

# THE CORAL GENUS *METRIOPHYLLUM* EDWARDS AND HAIME

by F. J. W. HOLWILL

ABSTRACT. The morphology of the genus *Metriophyllum* has been investigated with the aid of serial sections and the skeletal structure of the coral is described in detail. A review of all recorded species of *Metriophyllum* is made and a revised description is given of *M. bouchardi* and *M. gracile*; in addition a new species is described from the Ilfracombe Beds (Middle/Upper Devonian) of north Devon.

THE genus *Metriophyllum* was established by Edwards and Haime in 1850 with *M. bouchardi* as the type species; they did not, however, publish a full description with figures until the following year (Edwards and Haime 1851). The known range of the genus extends from Middle Devonian to Lower Permian, though the genus is particularly characteristic of the Middle and Upper Devonian. It includes some of the smallest corals yet described—*M. gracile* has an average length of 6–7 mm. and an average maximum diameter of 3–4 mm.

Edwards and Haime (1851) originally placed *Metriophyllum* in the Stauridae, but Hill (1939) proposed a new family—the Metriophyllidae, with *M. bouchardi* as type genus—to contain *Metriophyllum* and allied forms; subsequent writers, notably Stumm (1949) and Lecompte (1952), have accepted the new family though they differ in their opinions as to the genera which should be included.

Possibly because of the small size of most species, the morphology of *Metriophyllum* has not been studied in detail hitherto. Even in the present study, it has been found difficult to discover specimens in which the apical end is completely preserved, and the earliest ontogenetic stages are therefore still not fully known.

In preparing this paper, I have collected extensively from the type locality of *M. bouchardi* at Ferques (Boulogne, France) and also from the Gerolstein area of Germany. In addition, I have studied collections from the British Museum (Nat. Hist.) and the Geologisch-palaeontologisches Institut und Museum at Bonn; I have also had original photographs of type specimens from the New York State Museum available for comparisons.

*Techniques.* Thin sections were made in the normal way, except that because of the small size of most of the specimens, a dental cutting wheel, making a cut of less than 0.5 mm., was used instead of the normal petrological slicing wheel. For serial sections, the specimens were embedded in a transparent plastic such as 'CEEMAR'; the resulting block was then milled flat on both sides and all subsequent grinding was done by hand. The advantage of this is that the specimen can be kept under constant observation and drawings made at minute intervals to record the rapidly changing arrangement of the septa and the carinae. At convenient intervals, cellulose peels were taken and these were mounted between glass slides and used as photographic negatives. The peels were made by dipping the etched surface of the coral into a 2/1 solution of butyl and amyl acetate

and then pressing the saturated surface on to a piece of transparent cellulose 0.01 in. thick. The advantage of this method over the one described by Butler (1935) is its speed and the ease with which the peel can be removed from the coral. The interval between successive serial sections was found by measuring the total thickness of the specimen plus plastic, before and after grinding, by means of an engineer's micrometer.

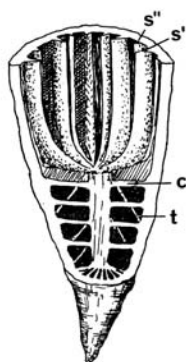
In some specimens there was little or no colour contrast between the coral structure and the infilling calcite. The latter was found to be slightly richer in iron than the coral itself, so that by dipping the polished surface of the coral into a solution of potassium ferricyanide and dilute hydrochloric acid (see Henbest 1931) it was found possible to stain the infilling material differentially. This greatly facilitated both photographic and microscopic examination of such specimens.

#### Genus *METRIOPHYLLUM* Edwards and Haime 1850

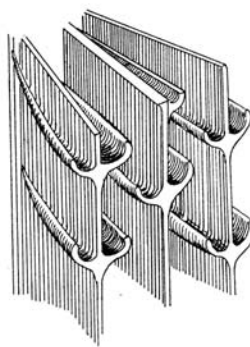
*Metriophyllum* Edwards and Haime 1850, p. lxi.

*Lopholasma* Simpson 1900, p. 206, figs. 19-21.

*Type species (by original designation). Metriophyllum bouchardi* Edwards and Haime 1850, p. lxi; 1851, p. 318, pl. 7, figs. 1, 1a, 1b, 2, 2b. Upper Devonian, Frasnian (Beaulieu Shales and Ferques Limestone), Ferques, near Boulogne, France.



TEXT-FIG. 1



TEXT-FIG. 2

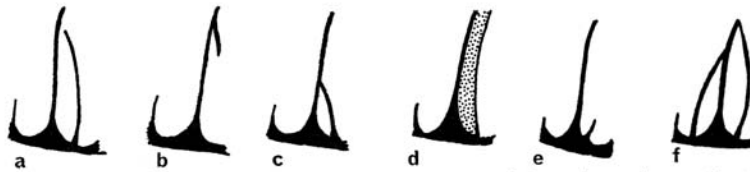
TEXT-FIG. 1. Exploded diagrammatic view showing the main morphological features of *Metriophyllum*.  
s' = major septa; s''—minor septa; t = tabulae; c = carinae.

TEXT-FIG. 2. Diagram showing the form of the horizontal trough-shaped carinae developed at alternating levels on adjacent septa.

*Description.* Small solitary turbinata to ceratoid corals. Calice deep and steep sided with septa projecting as sharp low ridges on the inner side. The floor of the calice is flat or slightly concave and the septa extend across this floor to meet at the axis where they are welded together with sclerenchyme to form a pseudo-columella (text-fig. 1; Pl. 16, fig. 2). The outer walls are also much thickened with sclerenchyme. The sides of the septa below the calice carry horizontal or nearly horizontal carinae which have upturned outer edges (text-fig. 2). The carinae may occur at the same or differing levels on either side of a septum but they always alternate in level with those on the neighbouring septa.

Tabulae are very thin and steeply inclined downwards away from the axis. Rejuvenation is uncommon but has been observed in *M. bouchardi*. It is doubtful whether true dissepiments are present in any species.

*Remarks.* The genus *Lopholasma* (type species *L. carinatum* Simpson 1900) is regarded as congeneric with *Metriophyllum* since transverse and longitudinal sections (Pl. 16, figs. 2 and 3) clearly show the presence of horizontal carinae so typical of *Metriophyllum*. (The dissepiments which Simpson (1900) described in *L. carinatum* are in fact the steeply sloping tabulae being cut by the transverse section; longitudinal sections confirm this.) I prefer to follow Stumm (1949) and Hill (1956) in regarding *Stereolasma* Simpson 1900 (type species *Streptelasma rectum* Hall 1876 (in part)) as a separate genus and not congeneric with *Metriophyllum* as Smith (1945) suggests; the horizontal carinae appear



TEXT-FIG. 3. Diagram showing some characteristic appearances of the carinae when cut by transverse sections.

to be a well marked and persistent character in the genus *Metriophyllum* and although *Stereolasma* is clearly a related form, the absence of any carinae makes it inadvisable to include it within the genus *Metriophyllum*. The same comments also apply to the specimens in the New York State Museum labelled *M. ungula* (Hall); longitudinal sections of this species clearly show that it lacks horizontal carinae and almost certainly belongs to the genus *Stereolasma*; (compare median longitudinal sections of *M. carinatum*, *S. rectum*, and '*M.*' *ungula*—Pl. 16, figs. 3, 5, and 7).

