TABULATE CORALS FROM THE ILFRACOMBE BEDS (MIDDLE-UPPER DEVONIAN) OF NORTH DEVON

by the late F. J. W. HOLWILL

ABSTRACT. Twenty species of tabulate corals from the Ilfracombe Beds of North Devon are figured and described; of these, Clauvella undulatula is a new species and most of the others are recorded for the first time from North Devon.

LITTLE or no systematic palaeontological work has been done on the Ilfracombe Beds for the last hundred years; Phillips (1841) and Edwards and Haime (1853) are the only authors who have figured corals from these beds though many others have published fossil lists; of these, Valpy (1867) and Etheridge (1867) are the most important, though Etheridge drew much of his information from Valpy's earlier work. Webby (1964) has described a number of rugose corals from the Ilfracombe Beds of Somerset but has only figured one tabulate coral.

The accompanying table shows all the tabulate corals previously recorded from North Devon (Table 1). Unfortunately, none of these corals is accurately localized and many of the original specimens have been lost; I have therefore re-collected throughout the whole coastal area and this work has largely substantiated previous records, but in addition sixteen other species have been recognized, one of which is new.

STRATIGRAPHY

The Ilfracombe Beds consist of a series of slates, often calcareous, with some arenaceous bands and occasional limestones. Four distinctive limestones have been named and described in earlier papers (Holwill 1962, 1964) and it is from these limestones that the corals have been obtained. The evidence for the age of the limestones has also been discussed in the above two papers and the conclusions are summarized in the following table:

<table>
<thead>
<tr>
<th>Limestone</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>David's Stone Limestone</td>
<td>Frasnian</td>
</tr>
<tr>
<td>Combe Martin Beach Limestone</td>
<td>?</td>
</tr>
<tr>
<td>Jenny Start Limestone</td>
<td>Givetian</td>
</tr>
<tr>
<td>Rillage Limestone</td>
<td></td>
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</tbody>
</table>

The limestones are separated by thick successions of unfossiliferous slate and the precise boundary between Middle and Upper Devonian cannot be defined.

In the Jenny Start Limestone there is an abundant fauna of rugose corals associated with occasional tabulates; in the David's Stone Limestone however, tabulate corals are locally numerous (for example at Broadstrand near Ilfracombe), while Rugosa are almost completely absent. The whole of North Devon is strongly folded and faulted so

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that the majority of the corals are distorted and frequently recrystallized. Corals form the dominant element in the fauna though crinoid fragments are widespread and there are occasional brachiopods (especially in the Combe Martin Beach Limestone), gastro-

**TABLE 1. Tabulate corals previously recorded from North Devon**

<table>
<thead>
<tr>
<th>Species</th>
<th>First recorded</th>
<th>Substantiated</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Favositites cervicornis (de Blainville)</td>
<td>Etheridge 1867</td>
<td></td>
<td>Thamnopena cervicornis</td>
</tr>
<tr>
<td>F. fibrosus Edwards and Haine</td>
<td>Phillips 1841</td>
<td></td>
<td>Thamnopena polynema</td>
</tr>
<tr>
<td>F. polymorpha (Goldfuss)</td>
<td>Phillips 1841</td>
<td></td>
<td>Thamnopena polymorpha</td>
</tr>
<tr>
<td>Heliolites pumilus Goldfuss</td>
<td>Etheridge 1867</td>
<td></td>
<td>Thamnopena pumilus</td>
</tr>
<tr>
<td>Alcadelia suborbicularis Lamarck</td>
<td>Etheridge 1867</td>
<td></td>
<td>Thamnopena polyformata</td>
</tr>
<tr>
<td>Favositites robusta Edwards and Haine</td>
<td>Etheridge 1867</td>
<td></td>
<td>Thamnopena robusta</td>
</tr>
<tr>
<td>Michelinia antiqua (M'Coy)</td>
<td>Valpy 1867</td>
<td></td>
<td>Thamnopena antiqua</td>
</tr>
</tbody>
</table>

**Syringopora sp.** Valpy 1867

**Cladorhmonia sp.** Valpy 1867

probably a synonym of *Aulopora* figured below.

![Map of the North Devon Coast between Combe Martin and Ilfracombe showing the localities mentioned in the text.](image)

**TEXT-FIG. 1.** Map of the North Devon Coast between Combe Martin and Ilfracombe showing the localities mentioned in the text.

pods and orthoceratids (in the Rillage Limestone). The main localities mentioned in the text are shown on the accompanying map (text-fig. 1).

**Acknowledgements.** The field work connected with this study was carried out with financial assistance from the Central Research Fund of the University of London; this help is gratefully acknowledged.

**Note.** Dr. C. T. Scrutton (British Museum (Nat. Hist.) has seen the manuscript through the press.
SYSTEMATIC DESCRIPTIONS

All the specimens discussed below are in the Murchison Museum, Imperial College, London, and their catalogue numbers are prefixed MM in the text. The only exception is *Pleurodictyum sp.* which is in the British Museum (Nat. Hist.).

**ORDER TABULATA**

Family *Chaetetidae* Edwards and Haime 1850
Sub-family *Chaetetinae* Edwards and Haime 1850

**Genus Chaetetes** Fischer (in Eichwald 1829)

1829 *Chaetetes* Fischer (in Eichwald), p. 197.
1899 *Litophyllum* Etheridge, p. 178.
1939 *Chaetetes*; Lecompte, p. 154 (em syn.).
1958 *Chaetetes*; Stasinska, p. 224.

*Diagnosis.* Massive tabulate corals with narrow, straight, or slightly curved, prismatic corallites making an angle of 90° with the outer surface. Septa are absent or represented by rudimentary spines. No mural pores. Tabulae horizontal and tending to occur at the same level in adjacent corallites. Increase by fission.

*Remarks.* Etheridge (1899, p. 178) erected the genus *Litophyllum* for chaetetid-like forms with thickened walls; in transverse section, the polygonal form of the calice appears rounded as a result of thickening. Lecompte (1939, p. 154) included these thickened forms within the genus *Chaetetes*; this seems justified for within the same colony, thickened and unthickened forms can occasionally be found.

