MARISASTRIDAE (RUGOSA) FROM SOUTH-EAST DEVONSHIRE, ENGLAND

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ABSTRACT. The family Marisastridae Różkowska 1965 is emended. Species of *Marisastrum*, *Haplothecia*, and *Billingsastraea?*, including *H. ogwellensis* sp. nov., are described from the Middle and Upper Devonian of south-east Devon.

THE species described in the present paper were examined in the course of a detailed consideration of the colonial phillipsastreids and related corals from south-east Devon. They belong to three different genera which are assigned to the family Marisastridae Różkowska as emended herein. Species and genera placed in the Phillipsastraeidae will be described elsewhere, together with a review of the localities from which the material was obtained.

The following abbreviations are used: BM, British Museum (Natural History); OUM, University Museum, Oxford; GS(Geol. Soc. Coll.), Geological Society Collection in the Geological Survey Museum, London; TM, Torquay Museum; TM(JB), Jukes-Browne Collection in the Torquay Museum.

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SYSTEMATIC PALAEONTOLOGY

The genus *Marisastrum* was erected by Różkowska (1965, p. 262) with *Cyathophyllum sedgwicki* Edwards and Haime as type species. At the same time she proposed (p. 261) the family Marisastridae to include the new genus and *Ceratophyllum* Gürich. Różkowska gave the principal diagnostic features of the family as possession of a full trabecular fan based on a reflexed dissepimentarium, the absence of horseshoe dissepiments, and the presence of an epitheca. She regarded the family as belonging to the Phillipsastraeacea *sensu* Schouppé 1958.

Różkowska laid stress on corallite wall structure in her familial classification. In the writer's opinion, however, this factor is not of sufficient importance to justify such usage, although it may be of some significance at the generic level. Thus, some species may have an epitheca in some parts and a pseudotheca, or a complete lack of any wall structures, in others. *Phillipsastrea lacunosum* (Gürich), interpreted by Różkowska (1953, p. 45, pl. 6, figs. 3, 4) as secondarily phaceloid, is one example; another is *Phillipsastrea cincta* Smith (1945, p. 43, pl. 22, figs. 4*a–c*), a rather remarkable coral in which a well-formed

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epitheca is present between some corallites whilst others are united by dissepimental tissue only.

The form of the dissepimentarium in these corals appears to be the most important factor in classification at the family level. This is now recognized by most workers in separating the horseshoe-bearing phillipsastreids from the disphyllids with normal dissepiments. On the other hand, the large group of corals with reflexed dissepimentaria (and consequent broad trabecular fans) but without horseshoes have not been so clearly distinguished. Schouppé (1958), Strusz (1965), and Różkowska (1965) have all given different interpretations of their importance and classification. Schouppé (1958, p. 217) included forms with trabecular fans, both with and without horseshoe dissepiments, in the suborder Phillipsastraeacea. He put all the species he considered to lack horseshoe dissepiments, however, in one genus, *Billingsastraea*, which he classified with *Phillipsastrea* in the same family. *Billingsastraea* as thus interpreted by Schouppé (1958, p. 235) was a collection of species belonging to at least three different genera—*Billingsastraea sensu stricto*, *Marisastrum*, and the '*Phillipsastrea*' *pentagona* group, which will be discussed in detail elsewhere. Strusz (1965, p. 523) did not mention the suborder Phillipsastraeacea but separated the horseshoe-bearing genera in the family Phacellophyllidae. He drew attention to the group of corals with reflexed dissepimentaria lacking horseshoes as having trabeculae developed in 'disphylloid' fans. He did not distinguish them at the family level, however, but classified them with the disphyllids *sensu stricto* (having trabecular 'half-fans') in the family Disphyllidae.

Różkowska (1965, p. 261) was thus first to give family status to part of the group of corals with 'disphylloid' fans by erecting the Marisastridae. The writer believes, however, that the family should include all the genera with this basic dissepimental plan, irrespective of wall structure, and the family diagnosis is emended accordingly. It is doubtful whether the phillipsastreids and marisastrids form a group of sufficient importance and definition to warrant a separate suborder and for this reason the use of the Phillipsastraeacea is discontinued here.

Family MARISASTRIDAE Różkowska 1965 emend.

1965 Marisastridae Różkowska, p. 261.
e.p. 1965 Disphyllidae; Strusz, p. 525.

Type genus. *Marisastrum* Różkowska 1965, p. 262.

Diagnosis. Simple, fasciculate, or massive rugose corals; the latter may be cerioid, astraeoid, or thamnasterioid. Septa of two orders, major and minor, usually with spindle-shaped dilatation. Dissepimentarium reflexed. Septal trabeculae arranged in a broad fan on the dissepimental surface. No horseshoe dissepiments.

Included genera. *Marisastrum* Różkowska 1965; *Ceratophyllum* Gürich 1896 (*sensu* Różkowska 1965); *Haplothecia* Frech 1885; *Billingsastraea* Grabau 1917; *Paradisphyllum* Strusz 1965; *e.p. Mansuyphyllum* Fontaine 1961 *sensu* Strusz 1965.

Genus MARISASTRUM Różkowska 1965

1965 *Marisastrum* Różkowska, p. 262.

Type species. *Cyathophyllum sedgwicki* Edwards and Haime 1851, p. 387; 1853, p. 231, pl. 52, figs. 3, 3*a*.

Diagnosis. See Różkowska 1965, p. 262.

Marisastrum sedgwicki (Edwards and Haime) 1851

Plate 40, fig. 1

1851 *Cyathophyllum sedgwicki* Edwards and Haime, p. 387.
1853 *Cyathophyllum sedgwicki* Edwards and Haime; Edwards and Haime, p. 231, pl. 52, figs. 3, 3*a*.
?1855 *Cyathophyllum sedgwicki* Edwards and Haime; F. A. Roemer, p. 29, pl. 6, fig. 11.
1885 *Cyathophyllum sedgwicki* Edwards and Haime; Frech, p. 42, pl. 4, fig. 6.
non 1904 *Cyathophyllum sedgwicki* Edwards and Haime; Penecke, p. 147, pl. 5, figs. 3*a–c*.
?1913 *Cyathophyllum* (*Hexagoniophyllum*) *sedgwicki* (Edwards and Haime); Paeckelmann, p. 340.
?1922 *Cyathophyllum* (*Hexagoniophyllum*) *sedgwicki* (Edwards and Haime); Reed, p. 11, pl. 1, fig. 6.
non 1939 *Spinophyllum sedgwicki* (Edwards and Haime); Soshkina, p. 33, pl. 6, figs. 59, 60; pl. 12, fig. 96.
1948 *Prismatophyllum sedgwicki* (Edwards and Haime); Dembińska-Różkowska, p. 208, figs. 18*a*, *b*.
non 1951 *Phillipsastraea sedgwicki* (Edwards and Haime); Soshkina, p. 96, pl. 18, figs. 3, 4; pl. 23, fig. 3.
non 1952 *Phillipsastraea sedgwicki* (Edwards and Haime); Soshkina, p. 101, pl. 41, fig. 144.
1954 *Hexagonaria sedgwicki* (Edwards and Haime); Moenke, p. 465, text-figs. 3–5, 7; pl. 1, figs. 3–6.
non 1954 *Phillipsastraea sedgwicki* (Edwards and Haime); Soshkina, p. 46, pl. 10, figs. 1, 2.
e.p. 1958 *Phillipsastraea sedgwicki* (Edwards and Haime); Bulvanker, p. 119, ?pl. 55, fig. 3; *non* pl. 56, figs. 1*a*, *b*.
1965 *Marisastrum sedgwicki* (Edwards and Haime); Różkowska, p. 262, text-figs. 1, 2.

