Heliolites* the septa and walls consist of regularly spaced trabeculae, usually inclined, while in *Heliopora* all the trabeculae are vertical, and in the "coenenchyma" are massed into pillars at the point of junction of three or more tubules.

In *Heliolites* the trabeculae of the septa may be in contact, so that the septa are lamellar as in *H. parvistella*, or free axially—i.e. acanthine —as in *H. daintreei*. Both monacanthine and rhabdacanthine types (Hill, 1936, figs. 14, 15) occur, but in *Heliopora* the trabeculae of the "pseudo-septa" are always in contact so that the "pseudo-septa" are always lamellar and never spinose. Many writers have considered that the radial plates of *Heliopora* differ from the "true septa" of the Rugosa and Hexacoralla and hence have termed them "Pseudosepta." It is difficult to discover in their writings any clear reasons for this differentiation, which appears to be based on the idea that the septa of the Rugosa and Hexacoralla arose later than, and independently of, the "theca" (i.e., the wall), whereas the "pseudosepta" of *Heliopora* are continuations into the tabularium of the walls of the small tubes and thus are an integral part of the walls. This argument is based on a misunderstanding of the micro-structure of the skeleton and of the manner in which it was formed by the soft parts. It is clear from the description and figures above that the radial plates in both *Heliopora* and *Heliolites* have a trabecular structure as in the vertical skeletal elements of all Rugosa and Hexacoralla; but whereas in *Heliopora* the

* This differs somewhat from the micro-structure described and figured by Bourne (1899, pp. 517-524, figure on p. 523).

septal trabeculae are vertical, in *Heliolites,* as in the Rugosa and Hexacoralla, they are inclined. We remain in doubt if this difference is sufficient to justify the use of the prefix "pseudo."

In the Anthozoa much classificatory importance has been attached to the mode of insertion of the septa, and the number, insertion, and arrangement of the mesenteries. Thus the Rugosa are distinguished by the pinnate insertion of the septa (in fours) and the Hexacoralla by the cyclical insertion of the septa and mesenteries, the cycles being six or multiples of six. Hickson (1924, pp. 31, 32) has suggested that the Hexacoralla may be divided into two groups—group B, one in which twelve mesenteries are developed—and the other, group A in which more than twelve appear. When small numbers of mesenteries are involved the number of septa usually corresponds to the number of mesenteries, but such a correspondence is not invariable when the numbers are large. In the Actinians no such easy generalisation in number of mesenteries and septa can be made.

The Alcyonaria are distinguished by eight mesenteries. In *Heliopora* while there are always eight mesenteries, the number of septa (or pseudosepta) varies but is usually between ten and sixteen (according to Lindström, sometimes seventeen) although according to Moseley the most common number is twelve. *Heliopora* is apparently the only Alcyonarian with radial vertical plates which might be compared with septa. This lack of correspondence in the number of septa and mesenteries has also been used as an argument for terming them "pseudosepta," but it appears to us possible that they represent two incomplete cycles of eight. It should be kept in mind that little is known regarding the insertion of septa in hystero-corallites of compound Rugosa and Hexacoralla, but it seems possible that the basic plan of insertion might be masked in such types (e.g., see Smith and Ryder, 1927, pp. 339-342, text fig. 2).

In the Heliolitidae, when septa are present they are invariably twelve in number. There is a strong contrast here with the variability in *Heliopora*; and the fixity of twelve in the Heliolitidae suggests comparison with the Madreporaria rather than the Alcyonaria and in particular with Hickson's Group B of the Hexacoralla (1924, p. 32).

The question of dimorphism in *Heliopora* is one which has been much discussed since first postulated by Moseley (1876) but it still remains unsettled, some text-books following Moseley's theory of dimorphism, others adhering to the views of Bourne (1895) that the "coenenchyme" viewed by Moseley as siphonozooids is in reality a complex system of solenia (i.e. a canal system with extensions downwards into the small tubes but no openings to the free surface). Nicholson (1879, p. 25) and others, accepting dimorphism in *Heliopora,* argued by analogy that *Heliolites* was dimorphic, and therefore, an Alcyonarian. Professor Hickson, the British authority on Alcyonaria, says (*in litt.*): "As regards the dimorphism of *Heliopora*; it is not dimorphic and there is no clear evidence that it ever was dimorphic." Accepting this view of Bourne and Hickson, Nicholson's argument based on dimorphism is invalid.

Thus we consider the Heliolitidae differ from the Alcyonarian *Heliopora* in the general arrangement of the trabeculae, and in having a fixed number (12) of septa; and that for the same reasons they cannot be Alcyonaria.

(2) *Zoantharia.*—

The Zoantharia are Anthozoa with mesenteries varying greatly in number, typically arranged in pairs, the longitudinal muscles of which face each other except in the case of two opposite pairs, the *directives*, in which the muscles are on opposite sides; the tentacles are usually simple, six or some multiple of six in number, and the mesenterial filaments are trefoil-shaped in section; the stomodaeum has two ciliated grooves; typically there is a calcareous exo-skeleton, but this may be entirely absent.

The Zoantharia are divisible into the Actinaria (sea anemones) which are usually single individuals always without a skeleton, and the Madreporaria, usually colonial, always with an ectodermal exo-skeleton.

To the present-day biologist, the Hexacoralla are Madreporarian, but the soft parts of Rugosa and Tabulata being unknown, these sections are given but little space in zoological classifications. To Edwards and Haime, the Rugosa and Tabulata were also Madreporarian. Not knowing the soft parts of Rugosa and Tabulata, we cannot be sure that they are Madreporaria, but the possession of an exo-skeleton which is trabeculate, septate and tabulate, as in the Hexacorals, indicates affinity with the Madreporaria. The Rugosa, Hexacoralla, and Tabulata will all be included herein as sections of the Madreporaria.

(*a*) *Hexacoralla.*—Madreporaria in which the pairs of mesenteries and the septa are inserted in cycles which are six or multiples of six.

In the Heliolitidae we have no information on the mesenteries; but in both Heliolitidae and Hexacoralla all the vertical skeletal elements consist of vertical series of curved, inclined, or rarely vertical trabeculae. The septa of Heliolitidae are constantly twelve, and there is a group of Hexacoralla recognised by Hickson (1924, p. 32) in which the septa number six or twelve; in this group, however, when twelve occur, they are divisible into a primary and secondary cycle, according to their length and period of insertion. In the Heliolitidae there is no good evidence that the twelve septa are divided into two cycles, although Lindström (1899, p. 55) has suggested that such is possible in *H. porosus*.

In the Heliolitidae there is a reticulum which may consist of trabeculate polyhedric tubes crossed by sola, or of testae supplemented by further free trabeculae. In the Hexacoralla a common tissue frequently occurs; it may consist of dissepiments supplemented by trabeculae, as in *Cyphastraea,* or of dilated trabeculae as in *Pocillopora* and *Stylophora,* which both belong to Hickson's group characterised by six or twelve septa; or it may be compact or spongy.

Thus there is very close morphological similarity between the Heliolitidae and Hickson's group B, but absolute identity is spoiled because the twelve septa of the Heliolitidae are not divisible into two cycles of six.

(*b*) *Rugosa.*—Madreporaria in which there are two series of septa inserted pinnately on a tetrameral plan. The soft parts are unknown.

The vertical skeletal elements of the Rugosa consist, like those of the Hexacoralla and the Heliolitidae, of vertical series of curved or inclined trabeculae. The septa of all adult corallites alternate in size, their insertion being pinnate, on a tetrameral plan (Hill, 1935, p. 504). It may be that in hystero-corallites the pinnate manner of insertion is masked, but nevertheless, the alternation in size of the septa is always visible. In the Heliolitidae the manner of insertion has not been investigated, and any results obtained by such an investigation could not be used for comparative purposes until the insertion of septa in the hystero-corallites of Rugosa and Hexacoralla is also known. But in the Heliolitidae there is no good evidence that the septa alternate in size.

In the Rugosa the arrangement of plates in plocoid coralla suggests corallites surrounded by common tissue, but the "corallites" are in this case the tabularia, and the "common tissue" the dissepimentaria; whether the reticulum of *Heliolites* also represents dissepimentaria depends on the possibility that minor septa are present in the Heliolitidae; for in the Rugosa the development of dissepiments is dependent on the presence of minor septa. But the evidence that minor septa occur in Heliolitidae is weak, and therefore, the evidence that the reticulum of the Heliolitidae is homologous with the "common tissue" of Rugosa is also weak. Nevertheless, Lindström considered this a strong possibility. His reasons were (1) that in one specimen of *H. interstinctus* (1899, pl. 1, figs. i.-iv.) he observed a single corallite with two "thecae," one enclosing what we propose to call the tabularium and one enclosing this and some "coenenchyma." But at a later stage the outer "theca" encloses a great number of "calicles" and becomes in fact the wall of the whole colony, or holotheca. He drew an analogy between the inner wall and the wall* in the dissepimentarium of *Acervularia.* (2) In some of the Heliolitidae from Gotland he observed

* *Walls in the Rugosa.*—Much confusion has arisen in the use of terms for walls in this group mainly because the method of formation of the skeleton was not understood by the earlier writers. A review of the terms used for the various walls in Madreporaria has already been made (Hill, 1935, pp. 497, 499, 508, 512); and the definitions given below are in amplification.

Epitheca and Holotheca.—In simple corals the term *epitheca* is applied to the sheath enclosing the whole of the lumen and situated immediately outside the peripheral ends of the septa; in compound corals it is applied in a similar manner to the sheath surrounding each corallite when the corallites are separable; *holotheca* is applied to the sheath surrounding the whole colony. Immediately inside the epitheca in Rugosa is a narrow *peripheral stereozone* (see below) which is fibrous, though not certainly trabeculate in structure, while the epitheca and holotheca probably are granular. Usually the peripheral stereozone is very narrow and has then been regarded as part of the epitheca, but in such a case it seems better to refer to the double structure as the *outer wall.*

It is, however, not certain that the epitheca and holotheca are separate structures. The holotheca may be but the sum of the epithecae over the outer parts of the peripheral corallites; further miscroscopic examination of conditions in massive coralla with inseparable and separable corallites is needed. Until this is done, we propose to continue using the two terms as defined above.

Peripheral Stereozone.—A stereozone (trabeculate or merely fibrous) of any width, at the periphery of a corallite.

Median Stereozone.—A new phrase to describe any stereozone which is within the dissepimentarium but does not extend to the periphery, e.g. the "inner wall" of *Acervularia.* It may be produced either by dilatation of the septa ("pseudotheca" of Heider, see Ogilvie, 1897) or by the growth of additional trabeculae between the septa ("eutheca" of Heider, see Ogilvie, 1897).

Wall of the Tabularium.—This is not a separate strucure but is the junction of the dissepimentarium and the tabularium.