Lecompte (1939) has given a very full review of the literature on *Chaetetes* and he recognizes the following five features as diagnostic of the genus:

1. Exclusively fissipartite (usually bipartite) increase.
2. Tabulae tend to occur at the same level in neighbouring corallites.
3. Mural pores are absent.
4. Corallites are narrow.
5. Walls between corallites are completely amalgamated.

On this last point he admits to some uncertainty. Okulitch (1936, p. 374) has observed a line marking the suture between corallites in *C. radians*; and Oakley (1936a, p. 442) has found an inclusion of dark granular material in the walls of *C. skaptokinesis* which he attributed to recrystallization along an original suture. In the species described below, there is some evidence of a suture and although the question remains open, it seems probable that the walls may sometimes be composite.

Smith and Lang (1936, p. 188) pointed out that the walls in *Chaetetes* may be incompletely formed and, in transverse section, the resulting projection gives the appearance of a single septum, or, in extreme cases, where the walls are locally absent, to a meandroid colony.

Sokolov (1955, p. 95) was not prepared to accept the *Chaetetidae* as a family of the Tabulata since the absence of true septa, the mode of increase and the trabecular structure of the walls, sometimes arranged in isolated columns, was not found in any
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other members of the order. He therefore referred them to the Hydrozoa; in this he was followed by Stasińska (1958, pp. 178 et seq., 224).

I have here placed the Chaetetidae in the Tabulata following Hill and Stumm (1956, p. 450) although there is no additional evidence from the North Devon specimens to confirm or contradict either point of view.

*Chaetetes lonsdalei* Etheridge and Foord 1884

Plate 14, figs. 6, 7

1884 *Chaetetes lonsdalei* Etheridge and Foord, p. 474, pl. 17, figs. 2, 2c.
1889 Calamopora piliformis Schütze, p. 93, pl. 11, fig. 6.
1892 *Chaetetes piliformis* (Schütze); Rominger, p. 62, pl. 3, figs. 15-16.
1939 *Chaetetes lonsdalei* Etheridge and Foord; Lecompte, p. 161, pl. 21, figs. 1-2.
1958 *Chaetetes* (†) lonsdalei Etheridge and Foord; Stasińska, p. 230, pl. 37, figs. 1-3.

**Diagnosis.** (Modified after Lecompte 1939, p. 162.) Large tabulate corals with straight prismatic corallites from 0.2-0.6 mm. in diameter. The calices may be polygonal or alveoloid in shape with small granular or pointed spines projecting from the surrounding walls. The tabulae are well developed—three or four in 1 mm. The walls are stout and increase is fissiparite.

**Remarks.** The North Devon form agrees in all important respects with the species described by Etheridge and Foord from the Middle Devonian of Queensland and by Lecompte from the Carvinian of the Ardennes, though the diameter may be greater than was suggested by Lecompte; the diameter is however very variable. I have also included in the diagnosis the alveoloid form which seems more typical of the species (the polyalveoloid form is common, but it is almost always associated with granular spines and these, as Lecompte pointed out, are indications of incipient fission).

The tabulae are not regularly spaced but tend to occur at the same height in adjacent corallites; although they are usually horizontal, they occasionally show a slight downward projection at their centres. The walls have no dark median line but they are slightly thickened.

*C. lonsdalei* differs from *C. multiabulata* in having much larger corallites and fewer tabulae and from *C. cf. rotunda* in having larger and straighter corallites.

In North Devon, all the specimens of *C. lonsdalei* were obtained from the David’s Stone Limestone (Frasnian); in the Ardennes, Lecompte found the species was typical of the upper Carvinian beds, while Stasińska (1958) records it from the Givetian of Skaly, Poland. The species therefore seems to have a longer range than was at first thought by Lecompte.

*Chaetetes multiabulata* sp. nov.

Plate 9, figs. 4-7

**Holotype.** MM 11195 from the David’s Stone Limestone of David’s Stone.

**Diagnosis.** *Chaetetes* with very numerous tabulae (about 10 in 1 mm.) and thickened walls from which occasional short spines project. Corallites have a diameter of about 0.25 mm.

**Description.** The holotype consists of a small fragment about 1 cm. square which is embedded in limestone; longitudinal (Pl. 9, fig. 5) and oblique (almost transverse)
sections (Pl. 9, fig. 6) have been cut. The corallites are slightly curved in longitudinal sections and the calices are perpendicular to the outer surface. The tabulæ are very thin and approximately correspond in height in neighbouring corallites; they may be horizontal, slightly concave or slightly convex. The wall structure is partially recrystallized but a dark median line is frequently visible suggesting a composite rather than fully amalgamated wall.

Remarks. *C. multistriatus* differs from *C. rotundus* in having more numerous and thinner tabulæ and in the greater thickening of the walls.

Horizon. The David’s Stone Limestone is considered to be of Frasnian age.

*Chaetetes cf. rotundus* Lecompte 1939

Plate 9, figs. 2, 3

cf. 1939 *Chaetetes rotundus* Lecompte, p. 163, pl. 22, fig. 2.

Description. The specimen is part of a massive branching or irregularly lamellar colony measuring approximately 20 x 15 mm. The specimen has been abraded to intermittent.

The corallites are in close contact and polygonal in transverse section though the calices are somewhat rounded due to thickening of the walls. The corallites are mostly curved in longitudinal section but the calices always reach the exterior at right angles to the surface of the corallum.

The diagonal measurements of fully developed corallites vary from 0.2-0.25 mm.; smaller ones can be seen in transverse sections, but that these are immature corallites is confirmed by their appearance in longitudinal section. The thickness of the walls shows a marked variation—the thickest is 0.04 mm., and the thinnest 0.01 mm.; a dark median line is sometimes visible showing that the walls are not fully amalgamated.

No spines or septa are visible, and mural pores are absent. The tabulæ are not regularly spaced (about five in 1 mm.) and they tend to become more numerous towards the distal ends of the corallites. Many of the tabulæ are slightly convex distally and they do not occur regularly at the same height in neighbouring corallites.

Remarks. The specimen is similar in many respects to *C. regularis* Lecompte [1939, p. 160, pl. 20, fig. 13]; however, the tabulæ are more widely spaced and less regular.

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**Explanation of Plate 9**

All figures are thin sections of specimens from the David’s Stone Limestone (Frasnian) of North Devon.

Fig. 1. *Thaumastopora polymorpha* (Goldfuss). Longitudinal and partly transverse sections cut from a large corallum; MM 11199 from Hilsborough. x 3.5.