Lectotype (see Soshkina 1951, p. 96). The original of Edwards and Haime (1853, pl. 52, figs. 3, 3*a*), which is BM 48451. The specimen is labelled 'Middle Devonian, Torquay' and was found on 'Babbacombe Beach' according to Edwards and Haime; it is almost certainly a beach pebble.

Diagnosis and description. See Moenke 1954, p. 465; Różkowska 1965, p. 263.

Remarks. The opportunity is taken here to figure the lectotype of *Marisastrum sedgwicki*. As Różkowska suggests, this specimen, judging by the known European distribution of the species, is probably derived from the Frasnian. However, the species has never been recorded *in situ* from England, all the known material being, like the lectotype, cut from beach pebbles.

Measurements of diameter and septal number made on the lectotype and BM 15269 (figured Różkowska 1965, fig. 1) are summarized in Table 1.

EXPLANATION OF PLATE 40

Fig. 1. *Marisastrum sedgwicki* (Edwards and Haime). Polished surface of lectotype; ?Frasnian, beach pebble, Torquay, south Devon. BM 48451; ×2·5.

Figs. 2–5. *Marisastrum marmini* (Edwards and Haime). 2, Cross-section, BM R46096A. 3, Longitudinal-section, BM R46096B. 4, Cross-section, BM R46097A. 5, Longitudinal-section, BM R46097B. All Frasnian; thin bedded limestones near the southern end of Saltern Cove (SX 8950 5842), near Paignton, south Devon; ×3.

Marisastrum marmini (Edwards and Haime) 1851

Plate 40, figs. 2–5

e.p. 1851 *Cyathophyllum marmini* Edwards and Haime, p. 386, pl. 9, figs. 2, 2*a* (*non* figs. 3, 3*a*).
e.p. 1853 *Cyathophyllum marmini* Edwards and Haime; Edwards and Haime, p. 231, pl. 52, figs. 4, 4*a*.
?1951 *Phillipsastraea sedgwicki* (Edwards and Haime); Soshkina, p. 96, pl. 18, figs. 3, 4; *non* pl. 23, fig. 3.
?1952 *Phillipsastraea sedgwicki* (Edwards and Haime); Soshkina, p. 101, pl. 41, fig. 144 (upper two illustrations only).
?1954 *Phillipsastraea sedgwicki* (Edwards and Haime); Soshkina, p. 46, pl. 10, fig. 1.
1961 *Hexagonaria marmini* (Edwards and Haime); Semenoff-Tian-Chansky, p. 299.

Type material. The specimens figured by Edwards and Haime (1851) appear to be lost. There are, however, three topotypic specimens in the Milne Edwards Collection at the Muséum National d'Histoire Naturelle (Z63b (2 specimens) and Z63e) which agree closely with their figures 2 and 2*a* and which have been compared with the English material. The polished slab figured by Edwards and Haime (1853) from Torquay also appears to be missing.

Diagnosis. Marisastrum with non-carinate, moderately dilated spindle-shaped septa. Mean tabularium diameter about 5 mm. with between 18 and 21 major septa; ratio of tabularium to corallite area high. Increase peripheral and non-parricidal.

Description. Marisastrum marmini occurs as cerioid colonies of variable size. Most of the present specimens, from impure limestone, appear to be colonies only 5 to 10 cm. in diameter. Weathered calices have a wide central pit surrounded by a narrow reflexed platform.

Corallites are separated by a straight, or somewhat zigzagged epitheca which varies between 0·15 and 0·25 mm. in thickness. In very rare instances, however, it may fail to form between adjacent calices. A thin, dark, median line, the axial plane of Flower (1961, p. 26), can be seen where the epitheca is well preserved.

The septa are of two orders, major and minor, and may be slightly expanded at the epitheca. Usually there is a zone of septal dilatation about one-third to one-half the distance to the axis. The thickening is normally spindle-shaped, up to 0·4 or 0·5 mm. thickness, although rarely the septa may widen abruptly and taper towards the axis. When the zone of thickening approaches the epitheca, the septa may become wedge- rather than spindle-shaped. The major septa are very thin in the tabularium, with their ends slightly withdrawn from the axis and occasionally deflected in a weak vortex. The minor septa reach half-way, or somewhat less, to the axis and are less dilated than the major. The septa are non-carinate.

Horizontal tissue is generally well spaced in cross-section but appears more crowded in the zone of septal thickening. The tabularium junction is not clearly defined but corresponds approximately to the inner edge of this zone.

In longitudinal-section, the dissepimentarium is composed of several series of well-arched dissepiments. Their arrangement is somewhat variable but in the larger corallites they dip outwardly in a narrow peripheral zone. From the crest of the dissepimentarium flatter dissepiments slope steeply into the tabularium. On this reflexed surface, the septal trabeculae are arranged in a broad asymmetric fan. In immature corallites the dissepimentarium is very narrow and the dissepiments slope towards the axis throughout.

The tabulae are incomplete. There is an axial series of broad flat plates, frequently with downturned peripheral edges, which may occupy from one-half to nearly the whole

diameter of the tabularium. In the peripheral zone, horizontal, distally concave tabulae are irregularly developed.

Increase is peripheral and non-parricidal. Daughter corallites arise in the dissepimental tissue of the parent and may not form an epitheca until a late stage in their development.

Measurements of diameter and septal number are summarized in Table 1.

TABLE 1. Comparative data for species of *Marisastrum*

		M. sedgwicki	*M. marmini*
	N	2	4
d_t (mm.)	*O.R.*	3·2–4·2	4·3–6·2
	$\bar{x}$	3·7	5·1
n	*O.R.*	15–17	18–21
A_t/A	$\bar{x}$	0·13	0·2

d_t, tabularium diameter; *n*, number of major septa; A_t/A, ratio of tabularium to corallite area. *N*, number of colonies; *O.R.*, overall range; $\bar{x}$, arithmetic mean.

Discussion. Edwards and Haime (1851, p. 386; 1853, p. 231) included both fasciculate and cerioid forms in their original diagnosis but the species is here limited to the latter. The diameter of the corallites and the number of septa as stated by them agree closely with measurements made on the present material.

The specimens figured by Soshkina (1951, pl. 18, figs. 3, 4; 1952, pl. 41, fig. 144 (upper two illustrations only); 1954, pl. 10, fig. 1) as '*Phillipsastraea sedgwicki*' appear to be very close to the present material. They are certainly more similar to *Marisastrum marmini* than to *M. sedgwicki* but cannot be definitely identified as conspecific with the former.