*Range.* Middle Devonian–Lower Permian.

*Carinae.* Edwards and Haime failed to recognize the true nature of the carinae and they interpreted the strong horizontal processes seen in the median section (text-fig. 1; Pl. 16, fig. 1) as tabulae. Barrois (1882) was the first to publish a diagram showing the spur-like appearance of carinae in longitudinal sections and Simpson (1900) recognized the existence of the horizontal carinae, but he did not appreciate the significance of the spur-like processes on the sides of the septa. Soshkina (1928) appears to have been the first to recognize their true significance.

Because of the unusual form of the carinae within the genus *Metriophyllum* much confusion may arise when interpreting their appearance in sections. In transverse sections they may simulate septa or appear as spurs on either side of the true septa (Pl. 18, fig. 2); they may also give the impression that a septum is splitting. Text-fig. 3 shows some of the appearances of carinae in transverse sections. Where the plane of section cuts through the junction between a septum and carinae the septum will appear to be much thickened (text-fig. 3d). In longitudinal sections the carinae commonly appear as lobed hooks or spurs but in median sections they show as strong horizontal bars.

In *M. bouchardi* and *M. gracile* the carinae are very delicate trough-shaped structures (Pl. 18, figs. 6, 10, and Pl. 19), but in *M. carinatum* they are stouter and less upturned at their outer edges (Pl. 16, fig. 3). In all the species which have been examined the outer upturned edges of the carinae tend to be thickened (text-fig. 2) so that they appear lobed in longitudinal sections.

Wang (1950) demonstrated that the carinae are built up of fibrous tissue, as are the septa; the outer wall is made up of lamellar tissue. These skeletal structures are clearly seen in the section of *M. bouchardi* (Pl. 16, fig. 6).

The carinae only start to develop at the base of the calice, and the septa extend across the floor of the calice before any carinae are formed. It is often possible to distinguish a suture between the septum and its attached carinae (see Pl. 16, figs. 3 and 6) where impurities have become trapped.

*Tabulae*. These are very thin and not always seen even in median sections. They slope at about 45° down from the axis (Pl. 16, fig. 1, and Pl. 19, fig. *a*) and may terminate against the carinae. In longitudinal sections, not passing through the axis, they appear as plates which link the carinae (Pl. 19, fig. *c*, and Pl. 18, fig. 6). Barrois (1882) recognized the true tabulae, though not in median sections; his figure (pl. vii, fig. 2*d*) shows very regularly developed tabulae linking the outer lips of neighbouring carinae and he described them as 'planchers ondulés'. Hill (1939) was the first to note that they are 'steeply domed' when seen in median section.

Plate 19 shows longitudinal serial sections from the axis to the outer wall of *M. bouchardi*. The form of the carinae can be appreciated by tracing them individually through the series from the strong horizontal cross-bar appearance (fig. *a*) to the spur-like appearance seen in off-median sections. The outward sloping tabulae are clearly seen in the median section (fig. *a*) and the way in which they cut the carinae is seen in fig. *b*. Later sections show the way in which tabulae extend between the carinae—very much less regularly than suggested by Barrois's figure in his description of the Asturian specimens.

#### *Metriophyllum bouchardi* Edwards and Haime 1850

Plate 16, fig. 6; Plate 17, figs. 1–6, 11; Plate 18, figs. 7, 11; Plate 19; text-fig. 4

1845 *Cyathophyllum mitratum* (Schlotheim); Michelin, p. 183, pl. xlvii, fig. 7 (*non Hyppurites mitratus* Schlotheim 1820, p. 352).

1850 *Metriophyllum Bouchardi* Edwards and Haime, p. lxxix (*nom. nud.*).

1851 *Metriophyllum Bouchardi* Edwards and Haime, p. 318, pl. 7, figs. 1, 1*a*–*b*, 2, 2*b*.

*Description*. Small solitary turbinata to ceratoid corals with a maximum diameter of about 10 mm. Overall length rarely exceeds 20 mm. The outer surface usually shows longitudinal striations corresponding to the internal positions of the septa, and about three well-marked transverse constrictions or wrinkles (Pl. 17, fig. 1); more rarely the outer surface is nearly smooth. The calice is deep and steep sided; it may occupy a third of the total length of the coral, but the walls are frequently broken off near the base of the calice (Pl. 19, fig. 11); the floor of the calice is flat or gently concave. Septa within the calice are short and project from the wall as sharp ridges; both major and minor septa are seen in the calice, the latter being slightly less prominent than the major ones (Pl. 17, figs. 3 and 4); subsequently the septa and the wall are thickened with the result

that the minor septa are completely embedded in sclerenchyme; however, it is at these minor septal positions that the carinae join the outer wall. The number of major septa is commonly 18–20, though Edwards and Haime (1851) give 22–24 as characteristic of the species; the septa are straight or only slightly flexed and they extend across the floor of the calice to meet at the axis; the axial ends are slightly swollen and they are cemented together by sclerenchyme to form a pseudocolumella. In some specimens the columella is narrow, while in others it occupies nearly one-third of the lumen (Pl. 16, fig. 6).

The major septa carry horizontal carinae which have upturned outer edges. They are developed at alternate levels on adjacent septa and usually at different levels on opposite sides of the same septum. The carinae are spaced at about 1 mm. intervals. Tabulae are thin discontinuous plates sloping downwards away from the axis; they are irregularly spaced.

Rejuvenation is rare but does occur (Pl. 17, figs. 2 and 5; Pl. 18, fig. 7).

*Horizon and locality.* Upper Devonian (Frasnian); from the Beaulieu Shales and Ferques Limestone, Ferques, near Boulogne.

*Discussion.* Lang, Smith and Thomas (1940) designated the specimen figured by Edwards and Haime (1851, pl. vii, figs. 1, 1a) as lectotype. The original specimen appears to be lost. Their figure shows 22 major septa though Edwards and Haime, in their text, mention 22 to 24 as typical. Topotype specimens have been figured by Smith (1945) and these show 19 septa. Of some 20 specimens from the type area which I have examined, only 2 have more than 20 septa and none has as many as 24; the vast majority have only 18 or 20.

Barrois (1882) described specimens of *M. bouchardi* from Moniello and Arnao (Asturia) in which the calice is very shallow. He suggested that the specimens may have broken before interment and this seems the most probable explanation, since the distal parts of the calice are thin, having no secondary stereoplasmic thickening.