Figs. 4-7. *Chaetetes multistriatus* sp. nov. 4: Colony growing on the outer surface of a larger ?bryozoan; the latter shows penecontemporaneous borings which are filled with calcite and pyrite crystals; MM 11196 from Hilsborough. 5, Longitudinal and 6, transverse sections of the holotype MM 11195 from Sandy Cove. 7, Paratype showing transverse and longitudinal sections; MM 11197 from Hilsborough. All x 6.
The specimen is closest to *C. rotundus* Lecompte, differing only in the form of the corallum and in the slight arching of the tabulae.

**Material.** One specimen (MM 11198) from the David's Stone Limestone (Frasnian) of Hillsborough near Ilfracombe.

*Family FAVORITIDAE Dana 1846*  
*Sub-family ALVEOLITINAE Duncan 1872*  
*Genus ALVEOLITES Lamarck 1801*

1933 *Alveolites* Lamarck; Lecompte, pp. 7–15 (cum syn.).  
1939 *Alveolites* Lamarck; Lecompte, pp. 17–19 (cum syn.).  
1953 *Alveolites* Lamarck; Schoupp, p. 45 (cum syn.).

**Diagnosis.** See Smith 1933, p. 135.

**Remarks.** Lecompte (1933, pp. 7–15, 1936, pp. 6–8 and 1939, pp. 17–19) has fully reviewed the literature pertaining to this genus and has pointed out the features which separate it from *Favosites, Thamnopora,* and *Coenites.* Although the obliquity of the calice is apparent in most species, occasional individuals within a single colony may open perpendicularly to the outer surface. Lecompte has questioned the reality of a single large septum, suggesting that it is the first stage in fissipartite increase. The material from North Devon is relatively poorly preserved and it is impossible to investigate this matter further.

**Range.** Silurian and Devonian.

*Alveolites suborbicularis* Lamarck 1801

*Plate 14, fig. 4; Plate 15, figs. 1–5*

1933 *Alveolites suborbicularis* Lamarck; Lecompte, pp. 15–18 (cum syn.).  
1939 *Alveolites suborbicularis* Lamarck; Lecompte, p. 19 (cum syn.).

**Diagnosis.** See Smith 1933, p. 137.

**Remarks.** Lecompte believed that granular spines were also developed at various positions in the corallite in addition to the prominent septum on the lower side. Smith, however, regarded the granular spines as a recrystallization phenomenon (see comments in Lecompte 1936, p. 7). The recrystallized appearance of the North Devon specimens (see for example, Pl. 15, fig. 1, in which the appearance of additional septa is an illusion resulting from recrystallization) suggest that Smith's interpretation is correct.

In North Devon, this species occurs in the Jenny Start, Combe Martin Beach, and David's Stone Limestones; one specimen collected measured 25 x 35 cm. All the specimens are at least partially recrystallized and distorted; specimens from the Jenny Start Limestone tend to have more widely spaced tabulae (about three in 1 mm.) and larger calices than those from the David's Stone Limestone (about four in 1 mm.). Specimens from the Combe Martin Beach Limestone are relatively small and are frequently found encrusting *Thamnopora*; they are common only at the east end of the Parlour, near Combe Martin; recrystallization has obliterated most of the original wall structure but occasionally the median dark line is discernible; the tabulae are thin and spaced irregularly—about four in 2 mm.
Range. Middle and Upper Devonian. In North Somerset Webby (1964) has identified this species from the Upper Givetian (Roadwater Limestone). In Belgium, Lecompte has not recorded the species below the base of the Frasnian; it is unknown from the Carboniferous.

*Alveolites suborbicularis* Lamarck forma *gemmata* Lecompte

Plate 16, figs. 1-2

1939 *Alveolites suborbicularis* forma *gemmata* Lecompte, pp. 22-23, pl. 1, figs. 1-12.

Remarks. Most commonly, *A. suborbicularis* is an encrusting coral which tends to develop in relatively thin layers around some convenient object—often another coral colony. Lecompte (1939) has noticed, however, a continuous series away from this simple form through those in which there are slight or moderate swellings on the outer surface (due presumably to the more rapid and successful growth of some corallites), into forms which have developed definite branches and have abandoned the lamellar form completely; the former he classed as *formam gemmata* and the latter as formae *suborbicularis* and *constricta*. The specimen figured from North Devon still has an essentially lamellar form but it has a marked swelling across its surface; it therefore falls within the morphological group, forma *gemmata*. It occurs in the Jenny Start Limestone (Givetian).

*Alveolites multiperforatus* Lecompte 1933

Plate 13, figs. 1, 2

1933 *Alveolites multiperforatus* Salée; Lecompte, pp. 39-42, pl. 3, figs. 1, 1a, 1b.
1945 *Alveolites multiperforatus* Salée; Smith, pp. 13-14, pl. 36, figs. 3-5 (card syn.).

Diagnosis. Massive or encrusting tabulate corals. Calices with polygonal or sub-alveolitoid form; septal spines rarely seen. The walls are irregularly thickened and mural pores are numerous throughout the corallum. The tabulae are thin, horizontal or slightly convex.

Remarks. The species was fully described by Lecompte (1933) but without a diagnosis. He attributed the authorship of the species to Salée (who named the species in an unpublished manuscript), as did Smith (1945, p. 13) who also discussed the species. However, as Lecompte’s is the first published description, the species must be attributed to him. The abundance of the mural pores, together with the irregular thickening of the walls,

Explanations of Plate 10

Figs. 1–5. *Thaumastopora polymorpha* (Goldfuss). 1. Longitudinal and 2, transverse thin sections of MM 11200 from the David’s Stone Limestone (Frasnian) to the West of the Coastguard Station above Hagginton Beach. 3. Longitudinal thin section of specimen MM 11175 from the David’s Stone Limestone (Frasnian) of Sandy Cove. The coral tissue is almost entirely recrystallized. 4. Longitudinal thin section of MM 11201 from the David’s Stone Limestone of Hillesborough. 5. A broken corallum weathering out from the David’s Stone Limestone at Sandy Cove. MM 11202. All x 3 except fig. 2: 4.