M. marmini differs strongly from *M. sedgwicki*. The former has considerably larger tabularia and a high ratio of tabularium to corallite area (see Table 1); in addition, the septa are non-carinate. Of the species described by Moenke (1954) as *Hexagonaria*, all but her *H. hexagona* and *H. basaltiformis* should be assigned to *Marisastrum*. *M. phillipsastraeiformis* (Moenke) differs from *M. marmini* through strong carination of the septa. The other species, *M. mirabilis* (Moenke), *M. sanctacrucensis* (Moenke), and *M. davidsoni* (Edwards and Haime) *sensu* Moenke (1954) are all readily distinguished from *M. marmini*, particularly by their lower ratios of tabularium to corallite area.

M. marmini is recorded from the Frasnian of Ferques, near Boulogne, France; from the lens of Givetian or Frasnian limestone at Sidi Daoud, Chénoua, Algeria; from Frasnian limestones and beach pebbles from South Devonshire, England; and possibly also from the Frasnian of the Russian Platform and the southern Urals, U.S.S.R.

Measured material. BM R46096–9. All from thin-bedded limestones near the southern end of Saltern Cove (SX 89505842), near Paignton, South Devon; Frasnian.

Genus HAPLOTHECIA Frech 1885

1885 *Haplothecia* Frech, p. 68.
1935 *Haplothecia*; Lang and Smith, p. 549.
1940 *Haplothecia*; Lang, Smith, and Thomas, p. 65.
e.p. 1951 *Phillipsastraea*; Soshkina, p. 95.
e.p. 1952 *Phillipsastraea*; Soshkina, p. 101.
1956 *Haplothecia*; Hill, p. 280.
e.p. 1958 *Phillipsastraea*; Schouppé, p. 233.
e.p. 1960 *Phillipsastraea*; Spassky, p. 65.

Type species. Haplothecia filata (Schlotheim); Frech 1885, p. 68, pl. 6, figs. 7, 7*a* = *Madreporites filatus* Schlotheim *partim* (var.) α 1820, p. 359.

Diagnosis. Colonial rugose corals, cerioid or astraeoid. Septa of two orders, more or less dilated against the tabularium boundary. Septa strongly carinate, usually degenerating to perforate or spongy tissue at the corallite margin. Dissepiments small, well arched; dissepimentarium surface strongly reflexed. Tabulae complete or incomplete, predominantly distally concave.

Discussion. In his original diagnosis, Frech (1885, p. 68) stressed the carination of the septa and the peculiar character of the wall separating the corallites. Lang and Smith (1935, p. 549) also discussed the carination of the septa in *Haplothecia*, comparing that in the type species with the septal structure in '*Phillipsastraea pengellyi*'. They regarded *Haplothecia* as congeneric with *Phillipsastrea* although they thought that '. . . it may be found desirable in the future to retain the name, perhaps as a genomorph, for the forms exhibiting the peculiar septal degeneration . . .'. Their conclusion was, in effect, based on their belief that the species *pengellyi* differed from *Phillipsastrea sensu stricto* only through the character of the septa. I agree with their implication that *H. filata* and '*P*'. *pengellyi* are congeneric, but consider both distinct from *Phillipsastrea*.

The latter genus should be restricted to forms possessing horseshoe dissepiments. Schouppé (1958, p. 235) was similarly of this opinion but he claimed that horseshoe dissepiments are also developed in the type species of *Haplothecia*. He wrote (op. cit., p. 203) that 'by reason of the existence of horseshoes and the corresponding basic structure, I thus regard *Haplothecia* as a synonym of *Phillipsastr.* d'Orb., 1849 *sensu*'. On careful examination, however, Schlotheim's original specimen of *Madreporites filatus* (var.) α (see Pl. 41, fig. 2) shows no sign of horseshoe dissepiments.

For this reason, *Haplothecia* is here regarded as not closely related to *Phillipsastrea* and is placed in a different family. Within the Marisastridae, *Haplothecia* is distinguished by its peculiar septal structure and the dominance of distally concave plates in the tabularium.

Distribution. Frasnian of Germany (Harz) and U.S.S.R. (Urals); upper Givetian and Frasnian of south-west England.

Haplothecia filata (Schlotheim) 1820

Plate 41, figs. 1, 2

e.p. 1820 *Madreporites filatus* Schlotheim (var.) α, p. 359.
1885 *Haplothecia filata* (Schlotheim); Frech, p. 68, pl. 6, figs. 7, 7*a*.
1935 *Phillipsastraea filata* (Schlotheim); Lang and Smith, p. 549.
non 1951 *Phillipsastraea filata* (Schlotheim); Soshkina, p. 98, text-fig. 36, pl. 18, fig. 1.
non 1952 *Phillipsastraea filata* (Schlotheim); Soshkina, p. 101, pl. 42, fig. 141.
non 1960 *Phillipsastraea filata* (Schlotheim); Spassky, p. 66, pl. 25, figs. 3, 4.

Lectotype (see Frech 1885, p. 68). The original of *Madreporites filatus* Schlotheim (var.) α 1820, p. 359, which is in the collections of the Institut für Paläontologie und Museum der Humboldt-Universität, East Berlin. From Ibergerkalk, Bad Grund, Harz, Germany; Frasnian.

Diagnosis. Cerioid *Haplothecia* with tabularium diameters ranging from 1·4 mm. to 2·0 mm. and with 11 to 15 major septa. Septa strongly carinate and failing between the carinae peripherally. Dissepiments small, globose. Tabulae incomplete, horizontal, and distally concave.

Description. Cerioid colony with a straight, rarely zigzagged epitheca. The axial plane of Flower (1961, p. 26) is clearly seen.

Septa strongly carinate in the dissepimentarium. Towards the periphery the carinae become irregular in form and distribution and the septa frequently bifurcate. The carinae are often connected by clear structureless calcite but, towards the periphery in particular, the septa are discontinuous. The minor septa do not enter the tabularium but the major continue, smoothly attenuated, to the axis. Here there may be some fusion between adjacent or opposite septal ends.

In cross-section, the dissepimental tissue appears somewhat crowded and, particularly in the peripheral parts, rather irregular in shape.

In longitudinal-section, the dissepiments are small, globose, and evenly developed. The dissepimentarium surface is strongly reflexed, and upon it the septal trabeculae are arranged in a broad fan. The tabularium is composed of horizontal, incomplete, distally concave tabulae. Any axial structure is obscured by septal traces.

Measurements of tabularium diameter and septal number made on the lectotype are summarized in Table 2.

Discussion. The brief description above is based on the lectotype only. It is included here as this specimen has not been described since Frech (1885, p. 68), and for comparison with the English species of *Haplothecia.*

The species is only so far definitely known from the Ibergerkalk in the German Harz. The specimen figured by Soshkina (1951, pl. 18, fig. 1; 1952, pl. 42, fig. 141) is not conspecific with *H. filata*, although very similar to it and undoubtedly congeneric.

Haplothecia ogwellensis sp. nov.