Wall of the Axial Structure.—This also is not a separate part, being the junction of the axial structure with the outer tabulae.

Aulos.—A distinct wall within the tabularium; a tube enclosing almost flat tabulae, and surrounded by inclined tabulae; supposed to have been formed either by down turning of the axial parts of the tabulae or by the conjunction of the curved axial ends of the septa. In the first case the micro structure of the aulos is that of the horizontal skeletal elements and in the second that of the vertical skeletal elements.

faint polyhedric markings in the coenenchyma suggestive of "outer walls" of the calicles. But Lindström's "inner theca" in *Heliolites* is the wall of the tabularium and his "outer theca" is the holotheca, and thus his first analogy with the Rugosa is invalidated. As for his second argument the faint polyhedric markings in the reticulum were observed on the weathered surface only of a few specimens and might equally well be explained as differential weathering.

Thus there being no good evidence of two orders of septa, and no evidence that the reticulum is a dissepimentarium, and Lindström's analogies on the walls being invalid, we conclude that there is no reason to place the Heliolitidae in the Rugosa.

(c) *Tabulata.*—The sub-order Tabulata was founded by Milne Edwards and Haime for a group of compound corals in which the septa are absent or rudimentary and the tabulae well developed.

The soft parts of both the Tabulata and Heliolitidae are unknown. In the Tabulata septa may or may not be present, but when present they are always rudimentary. This also applies to the Heliolitidae, but the constant number of twelve characteristic of the Heliolitidae is very rarely exhibited by the Tabulata, in fact, in the latter the number appears to be extremely variable.*

The micro-structure of the skeleton is similar—i.e. trabeculate with the trabeculae curved or inclined. In neither are dissepiments developed, unless the reticulum of the Heliolitidae is a dissepimentarium (see argument under Rugosa). In both, tabulae are well developed. Mural pores, hollow connecting processes or solid platforms are present in most but not all genera of the Tabulata, but not in the Heliolitidae.

The question whether the Tabulata is a natural group remains an open one in spite of detailed discussions by more than one author. But even if it is, the Heliolitidae cannot in our opinion be included in it with the Favositidae, for the constant number of septa, as opposed to the great variability in the Tabulata, the absence of mural pores or connecting processes, and the presence of a reticulum in the Heliolitidae are sufficiently important characters to separate them.

C. Conclusion.

To sum up, the Heliolitidae are not Alcyonaria, because the number of septa is fixed at twelve. Their skeletal morphology however indicates that they are Zoantharia Madreporaria. They are quite dissimilar to the Rugosa or the Tabulata in this septal fixity, but they might perhaps be placed in the Hexacoralla with the Seriatoporidae and Madreporidae. There is however no good evidence that their twelve septa are inserted

* The number may be fixed in some Tabulata but this is not yet proved and is di cult of proof, as. e.g. in *Favosites,* it is nearly impossible to get a transverse section which is exactly at right angles to the direction of growth of the corallites, and, the septa being spinose, a complete cycle would rarely, if ever, appear in any one section. This difficulty increases when the septal spines are flat and widely spaced vertically. The only Tabulata known with lamellar septa—*Fossopora,* Etheridge (1903, p. 16) and *Angopora* Jones (1936, p. 18)—have six and "about twelve" respectively. *Angopora* is possibly related to *Thecia* Ed. & H., in which however, the septa are much thicker, and to *Favosites hisingeri* group 111, Tripp (1933, pp. 114-5, text fig. 33), non Ed. & H., in which about twelve short lamellar septa are seen in the text figure. *Favosites tripora* Walkom has twelve vertical series of septal spines in each corallite.

TABLE I.

SUMMARISING AND COMPARING THE STRUCTURE OF CERTAIN CORALS.

—	Heliolitida.	Alcyonaria (*Heliopora*).	Hickson's Group B of Hexacoralla (Seriatoporidæ and Madreporidæ).	Rugosa.	Tabulata.
Mesenteries	?	8	6 pairs	?	?
Micro-structure of skeleton	curved, inclined or vertical trabeculæ	vertical trabeculæ	curved, inclined or possibly sometimes vertical trabeculæ	curved or inclined trabeculæ	curved or inclined trabeculæ
Perforation of the skeleton	in three genera only	not known	in one family only	in one family only	in several genera
Septa	12, one cycle (slight possibility of two cycles in *H. porosus*)	10–16, not arranged in cycles	6 (one cycle) or 12 (two cycles of 6)	alternate in size (major and minor) number varies with size of corallite	very variable in number even in different parts of the same corallite; no cycles recognisable
Reticulum	tubuli with sola, or testæ	trigonal or tetragonal tubes with transverse plates	compact, or spongy	None unless the dissepimentarium is such	none except possibly in *Halysites*
Dissepimentarium	none unless the reticulum is such	none	none	well developed	none
Tabulæ	well developed	well developed	well developed	well developed	well developed
Mural Pores	absent	absent	absent	absent	well developed in almost all
Connecting Processes	absent	absent	absent	in some genera	in some genera

in cycles of six, which is the chief diagnostic character of the Hexacoralla. The insertion and arrangement of the septa is of primary importance in the sub-division of the Madreporaria, and it seems to us that the fixed number 12 and the equality of these 12 septa denotes a section of the Madreporaria equally as distinct as the Rugosa or the Hexacoralla. For this section we propose the name Heliolitida.

The Anthozoa would then be sub-divided as follows:—

Class.	Order.	Sub-order.	Section.	
Anthozoa	*Zoantharia*	*Madreporaria*	*Rugosa*	
			Hexacoralla	Group A Group B
			Heliolitida	
			(*Tabulata*)	
		Actinaria		
	Alcyonaria			

This is essentially what Kiär (1903) proposed. Brackets are placed around the Tabulata as they may not be a natural group.

VII. Systematic Descriptions.

ZOANTHARIA MADREPORARIA HELIOLITIDA.

Family HELIOLITIDAE.

Typical Genus: *Heliolites* Dana.

Diagnosis.—Compound corals with tabularia each defined by a wall usually ridged by septa which, when present, always number twelve: the tabularia are separated by a reticulum of tubuli or testae; the tabularia and tubuli are transversely divided; dilatation of the walls of the tubuli and of the septa may suppress the walls of the tabularia and the transverse plates; carinae may occur.

Range.—The Heliolitidae first appear in the Upper Ordovician of Europe and North America; they are common in the Silurian of Europe, North America, China, and Australia; and die out at the end of the Middle Devonian.

Remarks.—Lindström (1899) and Kiär (1903) have suggested different groupings into sub-families of the genera in the Heliolitidae. Both classifications were necessarily based chiefly on morphology, but partly also on assumed phylogenetic lines, Kiär's arrangement giving a greater importance to his views on phylogeny. Thus he considered that the thickened genera arose from thin ones, and grouped those genera which are similar except for thickening into sub-families. The present writers consider it profitless to attempt a grouping of the genera of Heliolitidae into sub-families on the evidence at present available to them.

Variability.—Individual species of Heliolitidae may vary within wide limits, in many characters. Thus the width of tabularium varies between 1 mm. and 3 mm. in *Heliolites interstinctus.* The distance apart of the tabularia is most variable in *Propora tubulata* and *Propora conferta,* being sometimes six times as great as others. Septal spines in some corallites of *P. tubulata* may be two and a-half times as long as those in others. The extreme example of the shortening of the septal spines is found in *H. interstinctus,* where this, the *decipiens* trend, has given rise to the variety *decipiens* in which the septa are absent and even the crenulations in the walls of the tabularia are lost, leaving the walls cylindrical. In some species, especially in the genus *Propora*, rhabdacanths may be sporadically developed in the septa, instead of the usual monacanths. The dilatation of the vertical skeletal elements may be six times as great in some individuals as in others of the same species, e.g. *Propora conferta.*

Genus *Heliolites* Dana.

Heliolites Dana, 1846, p. 541.

Lonsdalia D'Orbigny, 1849, p. 12 (vide supra, p. 189).

Geoporites D'Orbigny, 1850, p. 49 (vide supra, p. 189).

Stelliporella Wentzel, 1895, p. 27; genotype (by designation) *S. lamellata loc. cit.*, p. 34, pl. iv., figs. 10-12; E2, Kozel, Bohemia (? = *Heliolites parvistella* Roemer).

Pachycanalicula Wentzel, 1895, p. 27; genotype (by designation) *H. barrandei* Hoernes, MS., in Penecke, 1887, p. 271, Taf. xx., figs. 1-3.

Nicholsonia Kiär, 1899, p. 37; genotype *Heliolites megastoma* Kiär (*loc. cit.* and pl. vi., figs. 8, 9, pl. vii., figs. 1, 2) non McCoy (= *H. hirsutus* Lindström, 1899, p. 64). Non *Nicholsonia* Waagen and Wentzel, 1866, which is *Escharopora* Hall, 1847. a Polyzoan.

Helioplasma Kettnerova, 1933b, p. 180; genotype (by monotypy), *H. kolihai* Kettnerova, *loc. cit.* p. 182, text figs. 1, 2. Lower Devonian, Bohemia.

Genotype.—*Astraea porosa* Goldfuss, 1826, p. 64, pl. xxi., fig. 7. Devonian. Eifel.

Diagnosis.—Heliolitida with tabularia each defined by a wall usually ridged by septa which number twelve; the tabularia are separated by a reticulum of tubuli; tabularia and tubuli are transversely divided by complete tabulae and sola respectively.

Range.—F_1 to Middle Devonian in Europe; Niagaran to Devonian in America; Silurian and Devonian in Asia; Silurian and Devonian in Australia. *H. depauperata* is recorded from the Ordovician of the Central Himalayas by Salter and Blanford, 1865, but we have seen neither description nor figures.

The species of *Heliolites* are long ranged. The *interstinctus* group (*H. interstinctus, H. fasciatus,* and *H. repletus*), which is characterised by tabularia with short lamellar septa with entire axial edges, by polygonal tubuli variable in number and by the frequent occurrence of a columella, first occurs in F_1 of Estland, and continues to the Middle Devonian. The *parvistella* group (*H. parvistella* and *H. liljevalli,* characterised by tabularia with lamellar septa reaching to the centres where they form an irregular network) extends from F_1 to the end of the Silurian. *H. daintreei* (characterised by septa which are long but axially are broken into numerous upwardly directed trabeculae, which may form a network) is first found in the Upper Valentian (Lindström's a of Gotland) and continues to the Middle Devonian: *H. hirsutus* (with a sparse discontinuous reticulum and upwardly directed septal spines) is confined to Stratum a of Gotland; *H. porosus* (with thick-walled tabularia and septa which are variable in length, spinose axially and sometimes alternating in size) is known only from the Lower and Middle Devonian.