Fig. 6. *Conitis esoutricolor* (Steininger) Exterior surface of several coralla showing their lamellar form and the slit-like nature of the calices. Specimen MM 11181 from the Jenny Start Limestone (Givetian) of Widemouth Quarry. X 2.
gives the appearance of 'boudins' in longitudinal section. In North Devon, the species has been obtained from the Jenny Start Limestone of Widmouth; the skeletal structure is partially recrystallized, but the thickening of the walls and the numerous mural pores are readily seen. The tabulae are irregularly spaced—about three in 1 mm.; this agrees well with the specimen figured by Lecompte (1933, pl. 3, fig. 1b). The growth of the coral is also irregular and the corallites are rarely straight or parallel for more than short distances. The exterior surface shows the dominantly polygonal form of the calices but with some assuming a more alveolitoid shape. Their diameter is commonly 0·4–0·6 mm., i.e. similar to the dimensions recorded by Lecompte but slightly larger than in the specimens from the Mackenzie River area. Smith (1945) has described 'numerous minute spines' from some (but not all) of the Canadian specimens and Lecompte mentions them in his description. They have not been observed in the North Devon species but their apparent absence may be the result of the indifferent preservation.

In Canada and in the Ardennes, the species occurs in the Frasnian; in the latter area, it is associated with Thaumophyllum, Stromatopora, and ? Hexagonaria; there is a somewhat similar association in the Jenny Start Limestone (Givetian) of North Devon.

*Alveolites obtusus* Lecompte 1939

Plate 17, figs. 4, 5

1939 *Alveolites obtusus* Lecompte, pp. 42–43, pl. 6, figs. 4–7.

**Diagnosis.** See Lecompte 1939, p. 43.

**Remarks.** One of the distinguishing features of this species is the arrangement of the corallites into fascicles which are irregularly disposed and often interlaced with each other; this feature is well seen in the North Devon specimens. Because of the poor preservation, however, it is not possible to see the concentration of mural pores in the outer parts of the fascicle; there is evidence that the tabulae are more numerous in these peripheral parts and there is some thickening of the corallite walls. The calices agree with the description given by Lecompte, being polygonal or sub-triangular, yet with diameters almost equal.

Lecompte records his species from the Frasnian of the Ardennes; in North Devon, the two specimens assigned to this species occur in the Jenny Start Limestone (Givetian).

**Genus Coenites** d'Eichwald 1829

1829 *Coenites* d'Eichwald, p. 179.

1939 *Coenites*; Lecompte, p. 62.

1955 *Pseudo*coenites Sokolov, p. 189.

**Diagnosis.** See Lecompte 1939, pp. 62–63.

**Remarks.** Some workers (e.g. Lindström 1876, p. 16, Hennig 1906, p. 26) regarded *Coenites* as a bryozoan; Oakley (1936b, pp. 25–26) showed conclusively that *Coenites* was, in fact, a tabulate coral. Lecompte (1939) stated that there are three main criteria for recognizing the genus and distinguishing it from *Alveolites* and *Thaumaporta*:

(a) It has considerable distal thickening of the walls.

(b) It has a slit-like calicular opening.
(c) It frequently shows three septal processes (though these are not always visible and sometimes, as Oakley observed, there may be six).

The genus is closer to Alveolites than to Thanmopora, and I agree with Hill and Stumm (1956, p. 466) in placing both Alveolites and Coenites in the same sub-family.

Sokolov (1955, p. 189) erected a new genus Platocoenites for coenoid-like corals having a lamellar form and a "certain peculiarity in the arrangement of their calicular rim". I do not regard these differences as significant enough to erect a new genus, especially as many species of Coenites have a tendency to grow in a lamellar form. I therefore regard Platocoenites as a synonym of Coenites.

In North Devon, tectonics and recrystallization (the latter being particularly marked in the preservation of this genus and Alveolites) have affected all the specimens to a greater or lesser degree making it difficult to assign specific names in every case; the two specimens described below are however, well represented.

The genus ranges from the Silurian to the Devonian (Hill and Stumm 1956, p. 466) but in the Ardennes, Lecompte found that it characterized the Middle Devonian. In North Devon also, it occurs in the Middle Devonian (Givetian—Jenny Start Limestone), but Coenites tractatus Lecompte is found in the Frasnian (David's Stone Limestone).

Coenites escharoides (Steininger) 1849

Plate 10, fig. 6; Plate 13, figs. 3–5

1849 Limoria escharoides Steininger, p. 11.
1855 Limoria escharoides Steininger; Steininger, p. 27.
1876 Coenites expansus Korinek, p. 74, pl. 2, fig. 3.
1886 Coenites expansus Frech, p. 137.
1889 Coenites escharoides (Steininger); Schützer, p. 126, pl. V, figs. 12–13.
1896 Coenites expansus Frech var. polonica Štách, p. 145, pl. V, figs. 8a–b.
1898 Coenites escharoides Korinek, p. 57, pl. 2, fig. 3.
1901 Coenites escharoides (Steininger); Petts (pars), p. 193, pl. II, figs. 8a–b.

EXPLANATION OF PLATE II

Figs. 1, 4, Thanmopora cervicornis (de Blainville). 1, Longitudinal and transverse section of MM 11204 from the Combe Martin Beach Limestone of The Parkour (near Combe Martin). 4, Longitudinal section of MM 11188 from the Rillage Limestone (Givetian) of Smallmouth Beach. Both ×5.
Figs. 3, 5, 16, Thanmopora irregularis Lecompte. All the specimens are from the Jenny Start Limestone (Givetian). 3, Oblique section of MM 11171 (Rillage Quarries). 5, longitudinal, and 16, transverse (partly longitudinal) sections of MM 11170 (Higginton Beach). All ×3.
Figs. 2, 6, 7, 17, Thanmopora transversa Lecompte. All the specimens are from the David's Stone Limestone (Frasnian) of Sandy Cove. 2, Transverse, and 6, longitudinal sections of MM 11169. 7, Longitudinal (partly transverse) sections of MM 11168. 17, Transverse section of MM 11168. All ×3.
Figs. 8–10, 12–15, Thanmopora pterygia (Schlotheim). The following specimens are from the Jenny Start Limestone (Givetian). 8, Longitudinal thin section of MM 11165 (Rillage Quarry). 10, Longitudinal thin section of MM 11166 (Widmouth Quarry). 12, Longitudinal thin section of MM 11164 (Rillage Quarry). 14, Transverse, and 15, longitudinal (partly transverse) sections of MM 11167 (Higginton Beach); the latter shows the strong development of spines in the region of bifurcation. All ×3.
The remaining specimens are from the David's Stone Limestone (Frasnian). 9, 12, Transverse thin sections of MM 11163 (Sandy Cove). Both ×3.
Fig. 11, Thanmopora? pterygia (Schlotheim). Polished longitudinal section of MM 11203 from the Rillage Limestone (Givetian) of Smallmouth. The coral structure is entirely recrystallized. ×2:5.
Diagnosis. See Lecompte 1939, p. 67.