Plate 41, figs. 3–6

Holotype. OUM D542; Lower Frasnian limestones, road cutting, 40 yd. west of Ramsleigh quarry entrance (SX 8441 7005), East Ogwell, near Newton Abbot, south Devon.

Diagnosis. Cerioid *Haplothecia* with mean tabularium diameter 1·9 mm. and with between 10 and 14 major septa. Septa strongly carinate, rarely discontinuous peripherally. Dissepiments small, well arched. Tabulae incomplete with a narrow axial series of dome-shaped plates.

Description. The colonies, the external features of which are unknown, are apparently cerioid although recrystallization obscures the structure of the wall. This is usually strongly zigzagged, delimiting polygonal corallites. Only rarely does the wall break down for a short length of the corallite margin.

EXPLANATION OF PLATE 41

Figs. 1, 2. *Haplothecia filata* (Schlotheim). 1, Cross-section, ×3. 2, Longitudinal-section, ×6. Both cut from lectotype; Frasnian, Ibergerkalk, Bad Grund, Harz, Germany. Specimen un-numbered in the collections of the Institut für Paläontologie und Museum der Humboldt-Universität, East Berlin.

Figs. 3–6. *Haplothecia ogwellensis* sp. nov. 3, Cross-section of holotype, OUM D542/p1, ×3. 4, Longitudinal-section of holotype, OUM D542/p2, ×6. 5, Cross-section of topotype, OUM D543/p1, ×3. 6, Longitudinal-section of topotype, OUM D543/p2, ×3. All from Lower Frasnian limestone, road cutting, 40 yd. west of Ramsleigh quarry entrance (SX 8441 7005), East Ogwell, near Newton Abbot, south Devon.

The septa, major and minor, are 0·05 mm. thick peripherally and straight to slightly flexed in the dissepimentarium. They are variably dilated, up to *c.* 0·2 mm. thickness, against the tabularium boundary. Some major septa, however, may be virtually unthickened and the minor septa, which do not enter the tabularium, are less dilated than the major and frequently uniformly attenuated throughout. The major septa taper in the tabularium to 0·02–0·04 mm. width. Their axial ends may curve sharply to become confluent with septa in the adjacent quadrant, or they may be free, or rarely fused in small groups. An axial area, 0·5 to 0·25 mm. in diameter, is usually clear of septa.

The septa are variably carinate, usually with five carinae, 0·15 to 0·2 mm. wide, developed in 1 mm. of septal length. Normally the carinae are separated by clear structureless calcite but rarely this is missing and the septa are discontinuous.

Dissepiments are commonly uniserial between adjacent septa. In cross-section, the tabularium boundary is clearly but not sharply defined.

In longitudinal-section, the dissepiments are small, well arched, and between 0·1 and 0·3 mm. apart vertically. The surface of the dissepimentarium is reflexed with the crest *c.* 0·5 mm. outside the tabularium junction. The swollen isolated trabeculae forming the carinae are arranged in an asymmetric fan on the dissepimental surface, bending over to enter the tabularium almost horizontally.

The tabulae are mainly incomplete. There is a peripheral horizontal series of flat to distally concave tabulae, with an axial series, one-third to one-quarter of the tabularium diameter across, of dome-shaped plates. The latter appear to be fairly continuous but unfortunately they are usually partially obscured by the traces of major septa.

Quantitative data for this species are summarized in Table 2.

TABLE 2. Comparative data for species of *Haplothecia* (for symbols see Table 1)

		H. filata	*H. ogwellensis*	*H. pengellyi*
	N	lectotype only	2	17
d_t (mm.)	*O.R.*	1·4–2·0	1·5–2·4	2·0–4·9
	$\bar{x}$	1·65	1·9	3·55
n	*O.R.*	11–15	10–14	13–24
A_t/A	$\bar{x}$	0·06	0·095	0·1

Discussion. Haplothecia ogwellensis is very similar in general appearance to *H. filata.* The limited data available for these two species (Table 2) show the most striking difference in the ratios of tabularium to corallite area. This contrast is immediately apparent on a cursory inspection of the two species. They also show slight differences in tabularium size and number of major septa but the variation in both species is virtually unknown due to lack of material.

H. ogwellensis also differs from *H. filata* in having a zigzagged wall separating the corallites as opposed to the straight epitheca of the latter. In addition, carination and septal degeneration is stronger in *H. filata* and begins to approach that seen in *H. pengellyi.*

H. ogwellensis is known so far only from the type locality.

Measured material. OUM D542–3.

Haplothecia pengellyi (Edwards and Haime) 1851

Plate 42, figs. 1–5; Plate 43, figs. 1, 2

e.p. 1840 *Astrea* (*Siderastrea*) *hennahii* Lonsdale, p. 697, pl. 58, fig. 3*a* (*non* figs. 3, 3*b*).
1851 *Smithia pengillyi* Edwards and Haime, p. 422.
1853 *Smithia pengellyi* Edwards and Haime; Edwards and Haime, p. 241, pl. 55, figs. 1, 1*a*, 1*b*.
1883 *Phillipsastraea pengellyi* (Edwards and Haime); C. F. Roemer, p. 390, text-fig. 91.
e.p. 1885 *Phillipsastrea hennahi* (Lonsdale); Frech, p. 59 (synonymy *pars*), pl. 5, ?fig. 4.
non 1951 *Phillipsastraea pengelli* (Edwards and Haime); Soshkina, p. 100, pl. 19, fig. 2.
non 1952 *Phillipsastraea pengelli* (Edwards and Haime); Soshkina, p. 102, pl. 41, fig. 146.

Lectotype (see Soshkina 1951, p. 100). The original of Edwards and Haime 1853, pl. 55, fig. 1; unfortunately this specimen is lost.

In their original description of the species, Edwards and Haime (1851, p. 422) quoted as synonymous Lonsdale's (1840, pl. 58) fig. 3*a*. Smith (1917, p. 289) was of the opinion that GS (Geol.Soc.Coll.) 6192 (Pl. 42, fig. 1) was probably the specimen figured by Lonsdale, although this cannot be definitely proved. If, however, Smith is correct, GS(Geol.Soc.Coll.) 6192 appears to be the only survivor of the original syntypes.

The lectotype was stated by Edwards and Haime to come from the Devonian of Torquay, south Devon.

Diagnosis. Astraeoid tending to thamnasterioid *Haplothecia* with tabularium diameter ranging from 2·0 to 4·9 mm. and between 13 and 24 major septa. Septa heavily carinate, usually degenerating at the periphery to a spongy state. Dissepiments small, globose; dissepimentarium surface strongly reflexed. Tabulae incomplete.

Description. The colonies, of which the external features are unknown, are astraeoid tending to thamnasterioid. The margins of individual corallites are usually indicated by a sharp geniculation of the peripheral septal ends although these seldom join together to form a distinct pseudotheca. The septa are irregularly, rarely perfectly, confluent from one corallite to the next. Varying degrees of peripheral septal break-down contribute to the diffuse nature of the pseudotheca.