Remarks.—We agree with Lindström (1899, p. 62) and Kiär (1899, p. 40) that *Stelliporella lamellata* is closely related to *Heliolites parvistella* if not identical with it and as we retain *parvistella* in the genus *Heliolites, Stelliporella* is a synonym of the latter. Wentzel (1895, p. 27) made *H. barrandei* the type of a new genus *Pachycanalicula.* Wentzel based this on specimens from Bohemia with thick walled tubuli; Lindström examining both Swedish and Bohemian specimens found that the Bohemian individuals had thicker walls, but considered this to be due to compression of the specimens. Kiär (1899, p. 43) considered the degree of thickening of the walls not to be of generic significance.

H. hirsutus, the type of *Nicholsonia* (which is in any case preoccupied) we place in the genus *Heliolites.* Although it resembles *Proheliolites* in having a sparse reticulum, the septal spines are directed distally as in *Heliolites.* There is a resemblance to *Propora* in cross section, but this is due solely to the discontinuity of portions of the tubuli walls, whereas in *Propora* tubuli are completely absent, the only vertical structure being single trabeculae. This discontinuity, which is very rare in *Heliolites,* may be a reflection of the rapid replacement of tubuli by tabularia. The horizontal elements in the reticulum are sola, not testae. As there are more than twelve tubuli surrounding each tabularium, this species cannot be referred to *Plasmopora.*

Helioplasma was founded for Bohemian specimens differing only slightly from normal *Heliolites.* The differences (the occurrence in parts of the reticulum of testae instead of sola, and a very slight discontinuity of the tubuli walls) is insufficient in our opinion to justify separation from *Heliolites.* Kettnerova considered the species intermediate between *Heliolites* and *Plasmopora* but it has not an aureola of twelve tubuli as is characteristic of *Plasmopora.*

The only well-defined trend we have observed in *Heliolites* is the "decipiens" trend, by which the walls of the tabularia lose their septa and septal crenulations. This is common and was fully described and illustrated by Lindström (1899) in *Heliolites interstinctus,* but it also acts in other species. The trend is developed unequally in different parts of the same corallum (see Lindström).

Heliolites daintreei Nicholson and Etheridge.

(Pl. VI., figs. 1-5; pl. VII., figs. 1-5; pl. VIII., figs. 1-8; pl. IX., fig. 1.)

Heliolites Daintreei Nicholson and Etheridge, 1879, p. 224, pl. xiv., figs. 3, 3a. Broken River, North Queensland. Devonian.

Heliolites plasmoporoides Nicholson and Etheridge, 1879, p. 225, pl. xiv., figs, 2, 2b. Broken River, North Queensland. Devonian. Lectotype (here chosen) 90246, British Museum (Natural History).

Heliolites Barrandei R. Hoernes *nom. nud.*, Penecke, 1887, p. 271, pl. xx., figs. 1-3; top of Lower Devonian of Graz, Austria. Type material: Kettnerova, 1932, p. 6, pointed out that Penecke's syntypes were lost at the University of Czernowitz in the War 1914-1918. She based her work on Penecke's material at the Geological Institute of Graz University. As we have not access to this, we are unable to choose a neotype and we accept Lindström's interpretation of the species.

Heliolites Daintreei; Jack and Etheridge, 1892, p. 61, pl. i., figs. 7, 8.

Heliolites plasmoporoides; Jack and Etheridge, 1892, p. 62, pl. i., figs. 9-11.

Pachycanalicula Barrandei; Wentzel, 1895, p. 27.

Heliolites Barrandei; Lindström, 1899, p. 58, pl. iii., figs. 8-12, 17-27.

? *Heliolites interstincta* (Linnaeus); Chapman, 1913, p. 222 [Devonian], Lilydale Limestone, Victoria.

non *Heliolites interstincta* var. *gippslandica* Chapman, 1914, p. 311, pl. lx.; from the Silurian (possibly Devonian) of Cooper's Creek, Thompson River, Victoria (specimens not examined. This is *Plasmopora*, see p. 206).

? *Heliolites interstincta* var. *gippslandica* Chapman, 1920, p. 185, pls. xxix., xxx.; Silurian, Cowombat Creek, Victoria (specimens not examined).

Heliolites yassensis Dun, 1927, p. 255, pl. xviii., fig. 1; Yass District, N.S.W.; upper Silurian. Lectotype (here chosen) the specimen in the Australian Museum F5176 with two sections, A.M. 62, from Hattons Corner, Yass, figured by Dun *loc. cit.*

Heliolites regularis Dun var. *humewoodensis* Dun, 1927, p. 257, pl. xviii., figs. 4, 5; upper Silurian. The syntypes including the specimen figured are lost.

Heliolites jackii Dun, 1927, p. 257, pl. xviii., fig. 6; pl. xix., figs. 1, 2; upper Silurian. Of the syntypes listed by Dun the following are in the Australian Museum—Section A.M. 261 (19), no specimen; F 5174, with two sections A.M. 57 from Yass; F. 4081 (not 4801) with two sections A.M. 60 from Humewood; and F 4498, with two sections A.M. 55 from Yarralumla. The rest are lost. We select as lectotype the specimen F 5174 with two sections A.M. 57 from Yass, N.S.W.

? *Heliolites wellingtonensis* (nom. nud.) Dun, 1927, p. 256.

Heliolites barrandei Penecke; Kettnerova, 1932, p. 2, figs. 1, 2; Devonian of Graz.

? *Heliolites vesiculosus* Penecke; Kettnerova, 1932, p. 7, figs. 3, 4; Osternig, north of Tarvis in the Carnic Alps, probably M. Devonian.

Heliolites praeporosus Kettnerova, 1933a, p. 1, figs. 1, 2; Koneprus, L. Devonian.

? *Helioplasma kolihai* Kettnerova, 1933b, p. 182, figs. 1, 2; Koneprus, L. Devonian.

Lectotype (here chosen).—The specimen 90248, British Museum (Natural History), figured Nicholson and Etheridge, 1879, pl. xiv., figs. 3, 3a. Devonian. Broken River, North Queenland. Pl. VII., fig. 2.

Diagnosis.—*Heliolites* with tabularia of variable size with twelve short lamellar septa having numerous long upcurved spines vertical near the axis and swollen at the apices in late forms; with distant regularly horizontal tabulae; with tubuli regularly polyhedric or vermiform, sometimes rounded in late forms; and with the walls of the tabularia and tubuli rather thickened in late forms.

Description.—Lindström (1899, pp. 58-60) has given an adequate description of the species based on European and American material. We supplement it with a description of the Australian specimens, which can be treated in four ill-defined groups.

First group (Plate VI., figs. 1-4).—The external form is unknown but the coralla probably are hemispherical or slightly domed. The tabularia have a diameter of 1 to 2 mm. and their distance apart is from 0·25 to 2·25 mm., with one to six rows of tubuli between. The walls of the tabularia are thin or slightly thickened and sometimes crenulate. The septa arise from the crenulations when these are present, and are short lamellae breaking up axially into long, sharply upcurved spines. The tabulae are thin, rather distant and usually horizontal. The reticulum consists of tubuli of variable transverse section; they may be polyhedric or have rounded angles and may be equal or unequal in size; their walls are equal in thickness to those of the tabularia. The sola are thin and rather closer than the tabulae.

Second group (Plate VI., fig. 5).—This is similar in all particulars to the first group except that the coralla are small and globular, and that one to three rows of tubuli separate the tabularia.

Third group (Plate VII., fig. 1).—This is similar to the first group except that the tabularia are 1 to 1·5 mm. in diameter, with one to four rows of tubuli between; the septal spines are well developed and have swollen apices; the walls of the tabularia are thickened and crenulate, the septa arising from the crenulations; and the tubuli are small, regular, and rather rounded.

Fourth group (Plate VII., figs. 2-5, plate VIII., plate IX., fig. 1).—The corallum is massive and hemispherical, and may be large (Dun records one corallum measuring 20 cm. in diameter and 12 to 15 cms. in height). The tabularia range in diameter from 0·5 mm. to 2 mm. and vary greatly in distance apart in different specimens. The distance between the tabularia varies between 0·25 mm. and 6 mm. and is in general least in those coralla with the largest tabularia. The walls of the tabularia are thin, but are usually a little thicker than those of the tubuli; they are not quite circular, having slight angles where two tubuli meet; the septa usually arise from the walls between these angles, occasionally from the angles themselves; rarely crenulations between the angles form the bases of the septa. The septa are lamellar peripherally but axially they consist of long upcurved spines, which are frequently obscured by recrystallisation. The tabulae are as in the other groups. The tubuli are small, polyhedric, rounded or sometimes vermiform in transverse section. In longitudinal section their walls are usually straight but they may be slightly constricted at the sola. The sola are complete, more numerous than the tabulae, usually horizontal, but sometimes curved, inclined or geniculate.

Remarks.—Lindström places in this species forms from the Upper Llandovery, Wenlock, Ludlow and Lower Devonian of Europe, and the Niagaran of America. He considered that, in spite of variation in size and distance apart of the tabularia and of the thickness of the walls, the group forms a single species by reason of the constant and characteristic nature of the septa. These are lamellar in the peripheral part of the tabularia, but in the axial region they are spines, curving to the vertical. This gives a characteristic transverse section showing linear septa at the edge of the tabularia and dot-like sections of spines at the axis.

Lindström considered that the later forms were distinguishable from the earlier by the swollen axial ends of the septal spines and that some, but not all, Devonian specimens showed thickened tubuli walls with rounded angles. This is in agreement with our observations on the Australian specimens. We agree with Lindström that all these forms are better regarded as a species rather than as a genus; we do not consider the character of the septa, which is the most characteristic feature of the group, to be of generic importance.

As will be seen from the description above, it is possible to divide the Australian forms at least, into ill-defined groups on the characters of the septa; if, however, the reticulum which is the most variable element be considered as a character of classificatory value, a useless multiplicity of forms could be named. We have not given names to the Australian groups, as we have no evidence as yet that the differences are either specific or stratigraphical in value; they are small and gradations occur.

Kettnerova has given descriptions of Bohemian Lower Devonian *Heliolites*; we have not seen specimens, but from her descriptions and figures, we consider *H. praeporosus* is *H. daintreei* and that *H. vesiculosus* and *Helioplasma kolahai* may also be synonyms of *H. daintreei*.

Of our Australian material we place in the first group single specimens from Clermont, Chillagoe, Mount Etna, and Jenolan. While the septal characters in this group are constant, the reticulum varies in different parts of the one specimen and from specimen to specimen. The tubuli are the most unequal and irregular in the Clermont specimen and are most nearly equal and regular in those from Mount Etna and Jenolan. This group appears to be the most similar to the Austrian forms described by Penecke and Kettnerova.

The second group is confined to the Cave Limestone at Wellington, New South Wales.

The third group is known only from Lilydale, Victoria, and the specimens show little variation.