Remarks. Steininger's brief original diagnosis was amplified by Schlüter (1889), but both described only the external characters. Neither Lecompte nor I have re-examined the type and Lecompte's diagnosis which included the internal characters, is based upon material collected in the Ardennes.

The North Devon specimens are partly affected by recrystallization which obscures the finer details of the structure; I have no hesitation however in identifying them with the specimens described and figured by Lecompte from the Ardennes. Plate 10, fig. 6 shows the foliated form of the colony and the scaly appearance of the exterior surface. Longitudinal sections show a relatively unthickened central area in which the corallities run parallel to the outer surfaces, and abruptly thickened marginal areas where the corallities are sharply bent to become perpendicular to the outer surfaces.

The individual lamellae of the coralla have a thickness of 2-5 mm. and the calicular openings, which are very restricted because of the stereoplasms, have a maximum diameter of 0.3-0.5 mm. The thickening of the surrounding walls may also be as much as 0.5 mm.

Because of recrystallization, the tabulae are not readily seen and in many cases have been completely destroyed; where they are visible, they are numerous, very thin and often slightly concave.

The species is widespread in the European Devonian. Steininger's original specimens were from the Middle Devonian beds of Gerolsstein. Lecompte obtained the species from the Covoninian and Givetian beds of the Belgian Ardennes while from Russia, Pets (1901) and Chernyshev (1951) record the species from the Kuznetsk Basin; from Poland, Stasińska records the species from the Covunian of the Holy Cross Mountains and the Givetian of Skaly. Outside Europe, Reed (1908) found the species in the Middle Devonian of the Shan States (India) and Le Maître (1947) in the Middle Devonian of Morocco. In North Devon it has been obtained from the Jenny Start Limestone (Givetian) of Widmouth Quarry and Hagginton Beach.

**Coenites gradatus** Lecompte

Plate 17, figs. 1-3

1939 *Coenites gradatus* Lecompte, pp. 69-70, pl. 11, figs. 11-17.

Diagnosis. See Lecompte 1939, p. 70.

Remarks. This is a very common species in the David's Stone Limestone of Broadstrand (Hillsborough). Some of the specimens are moderately well preserved and the zonation which is typical of the species can be well seen (Pl. 17, fig. 3). This zonation is frequently emphasized by the preservation—the exterior fringe of each zone being better preserved
than the interior parts which are entirely recrystallized. This suggests that recrystallization took place at an early stage, possibly even before the colony finally died. Tabulae are rarely seen, but in one corallum where they are preserved, they are closely spaced—(three in 0.5 mm.). The calices are crescent-shaped and may show a median spine. Sometimes the wall between adjacent corallites is absent (?? fissipartite increase) giving the colony a meandroid appearance in transverse sections.

In the Ardennes, the species occurs in both the Couvinian and Givetian. Its occurrence in the David's Stone Limestone indicates that its range extends at least up into the Frasnian.

Coelites sp.
Plate 14, figs. 1–3

Description. Branching corallum with corallites straight at the axis and bending round sharply outside this in order to meet the exterior surface at right angles. The calices are much restricted by the thickening of the walls but they are commonly crescent-shaped and sometimes contain a prominent spine projecting in from the lower side. The diameter of the branches varies from 2–14 mm., but the average is about 8 mm. Thickening is strong in the peripheral areas but is also present to a lesser extent in the axial zone where the tabulae are few and widely spaced (Pl. 14, fig. 3).

Remarks. Only one example of this species has been found. It was obtained from the Jenny Start Limestone of Samson's Cove. In the form of its corallum, it resembles C. eschericius, but the branches of the latter are much thinner and the number of corallites in the axial zone is fewer. Generically, it is similar to Pliographe Günther (= Sculipore—see Lang, Smith, and Thomas 1940, pp. 100, 118), especially P. kaisini Lecompte (Lecompte 1939, pp. 144–5, pl. 20, fig. 11), but it lacks polygonal calices with three spines and it has greater thickening of the corallite walls. It is probably a new species, but with such limited material, I have hesitated to erect one.

Sub-family PACHYPORINAE Gerth 1921

Genus THANNOSPORA Steininger 1831

1939 Thannospora Steininger; Lecompte, p. 102, (cum syn.).
1958 Thannospora Steininger; Lafuste, pp. 3658–40.

EXPLANATION OF PLATE 12

Figs. 1, 3, 5–8. Thannospora crenigera (d'Orbigny). All the specimens come from the Jenny Start Limestone (Givetian) of Widemouth and Rillage Quarries. 1, Longitudinal and partial transverse sections of MM 11139 (Widemouth). 3, Longitudinal, and 7, transverse sections of MM 11160 (Rillage). 5, Longitudinal, and 6, transverse sections of MM 11161 (Rillage). 8, Longitudinal section of MM 11162 (Rillage). All × 3.

Figs. 2, 4, 5. Thannospora boloniensis (de Blainville). 2, Longitudinal and partly transverse section of MM 11156, and 4, longitudinal section of MM 11155 from the David's Stone Limestone (Frasnian) of Sandy Cove. 9, Longitudinal and partially transverse sections of MM 11157 from the Jenny Start Limestone (Givetian) of Rillage Quarry. All × 3.

Fig. 10. Thannospora crenigera (de Blainville). Transverse polished section of MM 11153 from the Combe Martin Beach limestone of the Parlour. Alveolites suberectus is seen overgrowing the Thannospora colony.
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1959 Thamnopora Steininger; Chudinova, pp. 66-67 (cum syn.).
1965 Thamnopora Steininger; Schouppé, pp. 38-40 (cum syn.).

Diagnosis. See Lecompte 1939, p. 102.