The septa, both major and minor, exhibit excessive degeneration in the dissepimentarium characteristic of the species. Usually the septa are thick and solid only in a zone surrounding the tabularium where their width varies between 0·2 and 0·5 mm. In this zone septa may apparently be uni- or multi-trabecular. Peripherally, the trabeculae become separated, causing the septa to become strongly and irregularly carinate. The carinae are usually of the yard-arm type but may be xyloid when thickened trabeculae alternate on either side of the septal axis. Frequently individual trabeculae become completely isolated at the periphery with up to four across the septal width.

The character and extent of the septal degeneration is highly variable both within and between colonies. Some septa are uniformly thin with a light yard-arm carination of *c.* 0·2 mm. width throughout the dissepimentarium. In others, separation and isolation of the trabeculae towards the corallite margins may form a spongy mass of tissue up to 1 mm. in width.

The minor septa penetrate slightly into the tabularium but the major become smoothly attenuate and continue, *c.* 0·07 mm. thick, more or less to the axis. The axial ends of the

EXPLANATION OF PLATE 42

Figs. 1–5. *Haplothecia pengellyi* (Edwards and Haime). 1, Cross-section of suggested syntype, GS(Geol. Soc.Coll.) 6192, ×3. 2, Cross-section, BM R23257. ×3. 3, 4, Longitudinal-sections, BM R23257, ×4. 5, Cross-section, BM R23252, ×3. All from upper Givetian limestone, Barton quarry, Torquay, south Devon.

major septa are frequently slightly dilated and may fuse in small groups. Sometimes septa in adjacent quadrants are continuous or subconfluent periaxially, imparting a bilateral appearance to the tabularium.

Dissepiments are uniserial, becoming multiserial peripherally, between adjacent septa. In cross-section, the tabularium junction is usually clearly but not sharply defined.

In longitudinal-section, the dissepiments are small and fairly globose with an average vertical spacing of *c.* 0·2 mm. The surface of the dissepimentarium is strongly reflexed with the crest between 0·6 mm. and 1 mm. outside the tabularium. Septal trabeculae are arranged in a broad fan at right angles to this surface, curving over to enter the tabularium at a low angle.

The tabulae are incomplete. There is a broad peripheral series of horizontal plates, slightly distally concave and with a vertical spacing of between 0·2 and 0·3 mm. In some cases, steeply sloping periaxial vesicles are also present. The tabularium axis is frequently obscured by septal traces. There is evidence in some corallites, however, for a narrow, irregularly developed, axial series of dome-shaped plates.

Increase is peripheral and non-parricidal, the young individual developing in the dissepimental tissue equidistant from the surrounding adult tabularia.

Measurements made on representatives of this species are summarized in Table 2.

Discussion. Although the lectotype of *Haplothecia pengellyi* is lost, both Edwards and Haime's (1853, pl. 55, figs. 1, 1*a*, 1*b*) and Lonsdale's (1840, pl. 58, fig. 3*a*) illustrations are sufficiently characterized to allow the identification of the species.

There is only one, questionable, record of the species outside England, by Frech (1885, p. 59, pl. 5, fig. 4), who figured a specimen from the Upper Devonian of Löhren near Dillenburg. He considered *H. pengellyi* to be conspecific with *Phillipsastrea hennahi*, attributing the larger size and peculiar septal structure in the former to specific variation. Frech was also obviously unaware of the considerable difference in the longitudinal-sections of these two species.

The specimen figured by Soshkina (1951, pl. 19, fig. 2; 1952, pl. 41, fig. 146) as '*Phillipsastraea pengelli*' [*sic*] has a well-formed pseudotheca and lacks the septal degeneration characteristic of the species. It is not conspecific with the English material.

H. pengellyi differs from both *H. filata* and *H. ogwellensis* by its larger size and correspondingly large septal number (see Table 2), its grade of septal degeneration, and its poorly developed pseudotheca.

The species is known in England from the upper Givetian limestones of Lummaton and Barton quarries, Torquay, and was recorded by Edwards and Haime (1851, p. 422) from Plymouth, south Devon.

Measured material. TM(JB) numbers 106, 110, 121–2, 124–5, 129, 131–3, 133*a*, 136–8, 140–1, 143; all from Barton quarry.

Genus BILLINGSASTRAEA Grabau 1917

1917 *Phillipsastraea* (*Billingsastraea*) Grabau, p. 957.
1937 *Billingsastraea*; Stumm, p. 437.
1937 *Radiastraea* Stumm, p. 439.
1940 *Billingsastraea*; Lang, Smith, and Thomas, p. 27.
1940 *Radiastraea*; Lang, Smith, and Thomas, p. 113.
1949 *Billingsastraea*; Stumm, p. 35.
1951 *Billingsastraea*; Ehlers and Stumm, p. 85.

1953 *Billingsastraea*; Ehlers and Stumm, p. 1.
1956 *Billingsastraea*; Hill, p. 280.
e.p. 1958 *Billingsastraea*; Schouppé, p. 235.
1964 *Billingsastraea*; Oliver, p. 2.
1964 *Radiastraea*; Pedder, p. 446.
e.p. 1965 *Billingsastraea*; Strusz, p. 547.

Type species. Phillipsastrea verneuili Edwards and Haime 1851, p. 447, pl. 10, fig. 5. Their specimen (which appears to be lost) was stated by Edwards and Haime to have come from Wisconsin. It is thought to have been a drift specimen originating from the Onondaga or Bois Blanc Formations of Ontario, Canada, or Michigan, U.S.A. (see Stumm 1949, p. 35).

Diagnosis. Astraeoid, thamnasterioid, or slightly aphroid rugose corals. Septa of two orders, usually undilated throughout and frequently carinate. Dissepimentarium reflexed. Tabulae incomplete.

Discussion. Oliver (1964) has given a valuable review of this genus. Schouppé (1958, p. 235) assigned to *Billingsastraea* a number of species formerly classified with *Phillipsastrea* but lacking horseshoe dissepiments. As Oliver (op. cit.) has pointed out, this is unsatisfactory as *Billingsastraea* differs significantly in morphological detail from the European forms considered by Schouppé, particularly in the septal dilatation characteristic of the latter. Several of these species are placed in a new genus to be described elsewhere and others have been placed by Różkowska (1965) in *Marisastrum*. Only one English species, *Acervularia battersbyi* Edwards and Haime, is here tentatively referred to *Billingsastraea*.

Stumm (1937, p. 439) erected *Radiastraea* on the mistaken identification of an aulos in the axial area of the type species, *R. arachne* Stumm. He later (1949, p. 35) corrected his error and placed *Radiastraea* in his synonymy of *Billingsastraea*. Pedder (1964, p. 447), however, reconstituted *Radiastraea* on a distinction in dissepimental structure, stating that 'The dissepiments in *Billingsastraea* are very uneven in size and appear to bear septal crests, whereas in the other (*Radiastraea*) they are of the normal disphyllid type.' This distinction is very difficult to detect in Pedder's illustrations (compare Pedder 1964, pl. 73, fig. 1 with Ehlers and Stumm 1953, pl. 1, fig. 3 of *Billingsastraea verneuili*) and, in the writer's opinion, is insufficient to warrant generic separation.