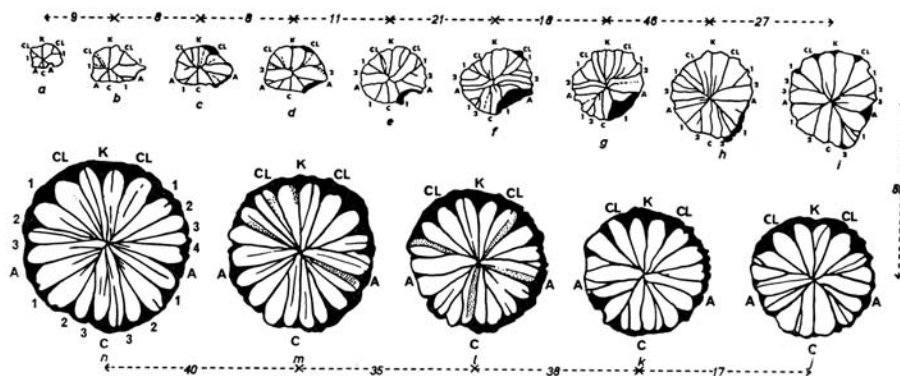
Smith (1945) stated that *Lopholasma carinatum* agrees with *M. bouchardi* in all essential characters and differs from it only in size and unimportant details. His remarks suggest that he regarded them as conspecific. There can be no doubt that *L. carinatum* is a species of *Metriophyllum*, but I cannot agree that they are conspecific, since *M.*

#### EXPLANATION OF PLATE 16

- Figs. 1–3. *Metriophyllum carinatum* (Simpson), Hamilton Beds, Livonia salt shaft, Livingstone Co., N.Y. 1, Longitudinal thin section (median) of a cotype showing the tabulae and horizontal carinae. NYSM 292,  $\times 3.3$ . 2, Transverse thin section of a cotype; major and minor septa are visible; the skeletal elements between the septa are sections through tabulae; NYSM 291,  $\times 3.3$ . 3, Longitudinal thin section (off median) showing the carinae appearing as spurs on either side of the septa. NYSM 290,  $\times 3.3$ .
- Figs. 4, 5. *Stereolasma rectum* (Hall). 4, Transverse thin section of hypotype, NYSM 320,  $\times 3.3$ . 5, Longitudinal thin section of hypotype, NYSM 322,  $\times 3.3$ .
- Fig. 6. *Metriophyllum bouchardi* (Edwards and Haime). Transverse thin section showing the lamellar structure of the outer wall and the fibrous structure of the septa and carinae. The suture between septa and carinae is well seen in the upper part of the plate. BMNH R16237,  $\times 7$ . Middle Devonian, Ferques, Boulonnais, France.
- Fig. 7. *Streptelasma unguolata* (Simpson). Longitudinal thin section of hypotype, NYSM 322,  $\times 3.3$ . Hamilton Beds, Hamburg-on-the-Lake, Erie Co., N.Y.  
(The original photographs of figs. 1–5, 7 were kindly supplied by the New York State Museum.)

*bouchardi* has only about twenty septa while *L. carinatum* shows thirty; also the carinae of *M. bouchardi* are larger and more strongly curved, thus producing deeper troughs; the carinae are also more widely spaced than in *L. carinatum*.

*Septal development.* Investigation of septal development in *M. bouchardi* presents unusual difficulties because, as has been pointed out above, the carinae simulate septa in transverse sections; in fact new septa and carinae arise in a similar way from the sides of the earlier formed septa. The fundamental difference between the two is that new septa arise only in four positions whereas the carinae may develop within any of the interseptal loculi. In making the present study it was found necessary to record sections at intervals of 0.003–0.005 inches and sixty-eight sections were made in a distance of 0.26 in. The sections were recorded by means of cellulose peels and a selection of critical



TEXT-FIG. 4. Selected serial sections to show the septal development of *M. bouchardi*. The figures indicate the distances between each section in thousandths of an inch. BMNH R16249,  $\times 4$ .

sections is reproduced in text-fig. 4. The septa in *M. bouchardi* show a radial arrangement in all stages of growth. However, there is a basic bilateral symmetry associated with a pinnate method of septal insertion.

The apical ends of several apparently complete specimens have been sectioned and the most juvenile arrangement of septa observed is that illustrated in text-fig. 4a. Two metasepta (marked I on the figure) are present in addition to the six protosepta (C = cardinal septum; K = counter cardinal septum; A = alar septa; CL = counter lateral septa; the septal nomenclature used here is that advocated by Hill (1935). The axial ends of the protosepta are swollen and welded together with sclerenchyme (this is not shown on text-fig. 4 as the sclerenchyme has been omitted for the sake of clarity). There is also thickening along the sides of the septa. The first formed metasepta are those which develop on the cardinal side of the counter lateral septa; those on the cardinal side of the alar septa follow almost simultaneously (text-fig. 4b and c), and this pattern is maintained with only minor exceptions throughout the development of the coral.

The newly formed septa grow until they almost reach the centre and their axial ends are within the central sclerenchyme. However, they always remain attached to the



protosepta from which they originated so that it is possible to distinguish four distinct groups of septa even in the mature corallite (see text-fig. 4n).

Within the calice the septa occur as longitudinal ridges; between these are a further series of ridges, usually somewhat less prominent, from which at a later stage of growth the carinae develop. These latter ridges occur in the position of minor septa and the outer surface of the epitheca has grooves which correspond to them. Because of the thickening of the epitheca below the calice, these ridges are not always apparent in sections made through the earlier formed parts of the corallite, but they can sometimes be distinguished embedded in lamellar tissue if the preservation is good. Whether or not these ridges should be regarded as true minor septa is open to question; they are closely linked with the subsequent development of the carinae and this suggests that they are not in fact minor septa. On the other hand, their regular position between the major septa, the septal grooves in the outer wall which correspond to them, and their formation from lamellar tissue would suggest a contrary interpretation. I incline to the view that they are true minor septa, and they are described as such in the systematic part of this paper.

Carinae are present in all but the earliest ontogenetic stages and each septum bears them. In the mature corallite the carinae run closely parallel to their parent septum, but in earlier stages they are more radially disposed and this increases the difficulty of distinguishing them from newly formed septa.

*Metriophyllum gracile* Schlüter 1884

Plate 17, figs. 7-10, 12, 13; Plate 18, figs. 1, 5, 6, 9, 10, 12-16

*Metriophyllum gracile* Schlüter 1884, pp. 82, 83.

*Metriophyllum gracile* Schlüter 1889, pp. 18-20, pl. 2, figs. 5-8.

*Metriophyllum laeve* Schlüter 1889, p. 18.

non *Lopholasma gracile* Soshkina 1928, p. 369.

*Lectotype.* Schlüter's species is based upon a number of syntypes in the Geologisch-palaeontologisches Institut und Museum at Bonn. From these syntypes the specimen illustrated in Plate 17, fig. 13 is here selected as the lectotype (Bonn, 161c).

EXPLANATION OF PLATE 17

Figs. 1-6, 11. *Metriophyllum bouchardi* (Edwards and Haime). Middle Devonian limestones and shales of Ferques, Boulonnais, France. 1, Exterior showing typical trochoid form and rugae; calicular margin is damaged. BMNH R18517,  $\times 5$ . 2, Calicular view of a specimen starting to rejuvenate. BMNH R18513,  $\times 5.4$ . 3, Specimen showing the deep steep-sided calice with major and minor septa appearing as ridges. BMNH R18517,  $\times 5.4$ . 4, Calicular walls have been broken revealing the form of the major and minor septa across the floor of the calice with carinae not yet formed at this level BMNH R16246,  $\times 4.7$ . 5, Specimen showing rejuvenation. BMNH R16248,  $\times 4.8$ . 6, Thin section (transverse) of a typical specimen; the flexure and thickening of the septa at the outer margin is well seen. BMNH R16249,  $\times 8$ . 11, Specimen in which the calicular walls have been completely abraded revealing the arrangement of septa across the calicular floor; some carinae are visible. BMNH R16231,  $\times 5.4$ .