In the fourth group we place specimens from Yass, Molong, and the Broken River. In the Yass specimens the variation in size of the tabularia and their distance apart is extreme and from our limited material it might be possible to distinguish two sub-groups, one in which the tabularia are 1·5 to 1·75 mm. in diameter and as little as 0·25 mm. apart; the other in which the tabularia are 0·5 to 1 mm. in diameter and as much as 6 mm. apart. There is, however, only a general and not a definite relationship between the size of the tabularia and their distance apart. Thus in two specimens with tabularia of approximately the same size (0·75 mm.) the distance between the tabularia is about 2·5 mm. and 1 mm. respectively. The most typical feature of the group is the shape in transverse section of the tabularia, which is somewhat similar to Lindström's Silurian *H. barrandei* var. *spongodes*. This has the least crenulation of the forms he examined, but it differs greatly in external form from the Yass specimens, and has slight crenulations where the septa join the walls. We place in this group *H. yassensis* Dun, *H. regularis* Dun var. *humewoodensis*, and *H. jackii* Dun. We have examined those of Dun's thin sections that have not been lost, and consider that he did not allow for the wide variation occurring within the various species of *Heliolites*. We have observed characters, which he considered diagnostic of different species, in the one specimen. Further, he appears to have failed to realise to what a great extent the septa of the Yass specimens are obscured by the recrystallisation of the matrix. In spite of this recrystallisation we have observed, under suitable illumination, septa of the characteristic *daintreei* type in nearly all his sections. The Molong material is even more crystalline and septa are observable in sections of one specimen only. The septa in this are quite characteristic and other characters leave no doubt that all four specimens belong to the same species. We place the lectotype of *H. daintreei* in this fourth group, although the diameter of its tabularia, 2 mm., is larger than in any specimen from other localities. *H. plasmoporoides* is *H. daintreei*, but we place it in the fourth group rather doubtfully as we have seen only one specimen and its preservation is poor. It has tabularia of 2 mm. diameter and the reticulum is mostly vermiform though regular in places.

Australian Localities.—1st Group: Portion 73, parish Copperfield, Clermont, Queensland, Lower Middle Devonian; Foot of Mount Etna, Rockhampton, Queensland, ?Lower Middle Devonian; Chillagoe, Queensland (Geol. Surv, No. F 1964), Silurian; Mount St. George, Jenolan, New South Wales (Australian Museum, F 4108, with two sections A.M. 61), Silurian. 2nd Group: Wellington Caves, New South Wales (Australian Museum, sections A.M. 259), ?Siluro-Devonian. 3rd Group: Lilydale, Victoria, Lower or Middle Devonian. 4th Group: Hatton's Corner, Yass, and Old Limekilns Ridge, Humewood, Yass, New South Wales, Upper Silurian; portion 3, parish Cudal, just west of Boree Creek on back road from Manildra to Cudal, near Molong, New South Wales, Lower Devonian (University of Queensland Collection, F 3408, with two sections); portion 170, parish Curra, near Wellington, New South Wales, Curra Creek, Crossing No. 2, east of road crossing, Lower Devonian (U.Q., F. 3409, with two sections); portion 174, parish Bell, county Ashburnham, Crystal Springs, near Molong, New South Wales, Lower Devonian (U.Q., F. 3410, with two sections); Mandagery's Creek, parish Brymedura, north of Garra, near Molong, New South Wales (probably portion 77), Lower Devonian (U.Q., F. 3411, with two sections on one slide); Broken River, tributary of Clarke River, North Queensland, Devonian (British Museum, Natural History specimens 90246 and 90248, with two slides of each).

Range.—Lindström described the species from Gotland in strata from a-f (Upper Llandovery to Ludlow), from the Lower Devonian (*barrandei* beds) of Austria and from the Niagaran of America. Kettnerova (1932, 1933) figured it from the Lower Devonian of Bohemia, and Le Maître (1934, pl. vii., figs. 5-8) recorded it from Ancenis in beds transitional from the Lower Devonian to the Middle Devonian. In Australia the first group is Lower Middle Devonian at Clermont, and possibly at Mount Etna also, Silurian at Chillagoe and at Jenolan. The second group is Siluro-Devonian. The third group is Devonian. The fourth group is Upper Silurian at Yass, Lower Devonian at Molong, and Devonian at Broken River.

Heliolites nicholsoni Eth. fil.

Heliolites sp. ind. Nicholson and Etheridge, 1879, p. 223.

Heliolites nicholsoni Etheridge, in Jack and Etheridge, 1892, p. 63, pl. 1, fig. 12.

We have been unable to trace this. Etheridge states it is in the British Museum, but Dr. H. D. Thomas in a letter says: "We have not got, nor is there any record that we ever had, the other specimen (i.e. *H. nicholsoni*). It is said to be in a large corallum of *Favosites* but I have examined all ours from Broken River, Queensland, and none contains a Heliolitid."

Judging from the figure in Jack and Etheridge it is quite possible that this species is *Plasmopora heliolitoides* Lindström.

Locality.—Broken River, tributary of the Clarke River, North Queensland. Devonian.

Heliolites interstinctus (Linnaeus). (Plate IX., fig. 2.)

Madrepora interstincta Linnaeus, 1767, p. 1276.

Heliolites interstinctus; Lindström, 1899, p. 41, pl. i., figs. 1-36; pl. ii., figs. 1, 2; pl. iii., figs. 1, 2.

Lectotype.—The specimen from Gotland described and figured by Linnaeus, 1745, p. 30, fig. xxiv. (chosen by Lindström, 1899, p. 42).

Diagnosis.—*Heliolites* with thin walled tabularia of variable size; usually with non spinose septa which arise from the crenulations; typically with a discontinuous columella; the tubuli are polygonal. In some coralla some or all of the tubularia are without crenulations, septa, or columella (*decipiens* variation).

Remarks.—A very crystalline specimen (University of Queensland, F 3437, with two slides) from the ?Silurian of Limestone Bluff, Mungana, North Queensland, may possibly belong to this species. It is probably of the *decipiens* morphology but this appearance may be due to its re-crystallisation.

Range.—Lyckholm beds of the Baltic, Gotlandian of Scandinavia, Wenlock and Ludlow of England and Bohemia, Silurian of Arctic Russia and Australia, and Niagaran of America; Lindström also records it as passing up into the Middle Devonian of the Carnic Alps.

Heliolites porosus (Goldfuss). (Plate IX., fig. 3.)

Astraea porosa Goldfuss, 1826, p. 64, pl. xxi., fig. 7; Devonian of the Eifel.

Heliolites porosus; Lindström, 1899, p. 53, pl. ii., figs. 29-37; pl. iii., fig. 3-7.

Heliolites porosa; Etheridge, 1899b, pp. 173-4, pl. xix., figs. 3, 4; pl. xxv., figs. 1, 2; Middle Devonian of Tamworth, N.S.W.

Heliolites porosus; Lecompte, 1936, p. 93, pl. xiv., figs. 2-5.

Type Material.—Goldfuss' syntypes from the Devonian of the Eifel and Heisterstein are in the University of Bonn. They were refigured and fully described by Lecompte *loc. cit.*

Diagnosis.—*Heliolites* with tabularia thick walled and crenulate, with unequal septa arising from the crenulations; the septal lamella have the axial edges obtusely denticulated or fringed with curved spines; the tubuli are small with thick walls.

Remarks.—All the vertical walls are thick but those of the tabularia are markedly more so than those of the tubuli. The septa are thick, straight lamellae, with short spines on the axial edge; the spines are not curved and are only slightly directed upwards so that in transverse section they form neither a network as in *parvistella* nor numerous dots as in *daintreei*. The septa are always unequal and are sometimes alternate in length.

Localities and Range.—In the Middle Devonian of New South Wales, at Moore Creek and Woolomol, near Tamworth, and on the Isis River, near Crawney; in the Givetian Burdekin Downs Limestone of North Queensland, at numerous localities on the Burdekin Downs and Fanning River Stations, and in the Reid Gap, near Townsville; in the Lower Middle Devonian Limestone at Elbow Valley, Silverwood, Queensland; and in the Middle Devonian Limestone in Kroombit Creek, 5 miles above Kroombit Station, near Biloela, Queensland.

Genus *Plasmopora* Edwards and Haime.

Plasmopora Edwards and Haime, 1849, p. 262.

Plasmopora; Lindström, 1899, p. 75.

Genotype (by monotypy).—*Porites petalliformis* Lonsdale, 1839, p. 687, pl. xvi., figs. 4, 4a. From the Wenlock shale. Walsall.

Diagnosis.—Heliolitida with each tabularium surrounded by an aureola of twelve tubuli, whose dividing walls typically continue into the tabularia as septa; additional tubuli whose walls may be discontinuous occur between the aureolae; testae may occur when the walls are discontinuous, otherwise sola are developed. Carinae may occur.

Range.—The range in Europe and America is Llandovery of Gotland, G1 of Estland; Wenlock of England, Gotland and Estland; Ludlow of Gotland; the Niagaran of America; and Middle Devonian of the Carnic Alps (Vinassa de Regny, 1918, p. 89). In Australia it occurs in the Upper Silurian of Yass, Lower Devonian of Molong, New South Wales, Silurian [?Lower Devonian] of Coopers Creek, Victoria, and Devonian of Johannsen's Caves, Rockhampton, Queensland, and of the Nundle road, Tamworth, New South Wales.

Table II. summarises the characters and range of the species recognised by Lindström. A full account of the micro-structure of the septa and walls has already been given, p. 187.

Plasmopora heliolitoides Lindström. (Plate IX., figs. 4, 5; pl. X., figs. 1-4.)

Plasmopora heliolitoides Lindström, 1899, p. 86, pl. vii., figs. 32-33.

Heliolites distans Dun, 1927, p. 258, pl. xix., figs. 3-6. Syntypes in the Australian Museum are F. 5173 (misprinted 5178 in explanation to plate) with two sections A.M. 56, from Yass, and F. 4082 with two sections A.M. 140, from Old Limekilns Ridge; upper Silurian. Lectotype (here chosen) F. 5173, A.M. 56, figured Dun, *loc. cit.*, figs. 5, 6.

Heliolites distans var. *humewoodensis* Dun, 1927, p. 261, pl. xx., figs. 3, 4. Syntypes in the Australian Museum are F. 4082, with two sections A.M. 43; F. 5547, with two sections A.M. 71; F. 5548, with two sections A.M. 72, all from the Old Limekilns Ridge, Humewood; upper Silurian. Lectotype (here chosen) F. 4082, A.M. 43, Dun, *loc. cit.*, figs. 3, 4.

Heliolites distans var. *intermedia* Dun, 1927, p. 261, pl. xx., figs. 5, 6. Syntypes in the Australian Museum are F. 5555, with two sections A.M. 75; F. 5556, with two sections A.M. 76; and F. 2433, with two sections A.M. 52; all from Old Limekilns Ridge, Humewood. Upper Silurian. Lectotype (here chosen F. 5556, A.M. 76, figured Dun, *loc. cit.*, figs. 5, 6.