Discussion. Contrary to most other workers (see especially Lang, Smith, and Thomas 1940, p. 92), Lecompte does not regard Pachypora Lindström as a synonym of Thamnopora. He argues that the lamellar structure seen in Pachypora lamellicornis is fundamentally distinct from the fibrous structure of Thamnopora. Lindström (1896, p. 29) himself argued most emphatically against the synonymy, and Chernyshev (1951) claimed that certain species of Pachypora (Thamnopora) possess two types of stereoplasmic microstructure—one concentric (i.e. lamellar) and the other fibrous. Chudinova (1959) has re-examined this material in addition to investigating over three thousand specimens of Thamnopora from the U.S.S.R. and she is emphatic that the stereoplasm always has a radial fibrous microstructure. The confused interpretation of the nature of the microstructure arises because incremental layers of fibrous CaCO₃ are laid down during growth and if the preservation is not good, the fibrous texture becomes lost and only the layers are readily apparent—hence the impression of a lamellar structure. This confirms the opinion of Hill (see Lecompte 1939, p. 103) that the lamellar structure is a recrystallization phenomenon. This being so, Pachypora must be regarded as a synonym of Thamnopora.

Range. Silurian to Trias, but it is most common in the Devonian and Permian.

*Thamnopora boloniensis* (Gosselet) 1877

Plate 12, figs. 2, 4, 9, Plate 14, fig. 5

1958 Thamnopora boloniensis (Gosselet); Stasievská, pp. 198-200, pl. 9-11 (cum syn.).
1965 Thamnopora boloniensis (Gosselet); Schouppé, pp. 42-45, pl. 3, fig. 5-9 (cum syn.).

Diagnosis. See Lecompte 1939, pp. 127-8.

Material. Three specimens from the Jenny Start Limestone and two from the David's Stone Limestone.

Description. (a) Jenny Start Limestone: specimens from the Jenny Start Limestone agree with the diagnosis of *T. boloniensis* except that the size of the calices is smaller (maximum diameter about 1.5 mm.). The corallites are, however, markedly larger than all other forms from North Devon. Only fragments of coralla have been collected and from MM 11157 a longitudinal section has been cut. The maximum diameter of the branch is 1.4 mm. and its length (incomplete) is 50 mm. (Pl. 12, fig. 9). The diameter of the corallites at the periphery varies from 1.1-1.5 mm., and the walls are thickened throughout, though most strongly at the periphery. The obliquity of the corallites varies from 60° to 90°. Mural pores are numerous and are approximately 1.2 mm. apart. Tabulae are moderately numerous in the axial region (4-5 in 2 mm.) but they tend to be irregularly grouped.

(b) David's Stone Limestone: two specimens have been sectioned longitudinally and these agree in all respects with Lecompte's diagnosis. The branches have a diameter of at least 15 mm. and the largest calices are over 2 mm. across. Mural pores are common
and have a diameter of about 0.15 mm. Tabulae are few and are slightly concave. The walls are thickened throughout but most strongly at the distal ends.

Remarks. In the Ardennes, Lecompte found that this species was characteristic of the Frasnian as did Sasińska (1958) in Poland; in Devon it occurs in both the Upper Givetian (Jenny Start Limestone) and the Frasnian (David’s Stone Limestone) but the earlier forms appear to show slight variations. Lecompte’s studies, however, showed that T. bolinensis is a very variable species even within the Frasnian, and its most persistent feature is the large size of the calices. I have, therefore, placed the two forms described above in the same species.

**T homorora coccinaria (de Blainville) 1830**

Plate 11, figs. 1, 4; Plate 12, fig. 10

1939 *T homorora coccinaria* (de Blainville); Lecompte, pp. 109–11 (cum syn.).

1945 *T homorora coccinaria* (de Blainville); Smith, p. 62, pl. 27, figs. 1a–c.

1958 *T homorora coccinaria* (de Blainville); Sasińska, pp. 200–2, pl. 12, figs. 1–3.

**Diagnosis.** See Lecompte 1939, pp. 110–11.

Remarks. The species has been identified from the Rillage and the Combe Martin Beach Limestones. The single specimen from the Rillage Limestone (Pl. 11, fig. 4) is remarkable because of its prominent spines seen in longitudinal section. The calices have a diameter of 1–1.2 mm. and the thickness of the walls is irregular, though most prominent at the distal ends of the corallites. The branch is irregular in diameter but reaches a maximum of 15 mm. Along the sides of the branch the corallites bend round to reach the exterior at right angles, but at its extremity, they make an angle of about 60°. Tabulae are irregularly spaced and may be slightly convex or concave.

In the Combe Martin Beach Limestone the species is locally common (especially at the entrance to the Parlour). Specimens are frequently overgrown by *Alveolites* and appear to be preserved in their growth positions (Pl. 12, fig. 10). The corallites are

**Explanation of Plate 13**

Figs. 1, 2. *Alveolites multiperforata* Lecompte. 1, Longitudinal thin section (×3) and 2, external surface (×2.4) of MM 11177 from the Jenny Start Limestone of Widemouth Quarry. The latter figure shows the form of the calices and the occasional breakdown of the walls between adjacent corallites. Figs. 3–5. *Coeetes escharoides* (Steininger). All are longitudinal sections of specimens from the Jenny Start Limestone, 3 and 5, MM 1192 from Hagginton Beach. Both ×4. MM 11681 from Widemouth Quarry. ×6.

**Explanation of Plate 14**

Figs. 1–3. *Coeetes sp*. MM 11190 from the Jenny Start Limestone (Givetian) of Samson’s Bay. 1, Transverse section showing the thickening around the calices. 2, Longitudinal and partly transverse section. 3, Longitudinal and transverse sections showing the form of the colony and the thickening in the axial and peripheral zones. All ×6.

Fig. 4. *Alveolites subcarinatus* Lamarck. MM 11150 showing the typical lamellar and encrusting form of the colony. ×1.8.

Fig. 5. *T homorora coccinaria* (de Blainville). Exterior surface of MM 11193 which has been distorted by tectonic pressure; from the Jenny Start Limestone of Widemouth Quarry. ×2.4.