Figs. 7-10, 12, 13. *Metriophyllum gracile* (Schlüter). Gerolstein area of Germany. 7, 8, Thin sections (transverse) showing the typical arrangement of the septa meeting at the axis and cemented by sclerenchyme. MM11120,  $\times 14$ . 9, Specimen showing the attachment groove which typifies individuals from a locality 1 km. south of Gerolstein (472.644). MM11119,  $\times 6$ . 10, Specimen with prominent root-like processes at the apical end. MM11117,  $\times 6$ . 12, Paralectotype showing the deep calice. Bonn,  $\times 7.7$ . 13, The lectotype, Bonn 161c,  $\times 6.5$ .

*Description.* Small solitary trochoid corals with an average length of 8 mm. and a diameter of 3–4 mm. The calice is deep and steep sided and may occupy as much as half the length of the corallite; the septa project into the calice as low ridges. The outer wall is relatively thick and marked by longitudinal grooves corresponding to the septal positions. There are 14–18 major septa in the average-sized specimen; these are slender and straight or only slightly flexed; at the axis they are welded together, though in ephelic stages they may withdraw slightly from the axis leaving a narrow aulos (compare Pl. 17, figs. 23 and 27). Minor septa are seen only in the calice, where they alternate with the major septa. Horizontal trough-shaped carinae occur on each septum though not within the calice; they are spaced at about 0.8 mm. intervals (Pl. 18, figs. 6 and 10). Tabulae are thin and slope steeply downwards away from the axis.

*Range.* *Metriophyllum gracile* has only been recorded from the Gerolstein area of Germany in beds which are of Upper Couvinian age. Hill (1939), in her remarks on *M. sp.* from Western Australia, suggests that *M. gracile* may extend up into the lower Givetian.

*Remarks.* Schlüter's original description records 16–18 septa but a re-examination of the syntypes and other specimens shows that there are not more than 18 septa and commonly only 14. No tabulae were observed in any of Schlüter's original specimens, but topotype material has been sectioned and this shows the thin, steeply inclined tabulae which are characteristic of the genus. The carinae are very delicate structures and they usually occur at the same level on opposite sides of a single septum, though they alternate in height with those on adjacent septa. The outer surface is usually strongly ribbed, though in larger specimens the distal end shows prominent transverse growth striae; this feature and some observations on the mode of attachment of the species have been the subject of a separate paper (Holwill 1963).

The main ways in which this species differs from *M. bouchardi* are in size, in number of septa, and in the positioning of the carinae.

*M. sp. cf. gracile* was recorded by Wade (1938) from the Rough Range of Western Australia; this record was based on a preliminary determination by Hill, who subsequently described the form (Hill 1939) merely as *M. sp.*, considering it inadvisable to give the form a name based on a single oblique section. Hill's figure of this specimen shows it to have well-developed minor septa, and on this basis alone it is to be distinguished from *gracile*. It is likely to be a new species, but until further material is available Hill is right in refraining from giving it a specific name.

#### *Metriophyllum gracile* (Soshkina) 1928

Soshkina recorded this species as *Lopholasma gracile* (Soshkina 1928, p. 368, pl. 12, fig. 14; text-fig. 12). Since *Lopholasma* is here regarded as synonymous with *Metriophyllum*, *M. gracile* Soshkina is a junior secondary homonym and as such the specific name must be rejected; I have communicated with Dr. Soshkina informing her of this and have invited her to publish a replacement name.

The form described by Soshkina is very small, having a maximum diameter of 2 mm. and a length of 5 mm. Only two individuals are recorded, both from the Lower Permian of the eastern Urals (Shchugor River). There are twelve major septa at this diameter and



no minor ones are apparent. The septa and outer walls are much thickened by sclerenchyme. The carinae are stout horizontal ridges developed irregularly from the sides of the septa; there is very little upturning of their outer edges. Tabulae are not seen.

*Metriophyllum laeve* Schlüter 1889

1889 *Metriophyllum laeve* Schlüter, p. 278(20), no figures.

Schlüter was uncertain whether *M. laeve* should be regarded as a distinct species. In his original description (Schlüter 1889) he describes the species as similar to *M. gracile* but nearly twice as large and with a smooth epitheca; he stated that *M. laeve* characterized a dolomite bed at the same horizon as the marl bed in which *M. gracile* occurs. A study of Schlüter's specimens shows that the smooth epitheca is not a consistent characteristic (compare Pl. 18, figs. 13 and 16); neither is size alone a reliable criterion for distinguishing species. However, thin and polished sections (Pl. 18, figs. 14 and 15) suggest that the septa are stout and slightly withdrawn from the axis leaving a small aulos; the axial ends of the septa are also swollen. At first sight these features would seem to be of specific importance, distinguishing *M. laeve* from *M. gracile*, but having examined several sections of *M. laeve* it was found that (i) the stout septa are caused by a recrystallization of the original calcite to form dolomite (some specimens were only partly recrystallized and these showed slender septa comparable with those typical of *M. gracile*). (ii) The swelling of the septal ends, and their slight withdrawal from the axis to form an aulos, can also be found in the epehebic stages of *M. gracile* (Pl. 18, fig. 5). It is true that the specimens of *M. laeve* are of larger average size than those of *M. gracile*, but it is not difficult to find specimens of *M. gracile* which are of comparable size; since *M. laeve* characterizes a particular lithology it is reasonable to suppose that the slightly different environment which facilitated dolomitization also tended to prolong the life of *Metriophyllum* so that a higher percentage of the individuals attained old age and developed senile characteristics.

*Metriophyllum lituum* sp. nov.

Plate 18, figs. 2-4, 8

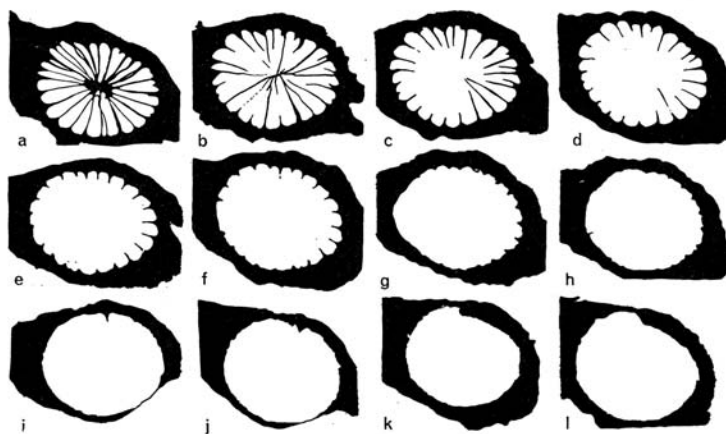
*Description.* Small solitary corals with a maximum observed diameter of 8 mm. At this diameter there are twenty-two major septa which are slender and usually slightly flexed; they reach the axis (except within the calice) and are welded together at the axis by a small amount of sclerenchyme, thus forming a pseudocolumella. Horizontal trough-shaped carinae are developed regularly up each septum; they are spaced at approximately 1.1 mm. intervals and are the same level on either side of any one septum, but alternate in height with those on adjacent septa. The septa are thickened just before reaching the outer wall, which is moderately thick. The calice is deep and steep sided; its floor is almost flat and the septa project into it as sharp ridges in the lower part; the distal end of the calice shows no evidence of septa on its inner surface (see serial sections, text-fig. 5). Minor septa are absent. The tabulae are steeply inclined downwards away from the axis and are numerous.