Billingsastraea differs from both *Marisastrum* and *Haplothecia* in possessing unthickened or faintly dilated septa. In addition, species of *Marisastrum* are exclusively cerioid, whilst species of *Haplothecia* are characterized by heavy carination and septal breakdown.

Distribution. Coblenzian to Givetian and ?Frasnian of North America (after Oliver 1964, p. 2); middle Givetian of south Devon, England.

EXPLANATION OF PLATE 43

Figs. 1, 2. *Haplothecia pengellyi* (Edwards and Haime). 1, Cross-section, BM R30983, ×3. 2, Longitudinal-section, BM R30984, ×4. Both from upper Givetian limestone, Barton quarry, Torquay, south Devon.

Figs. 3–5. *Billingsastraea? battersbyi* (Edwards and Haime). 3, Cross-section, ×3. 4, 5, Longitudinal-sections, ×4. Middle Givetian limestones, Wolborough quarry, Newton Abbot, south Devon; BM R23401.

Billingsastraea? battersbyi (Edwards and Haime) 1851

Plate 43, figs. 3–5

1851 *Acervularia battersbyi* Edwards and Haime, p. 419.
1853 *Acervularia battersbyi* Edwards and Haime; Edwards and Haime, p. 239, pl. 54, figs. 2, 2*a*.
1879 *Acervularia battersbyi* Edwards and Haime; Quenstedt, p. 535, pl. 162, fig. 37.
e.p. 1885 *Phillipsastrea ananas* (Goldfuss); Frech, p. 49 (synonymy *pars* only).

Type material. Edwards and Haime's original specimens are missing.

Diagnosis. Astraeoid tending to thamnasterioid *Billingsastraea?* with mean tabularium diameter 3·91 mm. and between 17 and 22 major septa. Septa, major and minor, may be uniformly attenuate, or more usually faintly dilated in a zone surrounding the tabularium; they are not carinate. Dissepiments low, elongate; dissepimental surface gently reflexed. Tabulae normally flat-topped domes.

Description. Colony shape and size is unknown but the largest fragment measured 14·5 cm. by 11 cm. in surface area.

The species is astraeoid tending to thamnasterioid. The peripheral septal ends are geniculate and abutting or more rarely confluent with those of neighbouring corallites. Sometimes septa may have free ends although these are never withdrawn from the corallite margins.

The septa, straight or slightly sinuous, are very thin peripherally, rarely exceeding 0·1 mm. and usually *c.* 0·05 mm. in thickness. Septal thickening is variable and some septa are uniformly attenuate throughout. Others are slightly dilated in a zone of up to 1·5 mm. width surrounding the tabularium. Septa may reach 0·3 mm. in this zone but usually they are 0·1 to 0·15 mm. thick.

Minor septa end more or less at the tabularium junction but the major continue almost to the axis. The axial ends of the major septa are usually free and may bear a slight elongate thickening.

Dissepiments are usually uniserial between adjacent septa. In cross-section, the tabularium boundary is clearly but not sharply defined.

In longitudinal-section, the dissepimentarium is composed of several series of rather low, elongate dissepiments. The dissepimental surface is gently reflexed with the crest usually *c.* 1 mm. outside the tabularium junction. Dissepiments forming the crest may be slightly more globose than the rest.

The tabularium structure is rather obscure in the available material. Tabulae appear to be complete or incomplete flat-topped domes with rare periaxial elements.

Quantitatively, the tabularium diameter ranges from 3·2 to 5·0 mm. with a mean value of 3·9 mm. There are between 17 and 22 major septa. The tabularia are evenly spaced and the ratio of tabularium to corallite area is *c.* 0·08.

Discussion. This material agrees well with the descriptions and figures of Edwards and Haime (1851, p. 419; 1853, p. 239, pl. 54, figs. 2, 2*a*). Particularly, they drew attention to the 'feeble development of the outer walls' and the 'very slender . . . slightly thickened' septa. Edwards and Haime gave the diameter of the calices (= tabularia) as 2 lines (= *c.* 4·2 mm.) or somewhat more, with 36 septa; this is comparable with the data for the present material.

Frech (1885, pl. 2, figs. 5*a*, *b*) illustrated a specimen from the Ibergerkalk (Frasnian;

Bad Grund, Germany) as a variety of *Phillipsastrea ananas* corresponding to *Acervularia battersbyi*. The character of the septal thickening and the strong external pseudotheca, however, distinguish Frech's specimen from the present material.

Acervularia battersbyi differs from the American species of *Billingsastraea* chiefly through the frequent, slight dilatation of the septa, which are also non-carinate. Uniformly attenuate septa are considered by Oliver (1964, p. 2) to be an important characteristic of the genus. Nevertheless, as the present species appears to agree in all other respects with typical members of *Billingsastraea*, it is tentatively assigned to that genus.

Edwards and Haime (1851, p. 419; 1853, p. 239) stated that the species is found both at Torquay and Newton. All the specimens examined by the writer, however, come from middle Givetian limestones in Wolborough quarry, Newton Abbot, which is probably their 'Newton'; no specimens are known from Torquay.

Measured material. OUM D288 (BM R1460 is cut from the same block), BM R23401, TM 120/7.

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ADDENDUM

Since this paper was written, Pedder (1966, p. 182) has published a description of *Haplothecia filata* also based on the lectotype. He provisionally places *Haplothecia* in the Disphyllinae, which he regards as a subfamily of the Cyathophyllidae.