Figs. 6, 7. *Coeetes lombardi* Etheridge and Foord. 6, Transverse and 7, longitudinal sections of MM 11770 from the David’s Stone Limestone of Hely Bay, near Ilfracombe. Both ×6.
smaller and more numerous in these coralla than in the specimen from the Rillage Limestone. The corallites have a diameter of about 0.9 mm. and make an angle of 50–60° with the outer surface at the extremity of the branches; along the sides, however, they are perpendicular or even directed posteriorly (see Pl. 13, fig. 1). Thickening of the walls is again irregular but most strong at the distal ends.

In North Somerset, Webby (1964, pp. 4–5) has identified the species from the Upper Givetian (Roadwater Limestone) and in the Ardennes too, Lecompte has found the species confined to the Givetian. Lecompte found that specimens from horizon Gib were smaller than those from Gib (Upper Givetian). This is most probably an ecological rather than evolutionary variation and although the North Devon specimens approximate more closely to Lecompte’s Gib specimens, the evidence is too uncertain to draw definite conclusions.

Stasińska (1958) also found the species confined to the Givetian but elsewhere it extends into the Upper Devonian. Smith (1945) records it from the Frasnian of North America and Chudinova (1959, p. 69) mentions its occurrence in Givetian and Frasnian beds of U.S.S.R., Mongolia, and the Sahara; it is however rarer in the higher stages.

_Thaumopora cronigera_ (d’Orbigny) 1850

1850 _Thaumopora cronigera_ (d’Orbigny); Lecompte, p. 107.

_Diagnosis._ See Lecompte 1939, p. 109.

_Remarks._ Lecompte (1939) regarded _T. cronigera_ as intermediate between _T. polymorpha_ and _T. cervicornis_ and he found difficulty in defining the precise limits of each species. Typically, the corallum of _T. cronigera_ is smaller and has less tendency to branch than _T. polymorpha_; it also has fewer tabulæe. However, it is less thickened by stereoplasm than _T. cervicornis_ and the calices are in consequence not so rounded.

The specimens from North Devon referred to this species are all broken fragments but are closely similar to those which were described and figured by Lecompte from the Dinant Basin; these differed from the type (Goldfuss 1831, pl. 27, fig. 3) selected by d’Orbigny (1850, p. 107) in being more ‘robuste’ and having calices more rounded in the axial zone.

In the Dinant Basin, the species occurs in beds Gib and G/ of the Middle Givetian. In North Devon, the species is common in the Jenny Start Limestone but has not been identified from any of the other limestones.

_Thaumopora polyforata_ (Schlotheim)

1820 _Milleporites polyforatus_ Schlotheim, p. 365, partim.
1826 _Calamopora polymorpha_ var. gracilis, var. gracillima, elongata Goldfuss, p. 79, pl. 27, fig. 5.
1936 _Fauvelites dubia_ (de Blainville); Lecompte, p. 54, pl. 10, fig. 1 (cum syn.).
1939 _Thaumopora dubia_ (de Blainville); Lecompte, p. 120, pl. 18, figs. 7–12.
1945 _Thaumopora polyforata_ (Schlotheim); Smith, p. 63, pl. 28, figs. 1, 2 (cum syn.).
1952 _Thaumopora polyforata_ (Schlotheim); Smith, p. 301.
1953 _Thaumopora dubia_ (de Blainville); Kropfíček and Schouppé, p. 95, pl. 1, figs. 2, 3 (cum syn.).
Remarks. The species is common in the Jenny Start Limestone of North Devon. Several specimens have been sectioned and these agree well with those figured and described by Lecompte (1939, pp. 120–2, pl. 18, figs. 7–12). The diameter of the branches is 6–8 mm., except for specimen MM 11167 which is slightly larger (10 mm.). The latter specimen (figured in Pl. 11, fig. 15) shows well the septal spines, though it is possible that recrystallization in the centre of the corallite has accentuated them. The thickening of the walls is well-marked in all the specimens. The average diameter of the calices is 1–7 mm.; none reaches the maximum diameter of 2 mm. mentioned by Lecompte in his diagnosis.

Lecompte (1936) made a detailed study of the species and refigured and described the original of Goldfuss (1826, p. 79), which shows no trace of septal spines. He accepted Queensell’s (1881, p. 37) view that the species should be interpreted more liberally and framed his diagnosis accordingly. Weyby (1964) has reviewed the recent literature and has pointed out that the reference of T. polyforata to the genus Pachypora, as advocated by Kropfisch and Schouppé (1953), is unsatisfactory, as the corallite walls show both fibrous and lamellar structure. In the light of the recent work by Chudinova (1959)—see discussion on genus above—Pachypora must be regarded as a synonym of Thamnopora.

In the Ardennes, the species ranges from Givetian to Frasnian. In North Devon it characterizes the Givetian Jenny Start Limestone though a single specimen from the David’s Stone Limestone (Frasnian) is doubtfully referred to this species.

_Thamnopora irregularis_ Lecompte 1939

Plate 11, figs. 3, 5, 16

1939 _Thamnopora irregularis_ Lecompte, p. 113, pl. 15, figs. 6–9.


Remarks. The specimens from North Devon agree very closely with the diagnosis and description given by Lecompte though the tabulate tend to be more closely spaced and the distal thickening is somewhat greater than in the holotype. The species has been found only in the Jenny Start Limestone where it frequently forms large ramifying masses. In the Dinant Basin the species occurs in the Gia and Gif beds of the Givetian.

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**EXPLANATION OF PLATE 15**

Figs. 1–5, _Atreoides suborbicularis_ Lamarck, 1, Transverse (partly longitudinal) thin section of MM 11166 from the David’s Stone Limestone of Broadstrand Beach, near Ilfracombe (×4). 2, Longitudinal, and 3, transverse sections of MM 11153 from the Parloir, near Combe Martin (×2–3). 4, Transverse and longitudinal sections of MM 11154 from the Jenny Start Limestone of Wilnemouth Quarry (×4). 5, Transverse and longitudinal sections of MM 11157 from the David’s Stone Limestone of Broadstrand Beach, near Ilfracombe (×4).

**EXPLANATION OF PLATE 16**

Figs. 1, 2, _Atreoides suborbicularis_ Lamarck forma _gemmatus_ Lecompte. 1, Transverse, and 2, longitudinal sections of MM 11178 from the Jenny Start Limestone of Rillage Quarries. Both ×3.5.
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_Thamnopora polymorpha_ (Goldfuss)

Plate 10, figs. 1-5

1939 _Favosites polymorphus_ (Goldfuss); Lecompte, pp. 44-40, pl. 7, figs. 1-2 (text syn.).
1939 _Thamnopora polymorpha_ (Goldfuss); Lecompte, pp. 104-7.
1964 _Favosites sp._; Holwill 1964b, p. 128.