*Holotype.* Specimen MM11113 from the Combe Martin Beach Limestone (Middle/Upper Devonian), Ilfracombe Beds, north Devon.

*Material.* Much of the material from north Devon is poorly preserved and no complete specimens of *M. lituum* have been obtained; hence the overall length and the form of the corallum are not known with certainty. Altogether eight specimens have been collected (MM11113, 4, 11122, 11125-9).

*Locality and horizon.* All the specimens have been obtained from the Combe Martin Beach Limestone in the neighbourhood of Newberry Beach, Combe Martin, north Devon. On the basis of the associated fauna the bed is dated as Upper Givetian or Lower Frasnian (see Holwill 1962 for a discussion of the probable age).

*Derivation of name.* From the Latin *lituus*—a curved staff or wand—referring to the thin flexed septa.



TEXT-FIG. 5. Serial sections through the distal parts of *M. lituum* sp. nov. The sections were taken at approximately equal intervals through a thickness of 0.14 in. MM11114,  $\times 4$ .

*Discussion.* *M. lituum* closely resembles *M. bouchardi*, but it differs from the latter both in size and in the number and slenderness of its septa; also in the very regular development of the carinae on either side of each septum. It differs from *M. gracile* in being larger and in having a greater number of septa.

Text-fig. 6 shows serial sections through a small specimen (probably in its nepionic stage, hence the small diameter and few septa). The sections show very clearly the way in which carinae may appear as spurs from the septa and even themselves simulate septa.

*Metriophyllum battersbyi* Edwards and Haime 1851

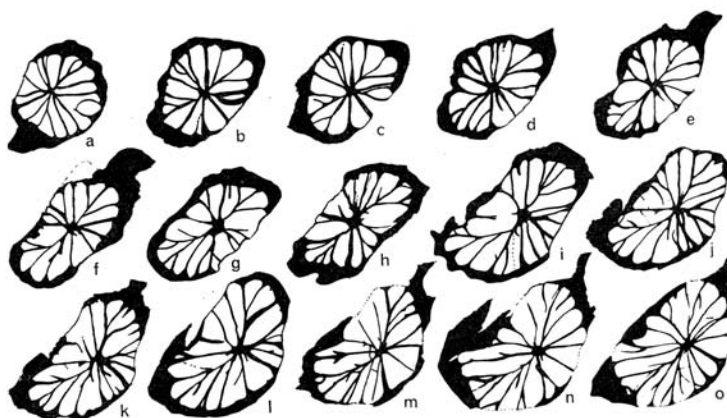
1851 *Metriophyllum Battersbyi* Edwards and Haime, p. 318.

1853 *Metriophyllum Battersbyi* Edwards and Haime, p. 222, pl. 49, fig. 4.

In 1851 Edwards and Haime recorded the coral *M. battersbyi* from the Middle Devonian Limestones of Torquay. They figured this specimen and gave a fuller description of it in their monograph of 1853. Many subsequent workers have referred to this identification and have doubted its validity (e.g. Hill 1939, Smith 1945). Apart from a species of *Metriophyllum* from north Devon (Holwill 1962), and a doubtful identification of *Metriophyllum* by Smith (1953) (see below), it is the only form of *Metriophyllum*

recorded in the British Isles and it differs in so many obvious characters from other known species of this genus that it is not surprising that doubt has been cast on the generic determination.

In describing it in 1853, Edwards and Haime made particular reference to the 'quadri-fascicular mode of arrangement of the septa' of which there were said to be forty-eight major ones, 'somewhat thickened', in a section taken just below the calice. These alternate with minor septa which are thinner. Dissepiments were also recognized. The authors distinguished the species from the type species by the more numerous septa and the fact that they were slightly thickened near the centre.



TEXT-FIG. 6. Serial sections through a juvenile specimen of *M. lituum* sp. nov. The sections were taken at approximately equal intervals through a thickness of 0.14 in. MM11114,  $\times 5$ .

Unfortunately the original specimen figured by Edwards and Haime has been lost, but their figure (pl. xlix, fig. 4) is closely similar to other specimens labelled *M. battersbyi* which are in the British Museum (Nat. Hist.) and which were obtained from the same area in south Devon as the holotype. A study of these specimens, from which several thin sections have been made, makes it clear that *M. battersbyi* is not a species of *Metriophyllum*; in fact Edwards and Haime's own description of the holotype is sufficient to show that it cannot be included in this genus as defined above. Briefly the chief characters which exclude it from the genus are as follows:

- (a) Absence of horizontal trough-shaped carinae.
- (b) The presence of minor septa extending half-way (or more) to the centre.
- (c) The presence of dissepiments.
- (d) The thickening of the septa in their central parts and their attenuation towards the periphery.
- (e) The presence of numerous inflated tabellae in a central tabularium.
- (f) The presence of an axial whorl.

Other less significant factors are the large size, the numerous septa, and the thin outer wall; none of these features characterizes any known species of *Metriophyllum*. It is

most probable that '*M. battersbyi*' should in fact be referred to the genus *Acanthophyllum* as redefined by Birenheide (1961).

*Metriophyllum carbonaria* (Grabau 1922)

1922 *Lopholasma carbonaria* Grabau, pp. 43–45, pl. i, figs. 5a–b, 6b, 7b, 7d, 8b, 8d, 9b, 9d, 10b, 10d, 11d, 12; text-figs. 54–56.

This species from the Viséan or Lower Moscovian of China differs from other known species of *Metriophyllum* in having a well-marked fossula and a cardinal septum which does not reach the axis. Grabau describes dissepiments which are 'fairly numerous, thin and for the most part cystiform, i.e. convex upwards', but later he writes: 'between the septa are cystose dissepiments . . . these probably being also in many cases sections of carinae.' His published figures do not support the suggestion that dissepiments are present and I consider that the structures observed by Grabau are either sections through the carinae as he himself suggests, or, even more probably, sections through the outward sloping tabulae. This contention is supported by a later remark of Grabau: 'the dissepiments break up into spines and finally these spines disappear'—this is the behaviour of the carinae in successive serial sections which has been demonstrated above.

*Metriophyllum carinatum* (Simpson 1900)

Plate 16, figs. 1–3

1900 *Lopholasma carinatum* Simpson, p. 206, figs. 19–22.

Some comments have already been made on this species in the foregoing descriptions and it is illustrated in Plate 16, figs. 1–3. Minor septa are well developed in addition to about thirty major ones which extend to the axis, where they are welded together by sclerenchyme. The minor septa extend slightly beyond the outer thickened wall and usually abut against a major septum (see Pl. 16, fig. 2). The carinae numerous and occur at alternate levels on either side of a septum; they are stouter and less upturned at their outer edges than in *M. bouchardi*.

The species is recorded from the Hamilton Shales (Middle Devonian) of U.S.A.

*Metriophyllum deminutivum* Easton 1944

1944 *Metriophyllum deminutivum* Easton, pp. 31, 32, pl. 3, figs. 1–3.