Heliolites distans var. *minuta* Dun, 1927, p. 262, pl. xxi., figs. 1-4. Syntypes in the Australian Museum are A.M. 237 (specimen apparently lost) from the Yass District, F. 5553, with two sections A.M. 73, F. 5554, with two sections A.M. 74, both from Old Limekilns Ridge, Humewood, and F. 2461, with two sections A.M. 53, from Bowning. Upper Silurian. Lectotype (here chosen) F. 5553, A.M. 73, figured Dun, *loc. cit.*, figs. 1, 2, 4.

Type Material.—In the Lindström collection in Stockholm; from Stratum d (Wenlock) of Ostergarn, Gotland.

Diagnosis.—*Plasmopora* with the tubuli of the aureola irregular and unequal in size frequently elongated parallel to the circumference of the tabularia, with septa absent or represented by blunt protuberances and with the walls in the reticulum continuous.

Description.—The corallum is large and spreading and the tabularia vary greatly in size and distance apart. Their diameter varies from 1·75 mm. to 1 mm. and their distance apart from 1·5 to 5 mm. The walls of the tabularia are slightly thicker than those of the tubuli. The septa are rudimentary, represented by knob-like swellings which are continuations of the radial walls of the aureola. They are not lamellar but are blunt rounded spines. The tabulae are complete, usually horizontal, 12 to 16 in a space of 5 mm. The twelve tubuli forming the aureola are frequently smaller than, occasionally equal to, or a little larger than the other tubuli. They often have their long axes parallel to the circumference of the tabularia and are unequal. The remainder of the reticulum consists of tubuli almost equal in diameter but of variable shape. The tubuli are not always parallel to the tabularia, frequently changing their direction of growth slightly. Some are polyhedric, others have rounded corners, and a few are alveolitoid frequently with a carina projecting from one side. The sola are horizontal, oblique or inosculating, about 24 in a space of 5 mm.

Remarks.—In this species the tubuli of the aureola are frequently elongated parallel to the circumferences of the tabularia whereas in all other species they are elongated in a radial direction. This, combined with the form of the septa (knob-like spines), gives the species its characteristic appearance. Carinae when present occur only in the reticulum and each probably represents the beginning of a new tubuli wall.

Range.—Stratum d (Wenlock) of Ostergarn, Gotland; Upper Silurian of Hatton's Corner and Derrengullen Creek, Yass, and of Old Limekilns Ridge, Humewood.

Plasmopora gippslandica (Chapman). (Plate X., fig. 5, pl. XI., fig. 1.)

Heliolites interstincta var. *gippslandica* Chapman, 1914, p. 311, pl. ix., figs. 35, 36. Silurian [? Devonian]. Cooper's Creek, Thomson River, Victoria.

non *Heliolites interstincta* var. *gippslandica* Chapman, 1920, see p. 200.

Heliolites regularis Dun, 1927, p. 256, pl. xviii., figs. 2, 3. Upper Silurian. Hatton's Corner, Yass, N.S.W.

Holotype.—The specimen described and figured by Chapman, loc. cit., thought to be in the National Museum, Melbourne, M.D. 746, Slide 1336.

Diagnosis.—*Plasmopora* with the tubuli of the aureola usually elongated radially, and neighbouring aureolae in contact or occasionally separated by one or two rows of tubuli; with tubuli walls continuous vertically, and septa absent.

Description.—The external form is unknown. The tabularia show in cross sections as smooth and round with no sign of septa. Their diameter ranges from 1 to 1·5 mm. and they are from 0·5 to 1·5 mm. apart. The walls of the tabularia are but little if any thicker than the walls of the tubuli. The tabulae are mostly complete and horizontal but a few may be inosculating; 10 occupy a space of 5 mm. The tubuli of the aureola are radially elongated when the tabularia are sufficiently distant, and are usually equal in size; they are polyhedric except in parts of some coralla where the walls are somewhat thickened when the angles are rounded. When tubuli occur between the aureolae they are smaller than those of the aureola; not more than two such rows are developed. The sola are mostly complete, a few are inosculating or geniculate, and there are 10 to 14 in a space of 5 mm. The tubuli walls are frequently constricted at their junctions with the sola.

Remarks.—The absence of septa, the continuity of the walls, and the shape of tubuli of the aureola (radially elongated) distinguish this species. Of the European Silurian species it is closest to *P. heliolitoides* (Wenlock of Gotland) and *P. rudis* (uppermost Ludlow of Gotland). It differs from both in the absence of septa, from *heliolitoides* in the shape of the tubuli of the aureola and from *rudis* in having the tubuli walls vertically continuous. It appears to be very similar to the Middle Devonian *P. carnica* Vinassa de Regny (1918, p. 89, pl. vii., figs. 4, 5) but the sections of the latter are oblique so that we cannot be sure of complete identity.

TABLE II.

SUMMARY OF CHARACTERS AND RANGE OF SPECIES OF *Plasmopora* RECOGNISED BY LINDSTROM.

Species.	Nature of Septa.	Nature of Tubuli Walls.	Size of Aureolar tubuli relative to size of other tubuli.	Horizontal Elements of Reticulum.	Range.
petalliformis	acanthine	discontinuous	larger	testæ	Wenlock of England and Wenlock and Ludlow of Gotland
forœnsis	acanthine	mostly continuous	larger	testæ	Ludlow of Gotland
calyculata	lamellar with spines	discontinuous	larger	testæ	Wenlock of Gotland and England
scita	rhabdacanthine	discontinuous (monacanths in vertical series)	larger	testæ	Wenlock of England and Gotland: Niagaran of America
follis	acanthine	continuous and wavy	larger	sola	Niagaran of America
stella	lamellar with spines	mostly continuous	larger	sola	Llandovery of Gotland
scala	lamellar with spines	mostly continuous	larger	mostly sola	Llandovery of Gotland
rosa	lamellar with short spines	mostly continuous and wavy	larger	some testæ, inosculating sola	Ludlow of Gotland
suprema	short, lamellar with spines	mostly continuous and wavy	larger	sola and testæ	Ludlow of Gotland
rudis	slight swellings on the wall	mostly continous	about equal	some testæ, inosculating sola	Ludlow of Gotland
heliolitoides	slight swellings on the wall	continuous	variable, unequal, usually smaller	sola	Wenlock of Gotland
? *reticulata*	absent	discontinuous (monacanths in vertical rows)	about equal	testæ	Llandovery of Gotland

Localities and Age.—Johannsen's Caves, Rockhampton, Devonian (F 5512, Australian Museum); Nundle road, near Tamworth, New South Wales, Devonian (F. 6936, Australian Museum); portions 31 and 174, parish Bell, county Ashburnham, near Molong, New South Wales, and portion 170, parish Curra, near Wellington, New South Wales. Lower Devonian; Hatton's Corner, Yass, New South Wales, Upper Silurian; Cooper's Creek, Thomson River, Victoria, Silurian [?Devonian].

We have been unable to trace the specimen figured by Dun (*loc. cit.*), said by him to be in the Mining Museum, Sydney, and his description is obscure and his measurements contradictory; he does not give the magnification of the figures. In large collections from Hatton's Corner, Yass, we have found no similar specimens. Nevertheless we have no doubt that it should be referred to this species.

The specimen figured by Chapman, *loc. cit.*, could not be *Heliolites interstincta* since it possesses the diagnostic character of *Plasmopora*, viz., an aureola of 12 tubuli.

Plasmopora sp. cf. *gippslandica* (Chapman).

(Plate XI., fig. 2.)

One poorly-preserved specimen from Boomerang Tank, Canbelago, near Cobar, New South Wales, in the Australian Museum, probably Silurian is similar to *gippslandica* but the walls of both the tabularia and tubuli are considerably thickened and the angles of the tubuli are rounded. Occasionally there is only one row of tubuli between adjoining tabularia. The tubuli are unequal in size.

Genus *Propora* Edwards and Haime.

Propora Edwards and Haime, 1849, p. 262.

Lyellia Edwards and Haime, 1851, p. 226.

Pinacopora Nicholson and Etheridge, 1878. Genotype *P. grayi* Nicholson and Etheridge, *loc. cit.*, p. 54, pl. iii., figs. 3-3j. Silurian. Girvan.

Propora; Lindström, 1899.

Genotype.—*Porites tubulata* Lonsdale, 1839, p. 687, pl. 16. figs. 3, 3a, 3b (non figs. 3c-f. See Edwards and Haime, 1850, p. lix.). Wenlock Limestone.

Diagnosis.—Heliolitida in which the reticulum consists of testae; with spinose septa; and with a variable development of discrete trabeculae throughout the tissue.

Range.—Upper Ordovician of North America, England, Scandinavia, and the Baltic States; Silurian (Valentian to Ludlovian) of Europe; Niagaran of America; Gotlandian of Korea; and Upper Silurian of Australia.

Remarks.—*Lyellia* was founded on two genosyntypes—*L. americana* Edwards and Haime (1851, p. 226, pl. 14, figs. 3, 3a) from Drummond Island, on Lake Huron, North America, Silurian, and *Sarcinula glabra* Dale Owen (1844, p. 76, pl. 11, fig. 11, see Edwards and Haime, 1851, p. 226, pl. 12, figs. 2, 2a-c) Upper Silurian, Iowa. Lindström (1899, pp. 92, 100) has shown that both these species rightly belong in *Propora* and therefore *Lyellia* is a synonym of *Propora*.

Pinacopora was founded for a number of small, concavo-convex, leaf-life expansions. We have not seen specimens but from the description and figures we agree with Lindström (1899, p. 99) that it is probably identical with *Propora*.

The morphology of the genus has been fully discussed above, see p. 187.

Propora conferta Edwards and Haime. (Plate XI., figs. 3-5.)

Propora conferta Edwards and Haime, 1851, p. 225. Borkholm (? F2), Chavli Canal de Windau, Russia.

Plasmopora australis Etheridge, 1899a, p. 33, pl. A, fig. 11; pl. B, figs. 5, 6. Silurian. Wombat Creek, Victoria. Figured specimen missing.

Propora conferta; Lindström, 1899, p. 93, pl. viii., figs. 32-39; pl. ix., figs. 1-23, 31, 32, 35.

Plasmopora shearsbyi Dun, 1927, p. 262, pl. xxi., figs. 5, 6. Lectotype, here chosen, the sections A.M. 256 (E. 21) in the Australian Museum, from Yass; upper Silurian. Other syntypes including the one figured are lost.

Syntypes.—Two specimens in the de Verneuil collection, Ecole de Mines, Paris, described by Lindström *loc. cit.*, p. 93.

Diagnosis.—*Propora* in whose tabularia the septa are extremely short or absent; with a reticulum of testae on which very short, thin separate trabeculae may occur; the walls of the tabularia may be crenulate, the outer angles being produced into the reticulum as short ridges.