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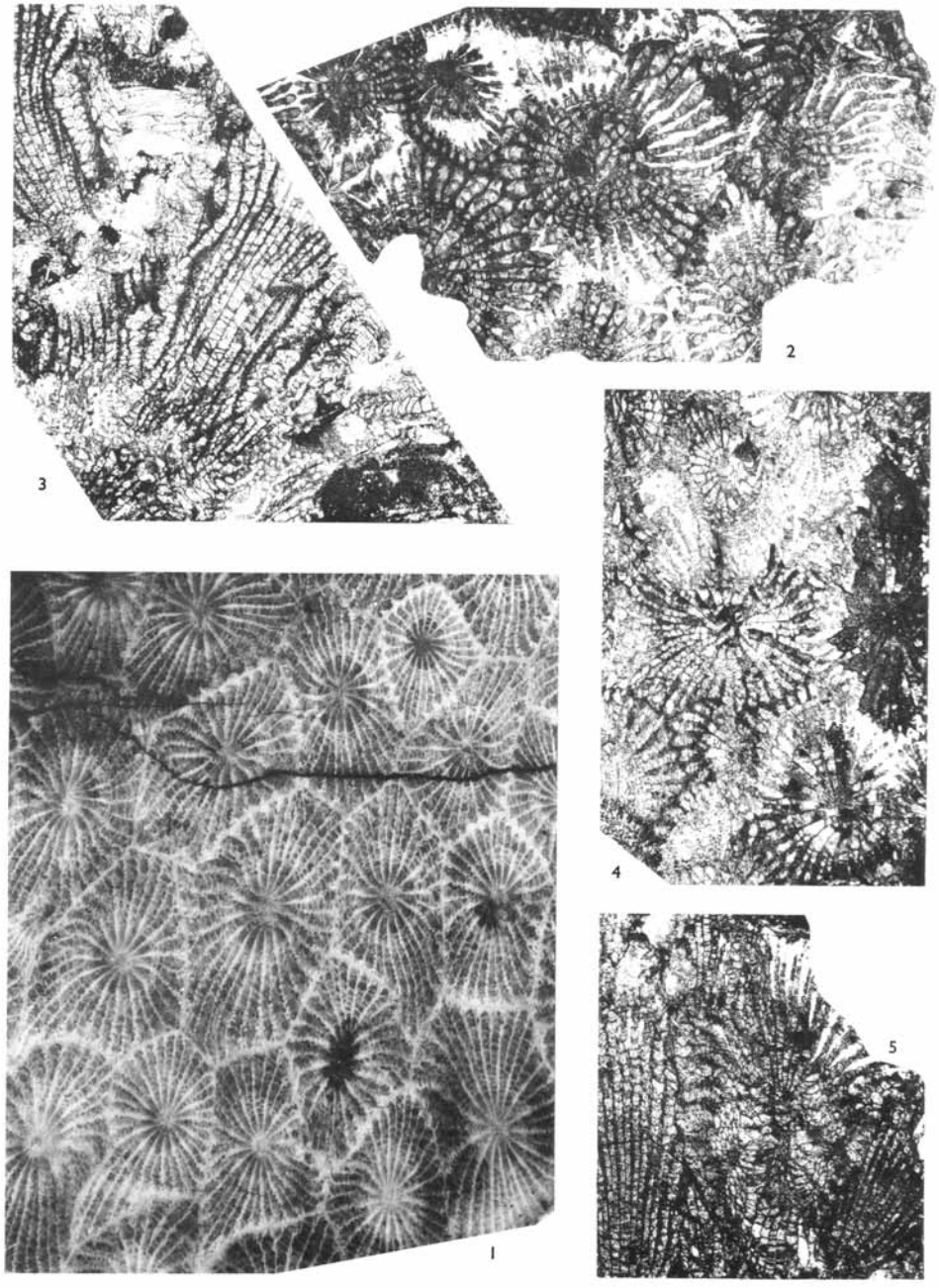
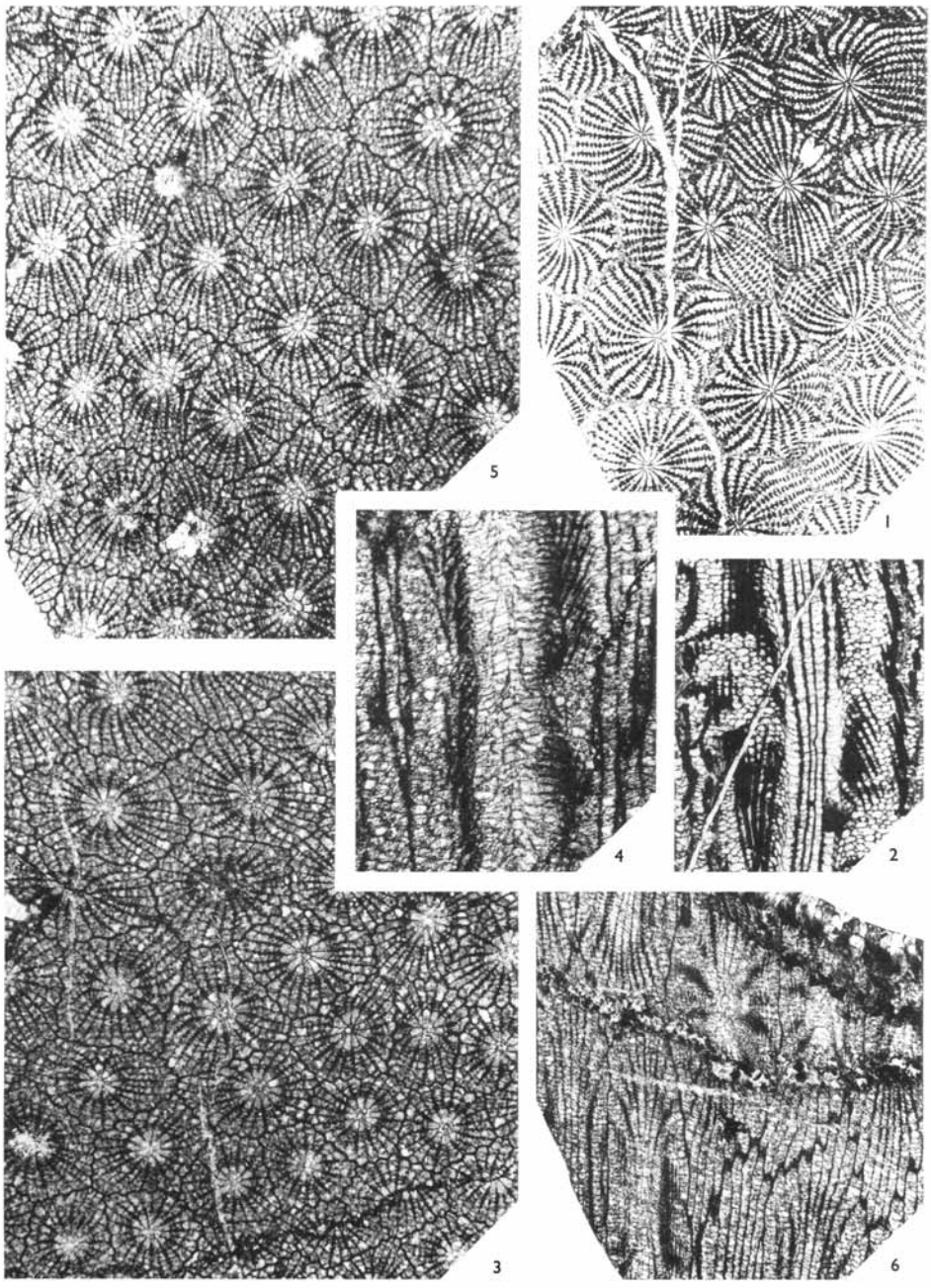
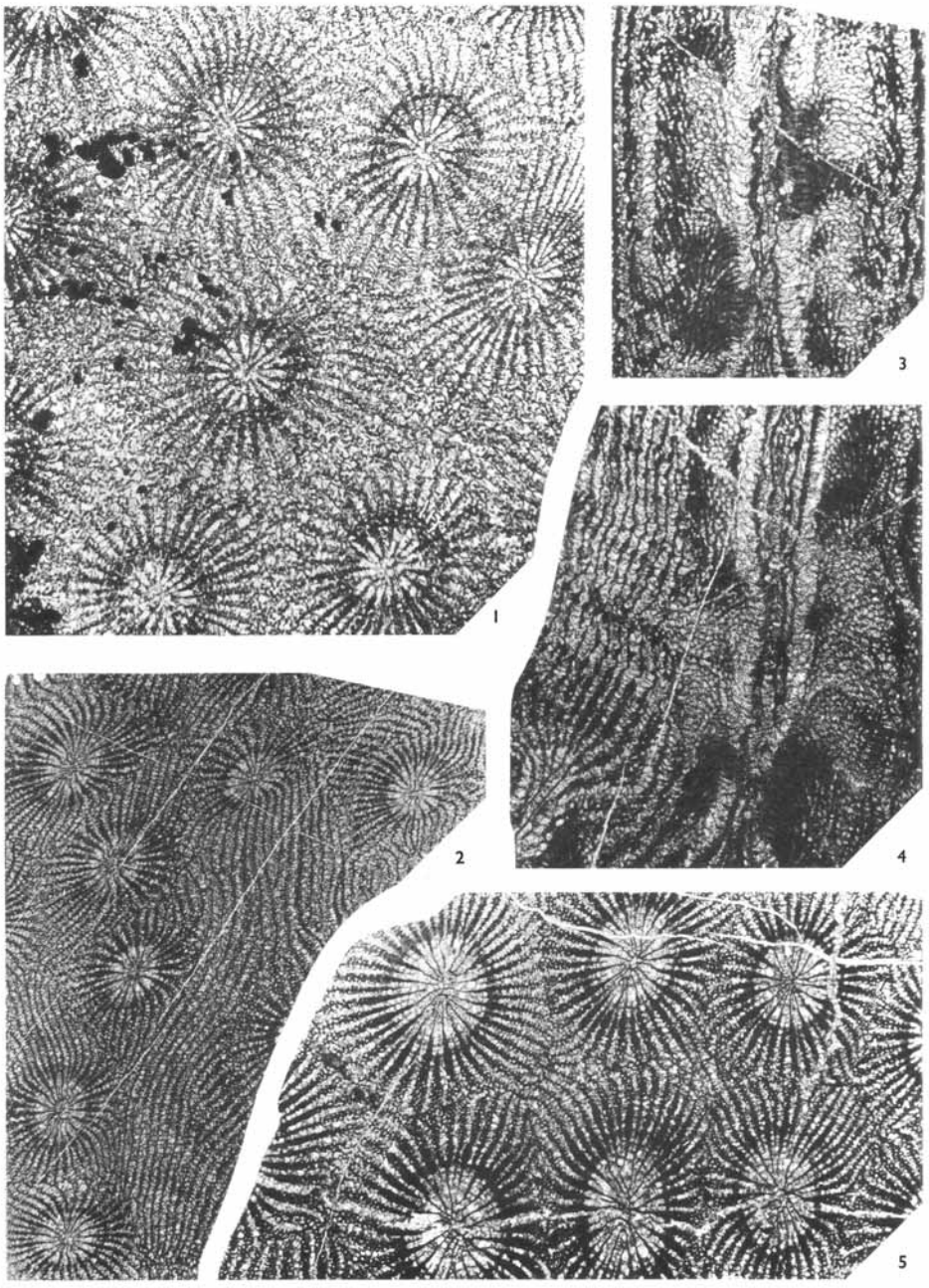