This species occurs in the lower part of the Chouteau Limestone (Mississippian) of Missouri, and must unquestionably be included within the genus *Metriophyllum* as defined above. In size and general form of the carinae, *M. deminutivum* resembles *M. gracile*, but at least one marked difference lies in the form of the septa during the middle ephebic stages: Easton describes them as 'grouped somewhat in pairs, five pairs on each side between single thick cardinal septum and thin counter septum with single minors joining it on either side to form tripartite counter system'. The presence of 'not more than three very fine dissepiments' is mentioned and, if true dissepiments are indeed present, this feature alone distinguishes it from other known species.

*Metriophyllum erisma* Hill 1949

1949 *Metriophyllum erisma* Hill, p. 142, pl. 6, figs. 11, 12.

Hill created this new species for forms in which the septal flanges (carinae) are inclined inwards and downwards and in which the inner tabulae sweep vertically downwards about the axis; there are also occasional outer tabulae. Hill does not indicate whether the carinae are of the trough-shaped variety which are typical of the genus, and unfortunately her figures do not clarify this point; the fact, however, that in the transverse section they 'appear as thickenings of the septa or as slender plates like extra septa running parallel to the septa' suggests that they may have upturned outer edges. The inclination of the carinae downwards towards the axis is exceptional (they make an angle with the horizontal of about 20°), and it has not been noted in any other species. The two sets of tabulae are also unique to this species.

*Metriophyllum (Aemulophyllum) exiguum* (Billings 1860)

1860 *Heliophyllum exiguum* Billings, p. 261, figs. 9, 10.

*M. (Aemulophyllum)* was erected as a subgenus of *Metriophyllum* by Oliver (1958) to contain forms of *Metriophyllum* with a calceoloid flattening; to the new subgenus he assigned the form *Heliophyllum exiguum* Billings. In his redescription of this species Oliver mentions the presence of a 'deep fossula on the convex . . . side which is occupied by a short cardinal septum'; he also describes crossbar carinae 'which descend gently

## EXPLANATION OF PLATE 18

- Figs. 1, 5, 6, 9, 10. *Metriophyllum gracile* (Schlüter). Gerolstein area of Germany. 1, Typical external appearance with longitudinal ridges prominent at the apical end and concentric growth striae in the distal parts. MM11115,  $\times 6.8$ . 5, Thin section (transverse) of a specimen in which the septa are slightly withdrawn from the axis leaving a narrow aulos. MM11121,  $\times 15$ . 6, 10, Thin sections (longitudinal) showing the deep calice with walls thickened near the base and the delicate carinae developed on either side of the septa, MM11124,  $\times 5.3$ ; 11123,  $\times 7$ . 9, Specimen showing the attachment groove which typifies individuals from a locality 1 km. south of Gerolstein (472.644). MM11116,  $\times 7$ .
- Figs. 2-4, 8. *Metriophyllum lituum* sp. nov. Combe Martin Beach Limestone (Ilfracombe Beds), Combe Martin, north Devon. 2, Polished section (transverse) of a paratype. Much of the outer wall has been abraded away but the form of the septa and carinae is well shown. MM11122,  $\times 6$ . Holotype. MM11113. 3, Transverse section,  $\times 6.3$ . 4, Median longitudinal section showing the horizontal carinae and steeply outward sloping tabulae,  $\times 6.3$ . 8, Off-median section showing the regular arrangement of the carinae on either side of the septa,  $\times 8.8$ .
- Figs. 7, 11. *Metriophyllum bouchardi* (Edwards and Haime). Middle Devonian limestones and shales of Ferques, Boulonnais, France. 7, Polished section of a specimen showing the early stages of rejuvenation. BMNH R18513,  $\times 4$ . 11, Thin section (transverse) of a specimen with a much thickened outer wall and axis. BMNH R16237,  $\times 5.3$ .
- Figs. 12-16. *Metriophyllum gracile* (Schlüter). Gerolstein area of Germany. All these are original specimens of Schlüter, in the Bonn Museum, which he named *M. laeve*; they are here regarded as conspecific with *M. gracile*. 12, Polished longitudinal section. Bonn 162b,  $\times 9$ . 13, A large specimen with relatively smooth epitheca. Bonn 162,  $\times 7$ . 14, Thin section (transverse) of a specimen which has recrystallized, thus destroying the original skeletal structure and creating the impression of much thickened septa. Bonn 162c,  $\times 10.75$ . 15, Polished transverse section of a specimen showing the septa slightly withdrawn from the axis and laterally in contact, thus forming an aulos. Bonn 162a,  $\times 8$ . 16, Same specimen, showing longitudinal ridges,  $\times 5$ .

towards the exterior' and are 'apparently limited to the peripheral zone'. These features suggest that the species is incorrectly regarded as a subgenus of *Metriophyllum*, which lacks a fossula, has horizontal carinae developed throughout its length (except in the calice), and has septa all of which reach the axis. Unfortunately I have not had the opportunity to examine the type material which is in the New York State Museum; however, the Museum has kindly sent excellent photographs of the holotypes, and these, together with Oliver's own figures and descriptions, suggest that the form should be regarded as a subgenus of *Heliophyllum* rather than of *Metriophyllum*.

*Metriophyllum ilitchense* (Soshkina 1928)

1928 *Lopholasma ilitchense* Soshkina, pp. 369–70, fig. 13a, b; pl. 12, figs. 12, 13.

This species is recorded from the Lower Permian of the eastern Urals. Soshkina has compared it with *M. carbonaria* (Grabau) but is reluctant to make the species synonymous because of their wide geographical separation and the fact that they occur in different geological systems. Only one incomplete specimen is recorded which has an elongate conical form and has seventeen major septa at a diameter of 6.5 mm.; there are a corresponding number of minor ones which are short and sinuous. The outer surface is covered by numerous spiny tubercles which are scarcely visible to the naked eye. Horizontal carinae typical of the genus are developed irregularly on either side of each septum. Soshkina specifically states that dissepiments occur running between the septa but that tabulae are absent. It is clear, however, from her figures that the structures she refers to as dissepiments are the same structures as Hill has interpreted as tabulae and which have been described as tabulae in this present paper; they run downwards away from the axis.

*Metriophyllum poshiense* Mansuy 1912

1912 *Metriophyllum poshiense* Mansuy, pp. 47, 48, pl. 7, fig. 8a–d.

Grabau (1922) doubts the generic identification of this species though his opinion was based only on a study of the published figures. The species, which has a maximum diameter of 7–8 mm., shows two series of septa: the major series meet at the axis and are welded together with sclerenchyme while the minor series are about half as long. The outer wall is thick and some of the septa show a thickening which may be the result of the section cutting through carinae. Unfortunately the reproduction of the plate is not clear enough to be certain on this point. I think Mansuy was probably correct in placing the species in *Metriophyllum*. The species occurs in the Middle Devonian of Indo-China.

? *Metriophyllum* sp. Smith 1953

1953 ? *Metriophyllum* sp. Smith, pp. 305–6, no figures.

Smith described a species of rugose coral from south-west Devonshire and assigned it tentatively to the genus *Metriophyllum*. The slates in which these fossils occur are thought to be of Lower Devonian age. All the specimens are somewhat compressed, and Smith did not feel justified in giving the form a specific name. I have examined the specimens, and I am very doubtful whether they should be referred to the genus *Metriophyllum* since carinae are completely lacking. The septa are much dilated in their axial parts



and laterally contiguous, thus forming a solid structure which fills most of the lumen; tabulae are absent. Smith suggested that the form probably represented an early species of *Metriophyllum* and this may well be, since it has already been noticed above that the Couvinian form, *M. gracile*, often shows septa which are swollen at the axis, sometimes with the development of a narrow aulos. (Such characteristics are also suggestive of *Syringaxon*—a fact which suggests that Lecompte (1952) is correct in placing *Metriophyllum* and *Syringaxon* in the same family (the Metriophyllidae.) However, until better-preserved specimens become available, I prefer not to regard ?*Metriophyllum* Smith as a species of *Metriophyllum* s.s.