Remarks.—The variation in the diameter of the tabularia and in their distance apart is very great in this species. In the Yass specimens the tabularia vary from just under 1 mm. in diameter to over 2 mm., and their distance apart varies from 0·25 mm. to 2·5 mm. In transverse section short breaks in the walls of the tabularia are sometimes seen. Of the individuals of this species figured by Lindström, his pl. ix., figs. 5 6, from the Upper Silurian (Ludlovian) of Tsien-shui River, China, is closest to the Yass form. This shows the same keeled crenulations and discontinuity of the tabularial walls. Etheridge's specimen from Victoria, which we have been unable to trace, is from the figures, obviously to be referred to this species.

Range.—*Propora conferta* has a long range—from the Upper Ordovician (?Trenton) of Iglulik Island (*Plasmopora lambei*) and stage 5a of Norway, through the Llandovery to the Wenlock of England, Estland and Gotland, the Niagaran of America, and the Upper Silurian of Tsien-shui of China, of Yass, New South Wales, and the Silurian of Eastern Victoria.

Upper Silurian Localities in Australia.—Yass, New South Wales (Australian Museum, A.M. 256); Derrengullen Creek, Yass (University of Queensland, F 3300); portion 161, parish Yass (Australian Museum, F 8233, A.M. 553); Old Limekilns Ridge, Humewood, near Yass (Australian Museum, F4083, A.M. 64 and A.M. 54); Wombat Creek, Victoria. Dun also records *P. shearsbyi* from Hatton's Corner, Yass, and from Bungonia, east of Goulburn, New South Wales, but we have been unable to trace the specimens.

VIII. Acknowledgments.

We are indebted for facilities for study to Professor H. C. Richards, D.Sc. During the course of the work, Miss Hill has held a Research

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EXPLANATION OF PLATES.

PLATE VI.

Heliolites daintreei Nicholson and Etheridge.

All figures approximately × 3 diameters.

First group.

Fig. 1.—F 3461, University of Queensland. Douglas Creek, Clermont, Queensland. Lower Middle Devonian. 1a, transverse section; 1b, vertical section.

Fig. 2.—F 3462, University of Queensland. Por. 120, par. Fitzroy (foot of Mount Etna), near Rockhampton, Queensland. ?Lower Middle Devonian. 2a, transverse section; 2b, vertical section.

Fig. 3.—F 1964, Geological Survey of Queensland. Chillagoe, North Queensland. Silurian. Transverse section.

Fig. 4.—AM 61, F 4108, Australian Museum. Mount St. George, Jenolan, N.S.W. ?Silurian. 4a, b, transverse section; 4c, vertical section.

Second group.

Fig. 5.—AM 259, 2608, Australian Museum. Wellington Caves, N.S.W. ?Lower Devonian. 5a, vertical section; 5b, transverse section.

PLATE VII.

Heliolites daintreei Nicholson and Etheridge.

All figures approximately × 3 diameters.

Third group.

Fig. 1.—L. 4, Melbourne University. Lilydale, Victoria. Lower Devonian. 1a, transverse section; 1b, vertical section.

Fourth group.

Fig. 2.—90248, British Museum, London. Holotype. Broken River, North Queensland. Devonian. 2a, transverse section; 2b, vertical section.

Fig. 3.—90246, British Museum, London. Lectotype of *Heliolites plasmoporoides* Nicholson and Etheridge. Broken River, North Queensland. Devonian. Transverse section.

Fig. 4.—AM 62, from F 5176, Australian Museum. Lectotype of *Heliolites yassensis* Dun. Hattons Corner, Yass, N.S.W. Upper Silurian. 4a, transverse section; 4b, vertical section.

Fig. 5.—AM 57, from F 5174, Australian Museum. Lectotype of *Heliolites jackii* Dun. Yass, N.S.W. Upper Silurian. 5a, transverse section; 5b, vertical section.

PLATE VIII.

Heliolites daintreei Nicholson and Etheridge.

Fourth group.

All figures approximately × 3 diameters.

Fig. 1.—AM 261 (19), Australian Museum. Syntype of *Heliolites jackii* Dun. 1a, transverse section; 1b, vertical section.

Fig. 2.—F 3294, University of Queensland. Hatton's Corner, Yass, N.S.W. 2a, transverse section; 2b, vertical section.

Fig. 3.—F 1024, University of Queensland. Hatton's Corner, Yass. N.S.W. 3a, transverse section; 3b, vertical section.

Fig. 4.—Tranverse section, Hatton's Corner, Yass, N.S.W.

Fig. 5.—F 3410, University of Queensland. Por. 174, par. Bell, co. Ashburnham (Crystal Springs), near Molong, N.S.W. Lower Devonian. Transverse section.

Fig. 6.—F 3411, University of Queensland. Mandagery's Creek, par. Brymedura, north of Garra, near Molong, N.S.W. Lower Devonian. Vertical section.

Fig. 7.—F 3408, University of Queensland. Por. 3, par. Cudal, just west of Boree Creek, on road from Manildra to Cudal, near Molong, N.S.W. Lower Devonian. Transverse section.

Fig. 8.—F 3463, University of Queensland. Spring Creek, near Mount Canoblas, N.S.W. Upper Silurian. Transverse section.

PLATE IX.

All figures approximately × 3 diameters.

Heliolites daintreei Nicholson and Etheridge, fourth group.

Fig. 1. F 3464, University of Queensland. Spring Creek, near Mount Canoblas, N.S.W. Upper Silurian. Transverse section.

Heliolites ?interstinctus (Linnaeus).

Fig. 2.—F 3437, University of Queensland. Limestone Bluff, Mungana, North Queensland. Silurian. 2a, transverse section; 2b, vertical section.

Heliolites porosus (Goldfuss).

Fig. 3.—Geological Survey of Queensland. Five miles above Kroombit Station, Kroombit Creek, near Biloela, Queensland. Middle Devonian. 3a, transverse section; 3b, vertical section.

Plasmopora heliolitoides Lindström.

Fig. 4.—AM 43, from F 4082, Australian Museum. Lectotype of *Heliolites distans* var. *humewoodensis* Dun. Old Limekilns Ridge, near Yass, N.S.W. Upper Silurian. 4a, transverse section; 4b, vertical section.

Fig. 5.—AM 56, from F 5173, Australian Museum. Lectotypes of *Heliolites distans* Dun. Yass. Upper Silurian. 5a, b, transverse sections.

PLATE X.

All figures approximately × 3 diameters.

Plasmopora heliolitoides Lindström.

Fig. 1.—AM 56, from F 5173, Australian Museum. Lectotype of *Heliolites distans* Dun. Yass. Upper Silurian. 1a, transverse section; 1b, vertical section.

Fig. 2.—AM 76, from F5556, Australian Museum. Lectotype of *Heliolites distans* var. *intermedia* Dun. Old Limekilns Ridge, Humewood, near Yass, N.S.W. Upper Silurian. Transverse section.

Fig. 3.—AM 73, from F 5553, Australian Museum. Lectotype of *Heliolites distans* var. *minuta* Dun. Old Limekilns Ridge, Humewood, near Yass, N.S.W. Upper Silurian. 3a, transverse section; 3b, c, vertical sections.

Fig. 4.—F 3296, University of Queensland. Hatton's Corner, Yass, N.S.W. Upper Silurian. 4a, transverse section; 4b, c, vertical sections.

Plasmopora gippslandica (Chapman).

Fig. 5.—AM 271, from F 6936, Australian Museum. Nundle road, near Tamworth, N.S.W. Devonian. Transverse section.

PLATE XI.

All figures approximately × 3 diameters.

Plasmopora gippslandica (Chapman).

Fig. 1.—AM 66, from F 5512, Australian Museum. Johannsen's Caves, near Rockhampton, Queensland. ?Lower Middle Devonian. 1a, transverse section; 1b, vertical section.

Plasmopora cf. *gippslandica* (Chapman).

Fig. 2.—Australian Museum. Limestone beds at Boomerang Tank, Canbelago, near Cobar, N.S.W. ?Silurian. Transverse section.

Propora conferta Edwards and Haime.

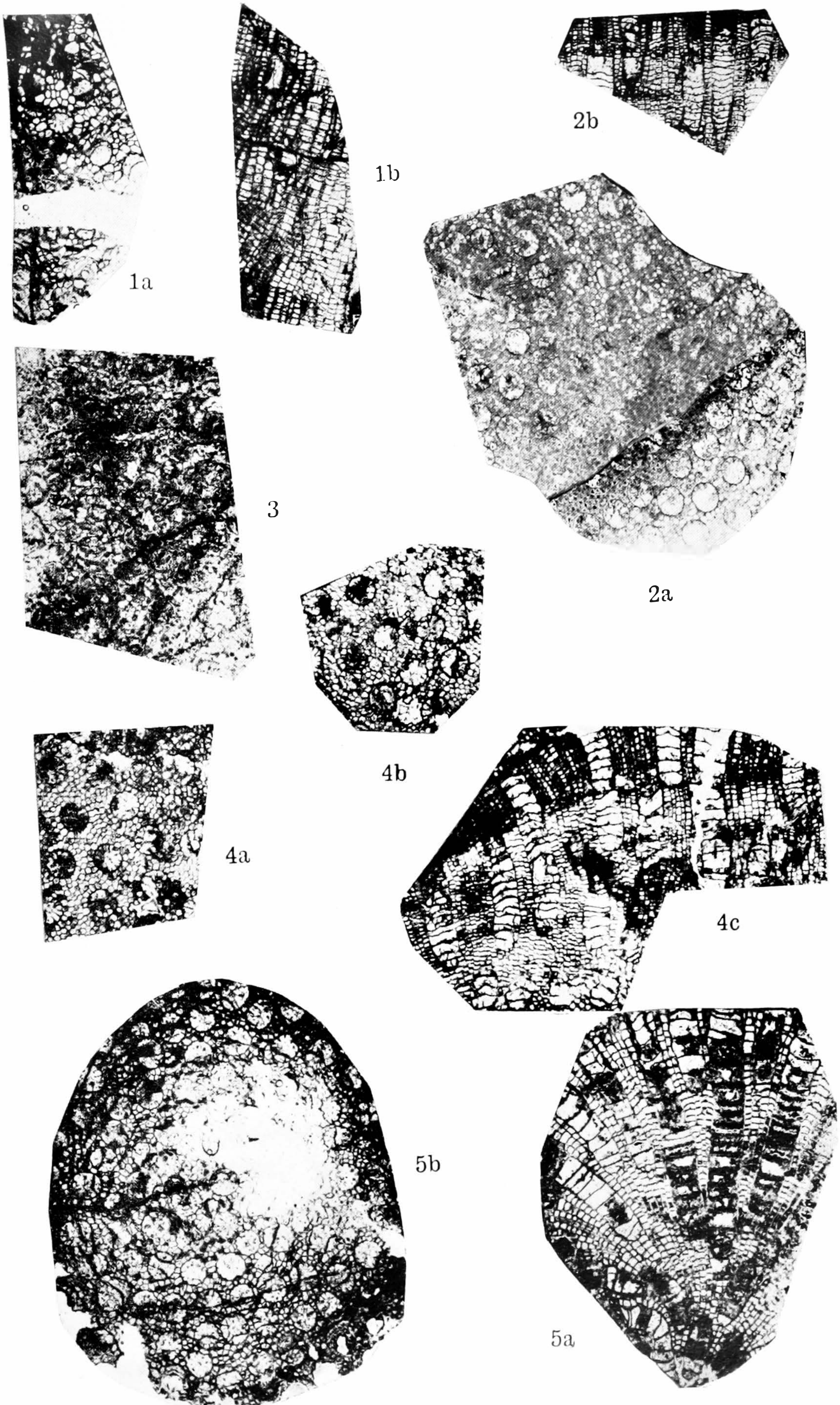
Fig. 3.—F 3300, University of Queensland. Hatton's Corner, near Yass, N.S.W. Upper Silurian. Transverse section.