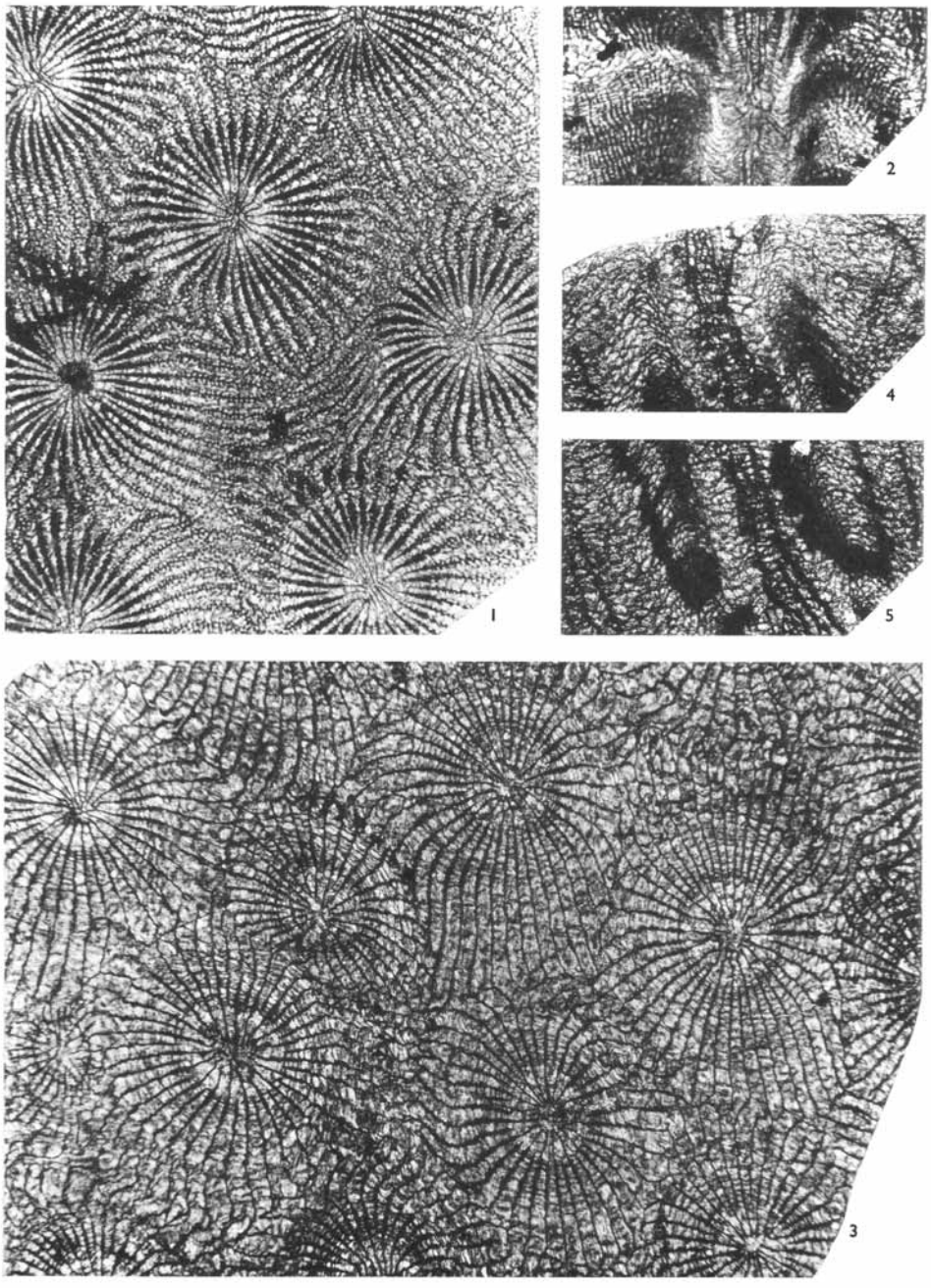
SCRUTTON, Devonian Marisastridae



SCRUTTON, Devonian Marisastridae



SCRUTTON, Devonian Marisastridae



SCRUTTON, Devonian Marisastridae