_Diagnosis._ See Lecompte 1939, p. 107.

**Remarks.** This species is very characteristic of the David's Stone Limestone and has not been found in any of the other limestones of the Ilfracombe Beds. The original fibrous structure is still visible in most of the examples collected. The form of the corallite is irregular but it tends to be branching or lamellar with marked bulbous projections.

The average diameter of the corallites is slightly smaller than in the examples from the Ardennes, but otherwise the North Devon specimens agree closely with the type.

In placing the species within the genus _Thamnopora_, I am following Lecompte (1939, pp. 81-83), who argued that the internal thickening, resulting in rounding of the calice, is never found in true favositids, only in species of _Thamnopora_. He admits, however, that _T. polymorpha_ forms a transition between indiscernible species of _Favosites_ with thin walls and angular calices, and typical _Thamnopora_ with well-rounded calices and branching corallum. Lecompte makes the point that _Favosites_ is typical of Middle Devonian strata, and does not extend into the Upper Devonian except for occasional aberrant forms, while _Thamnopora_ (which he considered to be generically distinct from _Parthypora_) showing intermediate characteristics appears in the Couvinian and by the Givetian and Frasian has developed the typical thamnoporid features. This leads him to suggest that _Thamnopora_ may have evolved from _Favosites_ during the Lower Couvinian. Other workers have found similar difficulty in deciding the precise boundary between _Favosites_ and _Thamnopora_. Swann (1947, p. 259) in studying his _alpensis_ lineage, found a complete morphological series between favositid and thamnoporid forms. In consequence, he felt it logical to place all the forms in _Favosites_, but he recognized that the thickening of the corallite walls was an evolutionary, not environmental, feature, characteristic of Devonian beds. Hamada (1959, pp. 206 et seq.) agreed that it was an evolutionary feature, but unlike Swann, he found it convenient to retain the generic name _Thamnopora_ for (p. 208) ‘favositids with wall thickening which makes the cross section of the visceral chambers rounded in the axis as well as the peripheral parts of the corallum’.

I agree with Lecompte and Hamada (1959, p. 208) that the genus _Thamnopora_ should be retained, as at the least it provides a useful morphological category, and in most cases the thickening (or lack of it) enables _Thamnopora_ and _Favosites_ to be separated without difficulty. Earlier, I (Holwill 1964) reported the presence of _Favosites_ in the David's Stone Limestone, but I was then interpreting _T. polymorpha_ as a favositid; no other species of _Favosites_ occurs in this limestone.

In Belgium, _T. polymorpha_ occurs in Couvinian and Givetian beds (including bed Gld—uppermost Givetian). In North Devon the species appears to persist into the Frasian, though its presence suggests that the David's Stone Limestone is at a low horizon within the Frasian.
**Thannopora tunefacta** Lecompte 1939

Plate 11, figs. 2, 6, 7, 17

1939 *Thannopora tunefacta* Lecompte, pp. 117–18, pl. 16, figs. 15–16.
1952 *Thannopora tunefacta* Lecompte; Sokolov, pp. 61–62, pl. 13, fig. 1.
1959 *Thannopora tunefacta* Lecompte; Chudinova, pp. 84–85, pl. 26, figs. 2–4.

**Diagnosis.** See Lecompte 1939, p. 118.

**Remarks.** Three specimens have been referred to this species from North Devon. All of them are fragments but they agree closely with Lecompte’s diagnosis and description except that they are somewhat smaller—the maximum diameter of the corallites being 6–7 mm. The maximum diameter of the corallites is 0.9 mm., but the walls are strongly thickened, especially distally, so that the aperture may be reduced to 0.2 mm. or less. The corallites bend round so as to meet the outer surface at right angles.

The type specimen comes from the upper Couvinian beds (Co2d) of Couvin but Lecompte also records it from the Givetian. In Russia, Chudinova (1959) reports it from the Middle Devonian of the Eastern Urals, while in North Devon it occurs in the David’s Stone Limestone (Frasnian).

**Subfamily MICHELININAE** Waagen and Wentzel 1886

**Genus PLEURODICYTUM** Goldfuss 1829

*Pleurodictyum* sp.

Plate 17, fig. 6

**Remarks.** Valpy (1867, p. 35) recorded *Pleurodictyum* sp. as *Michelina antiqua* from the Ilfracombe Beds probably at Hagginton Beach. I have not been able to trace his specimen with certainty, but it may be BM R6421; this is the specimen figured. It consists of a very poorly developed mould into which dolomite crystals have grown. There is no precise record of its locality, but its preservation and the nature of the limestone matrix make it almost certain to have been obtained from the Combe Martin Beach Limestone which crops out at many places along Hagginton Beach. Specific identification is impossible.

**Family AULOPORIDAE** Edwards and Haime 1851

**Genus Aulopora** Goldfuss 1829

**Explanation of Plate 17**

Figs. 1–3. *Cocytites gradatus* Lecompte, 1, Transverse and partly longitudinal section of MM 11183 from the David’s Stone Limestone of Hillborough near Ilfracombe. 2, and 3, longitudinal sections of MM 11185 and MM 11184 respectively; the latter shows the lamellar form of the colonies emphasized by the preservation. All × 3.

Figs. 4, 5. *Machetis oblongus* Lecompte, Transverse and longitudinal sections through specimens from the Jenny Start Limestone of Widemouth Quarry. 1, MM 11179 and 2, MM 11180. Both × 3.

Fig. 6. *Pleurodictyum* sp. Mould, BM R6421, probably from the Combe Martin Beach Limestone of Hagginton Beach. × 6.

Remarks. Only two small and very incomplete colonies have been collected—both of them from the David's Stone Limestone of David's Stone. One of them (MM 11188), shows two partly broken corallites, revealing a thin horizontal tabula. The other specimen is slightly larger, but is embedded in argillaceous limestone and is not seen in relief. The diameter of the calices is about 1.5 mm., and they are about 5 mm. long; they are linked together in a single chain. The preservation prevents any other specific details of the specimens being observed but the size and the shape of the corallites agree with those of A. tubiformis.

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