Fig. 4.—F 3465, University of Queensland. Bowspring Limestone, Hatton's Corner, N.S.W. Upper Silurian. Transverse section.

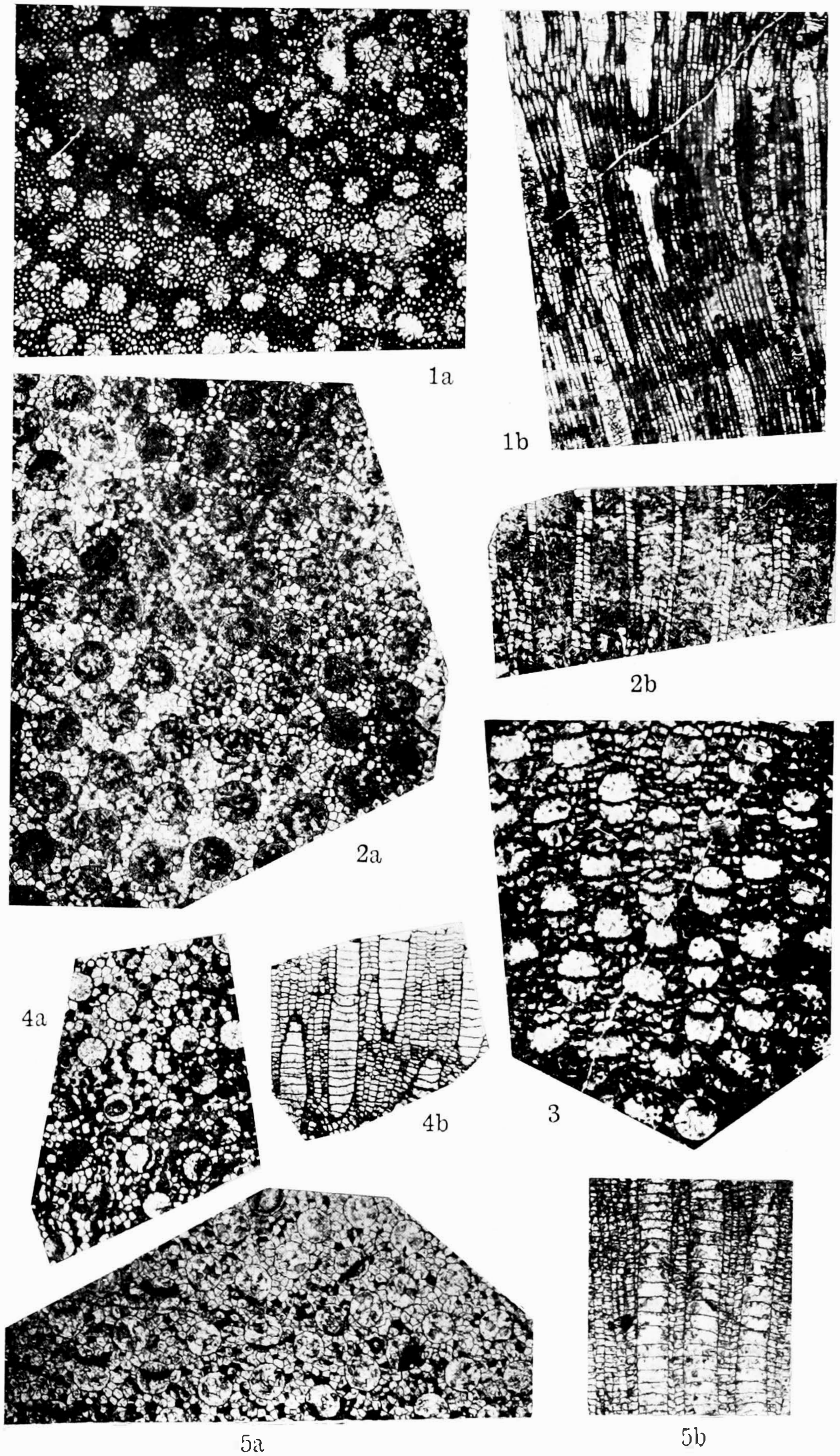
Fig. 5.—AM 256 (21), Australian Museum. Yass, N.S.W. Upper Silurian. 5a, transverse section; 5b, vertical section.

Heliopora coerulea (Pallas, Ellis and Solander).

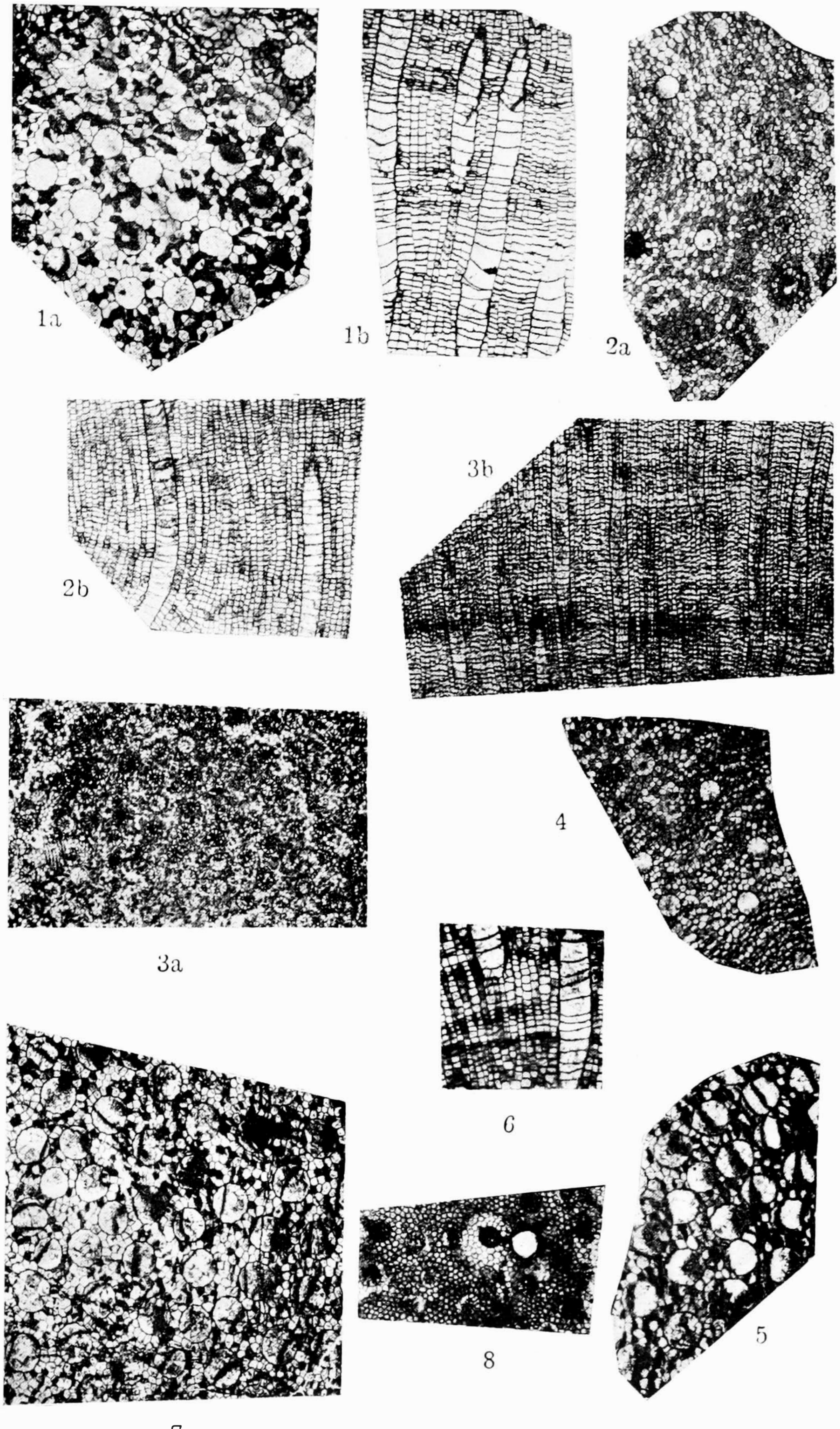
Fig. 6.—F 3466, University of Queensland. Recent. Great Barrier Reef.