*Repositories.* Corals illustrated in this paper are located in the following museums:

The New York State Museum, Albany 1, U.S.A. (NYSM).

The British Museum (Natural History), London (BMNH).

The Geologisch-palaeontologisches Institut und Museum, Bonn (Schlüter collection) (Bonn).

The Murchison Museum, Dept. of Geology, Imperial College, London (MM).

*Acknowledgements.* I have very much appreciated the co-operation given to me by the staffs of the British Museum (Nat. Hist.) and the Geologisch-palaeontologisches Institut und Museum at Bonn, who have permitted the loan of numerous specimens in their charge; and also the kindness of the New York State Museum in supplying me with excellent photographs of type specimens in that museum. I also express my sincere thanks to Dr. Gwyn Thomas for helpful criticism during the preparation of this paper. The help given by Mrs. J. Creighton and Miss M. Simpson in the preparation of material and by Mr. J. Gee in photographing it, is also gratefully acknowledged.

#### REFERENCES

- BARROIS, C. 1882. *Recherches sur les Terrains Anciens des Asturies et de la Galice*. Lille.
- BILLINGS, E. 1860. On the Devonian fossils of Canada West. *Canad. J.*, n.s., **5**, 249–82.
- BIRENHEIDE, R. 1961. Die Acanthophyllum-Arten (Rugosa) aus dem Richtschnitt Schönecken—Dingdorf und aus anderen Vorkommen in der Eifel. *Senckenbergiana leth.* **42** (1, 2), 77–146.
- BUTLER, A. J. 1935. On the Silurian coral *Cyathaxonia siluriensis* M'Coy. *Geol. Mag.* **72**, 116–24.
- EASTON, W. H. 1944. Corals from the Chouteau and related formations of the Mississippi Valley region. *Ill. State Geol. Surv. Rep. Invest.* **97**.
- EDWARDS, H. M. and HAIME, J. 1850–5. A monograph of British Fossil Corals, Pts. I–V. *Palaeontogr. Soc. (Monogr.)*.
- 1851. Monographie des Polypiers fossiles des Terrains palaeozoiques. *Arch. Mus. Hist. nat. Paris*, **5**.
- GRABAU, A. W. 1922. Palaeozoic corals from China. Pt. I. Tetrseptata. *Palaeont. Sinica*, **B 2** (1), 1–76.
- HALL, J. 1876. Illustrations of Devonian Fossils . . . of the Upper Helderberg, Hamilton and Chemung Groups. *Geol. Surv. State New York, Palaeont.*, **1–7** (but see Lang *et al.* 1940 for a full discussion on the date of this paper).
- HENBEST, L. G. 1931. Methods and techniques. *J. Paleont.* **5**, 355–64.
- HILL, D. 1935. British terminology for Rugose corals. *Geol. Mag.* **72**, 481–519.
- 1939. Western Australian corals in the Wade Collection. *J. roy. Soc. W. Australia*, **25**, 141–52.
- 1949. Middle Devonian corals from the Buchan District, Victoria. *Proc. roy. Soc. Victoria*. **62**, 137–64.
- 1956. Rugosa. In MOORE, R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part F, Coelenterata, **F 233–324**.

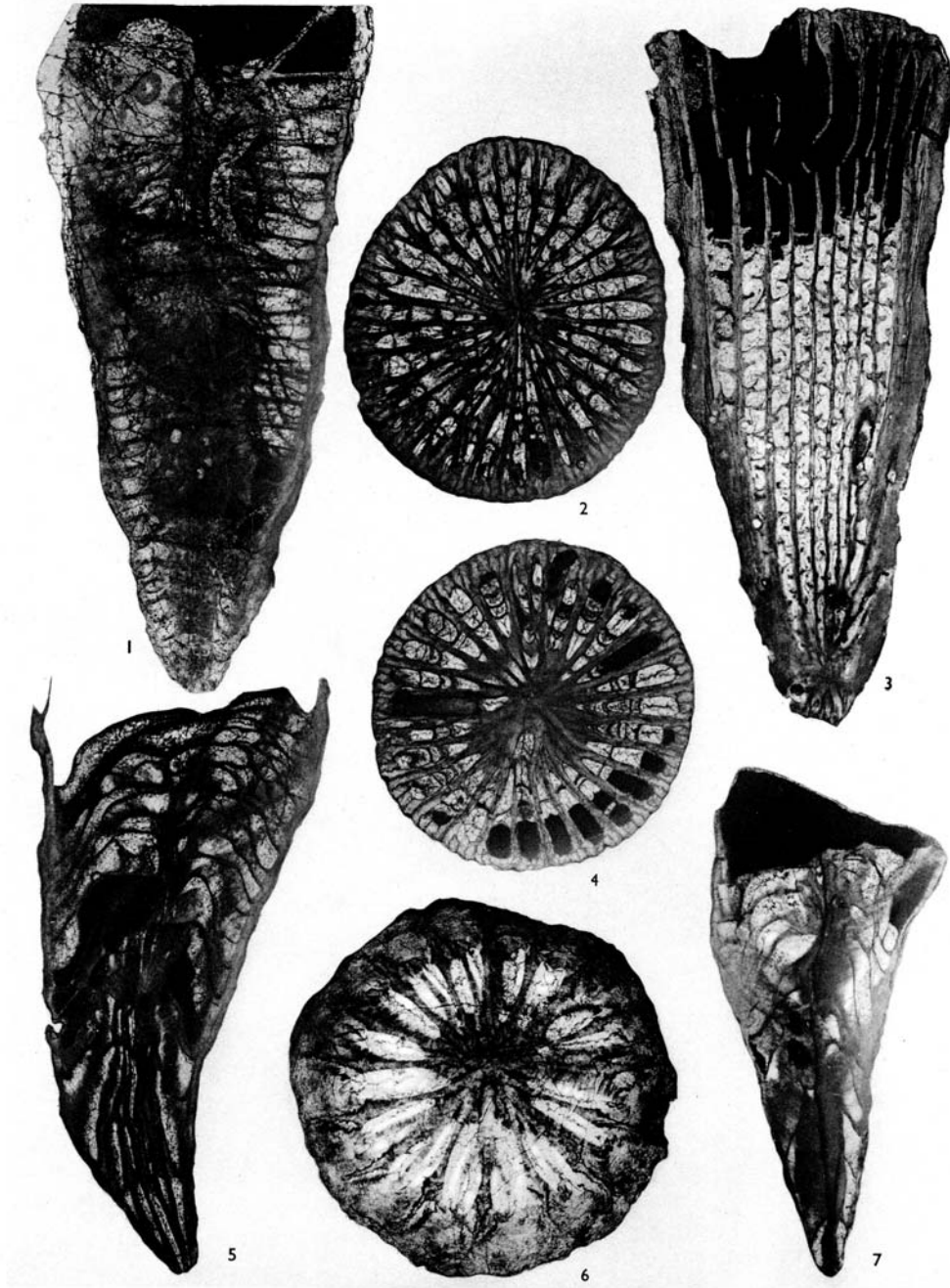
#### EXPLANATION OF PLATE 19

*Metriophyllum bouchardi* (Edwards and Haime). Sequence of longitudinal sections from the axis (fig. a) to near the outer wall (fig. p). The outward sloping tabulae are well shown in the near axial sections. BMNH R16242, ×4.