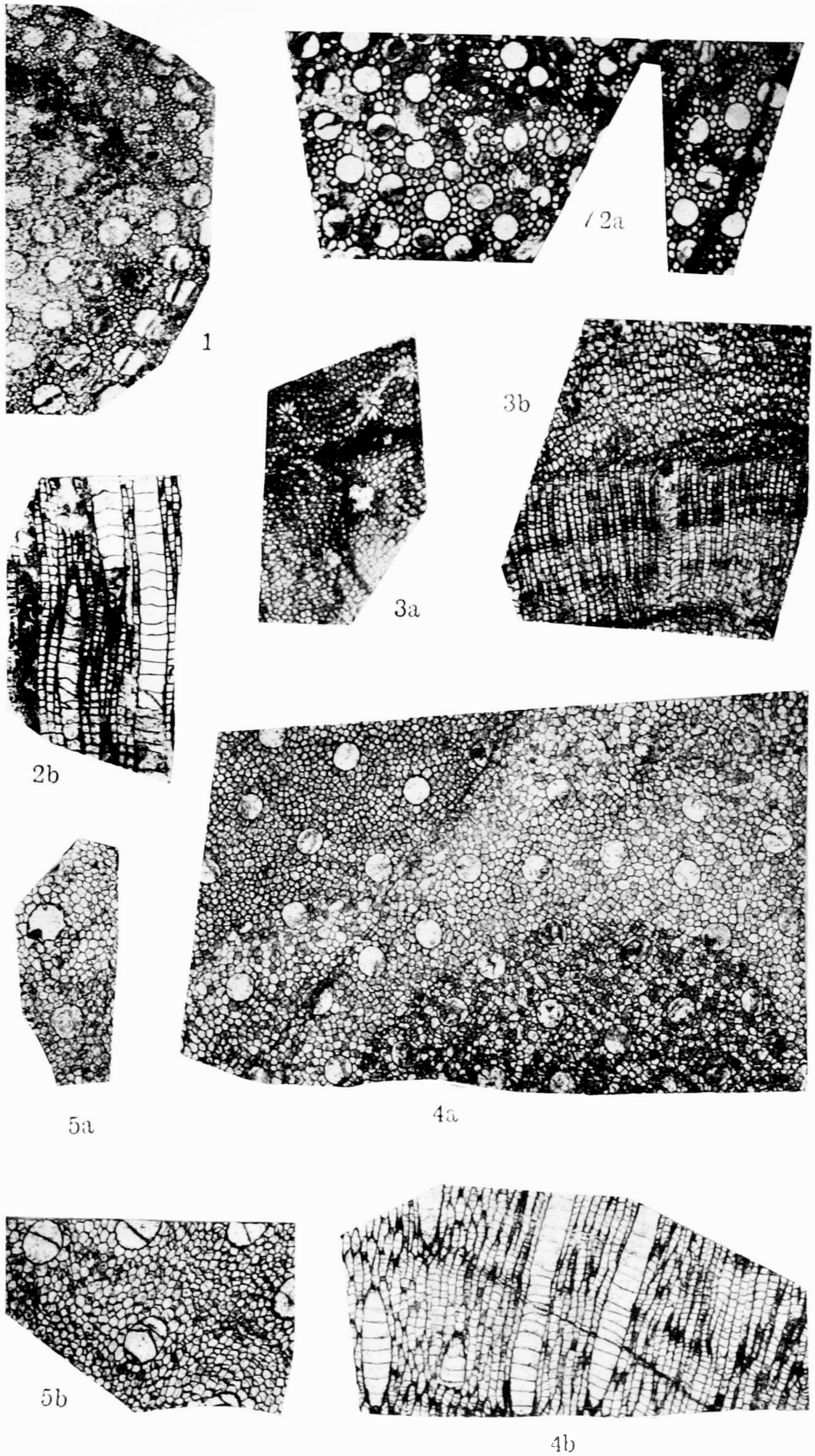
Heliolites daintreei Nicholson and Etheridge.



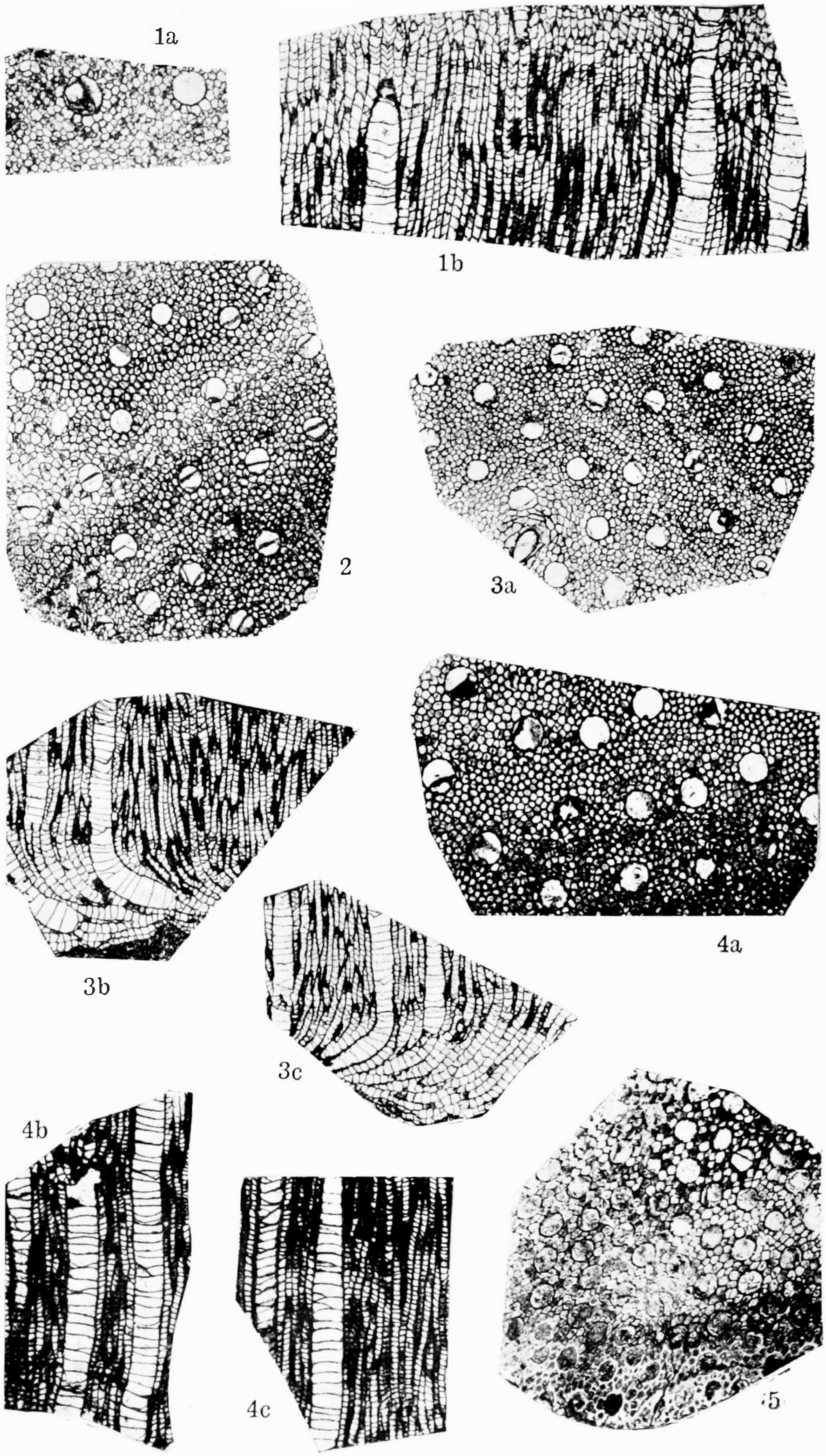
Heliolites daintreei Nicholson and Etheridge.



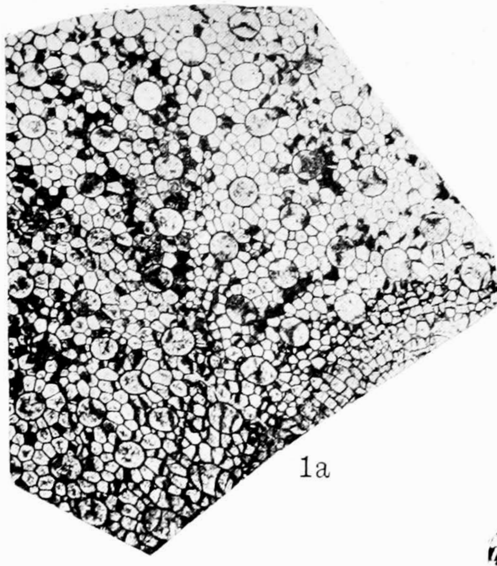
Heliolites daintreei Nicholson and Etheridge.



Heliolites and *Plasmopora*.



Plasmopora.



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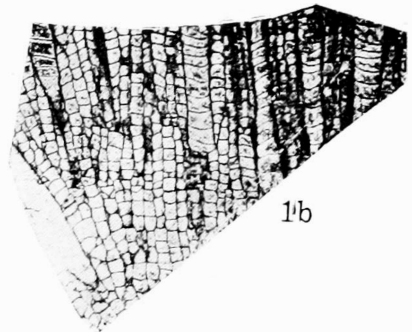

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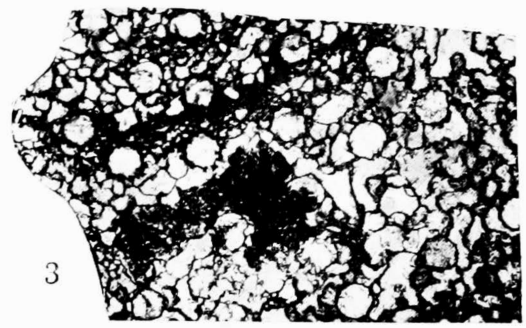

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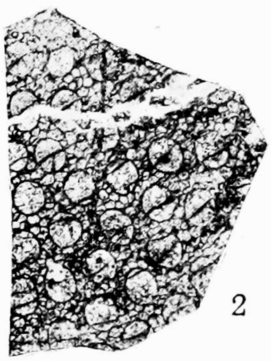
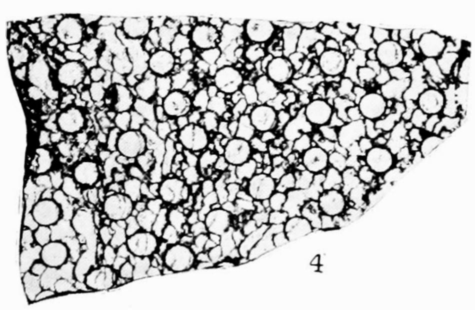


2



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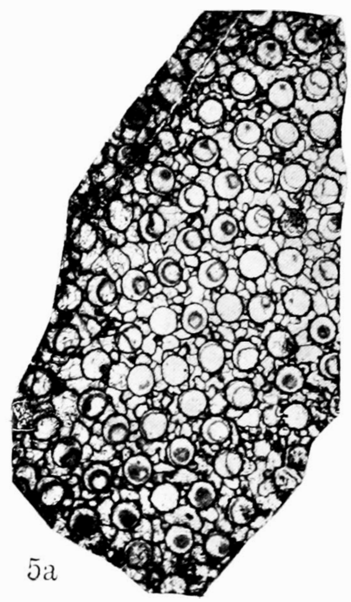

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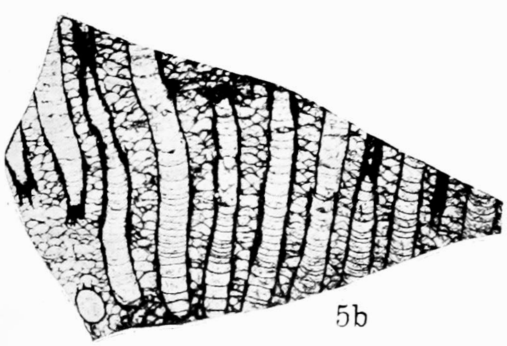
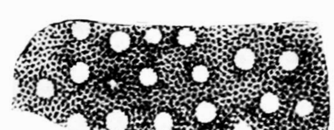


5b



6

Plasmopora, Propora and Heliopora.