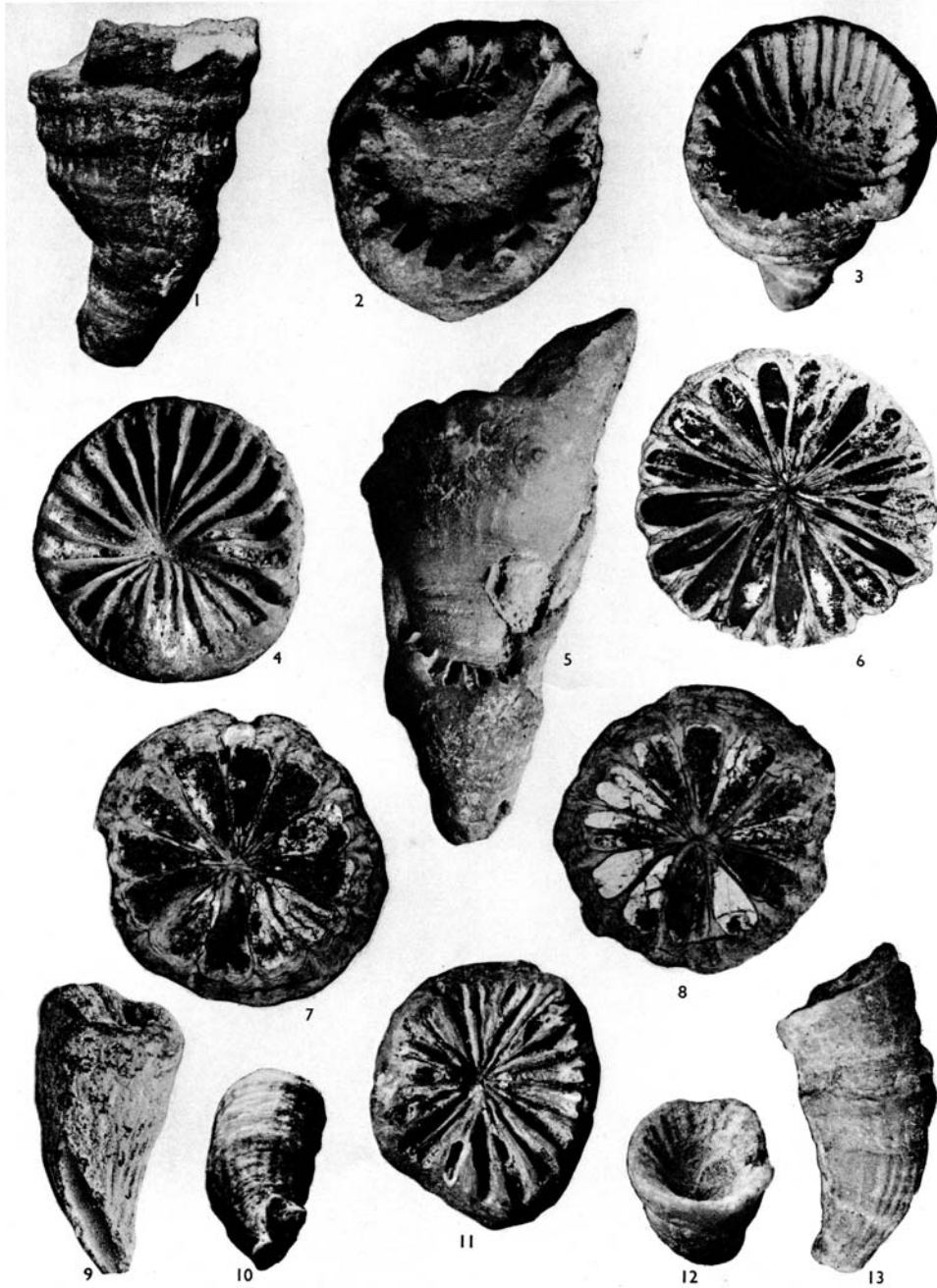
- HOLWILL, F. J. W. 1962. The succession of limestones within the Ilfracombe Beds (Devonian) of north Devon. *Proc. geol. Ass. Lond.* **73**, 281-94.
- 1963. A note on the mode of attachment and growth of the coral *Metriophyllum gracile* Schlüter. *Geol. Mag.* **100**, 503-6, pl. 33.
- LANG, W. D., SMITH, S. and THOMAS, H. D. 1940. *Index of Palaeozoic Coral Genera*. Brit. Mus. (Nat. Hist.). London.
- LECOMPTE, M. 1952. Madreporaires paléozoïques. In PIVETEAU, J. (ed.), *Traité de Paléontologie*, **1**, 419-538. Paris.
- MANSUY, H. 1912. Étude Géologique du Yun-Nan Oriental. Pt. II. Paléontologie. *Memoires du Service Géologique de l'Indochine*, **1** (2).
- MICHELIN, J. L. H. 1845. *Iconographie Zoophytologique*. . . . Paris. (8 parts, published yearly from 1841-8.) Part 5, 183-4, pl. 47, fig. 7.
- OLIVER, W. A. 1958. Significance of external form in some Onondagan Rugose corals. *J. Paleont.* **32**, 815-37, pls. 104-5.
- SCHLOTHEIM, E. F. 1820. *Die Petrefactenkunde*. . . . Gotha.
- SCHLÜTER, C. 1884. Ueber interessante neue Petrefakten. *Verhand. Naturhist. Preuss. Rheinlande*, **41**, 82-83.
- 1889. Anthozoen des rheinischen Mittel-Devon. *Abh. geol. Specialk. Preuss. Thuring. Staat.* **8**.
- SIMPSON, G. B. 1900. Preliminary descriptions of new genera of Palaeozoic Rugose corals. *Bull. N.Y. St. Mus.* (39), **8** (Palaeont. pap.), 199-222.
- SMITH, S. 1945. Upper Devonian corals of the Mackenzie River Region, Canada. *Spec. Pap. geol. Soc. Amer.* **59**, 1-126.
- 1953. Notes on corals from the Lower Devonian Rocks of S.W. Devonshire. In HENDRIKS, E. M. L., Geological succession and structure in western south Devonshire. *Trans. roy. Geol. Soc. Cornwall*, **18**, 299-308.
- SOSHKINA, E. D. 1928. Die unterpermischen Korallen von westlichen Abhang des nordlichen Uralgebirges. *Bull. Soc. Nat. Moscou* (sect. geol.), **6**.
- STUMM, E. C. 1949. Revision of the families and genera of the Devonian Tetracorals. *Mem. geol. Soc. Amer.* **40**.
- WADE, A. 1938. The geological succession in the west Kimberley District of Western Australia. *Rep. Aust. Ass. Adv. Sc.* **23**, 93-95.
- WANG, H. C. 1950. A revision of the Zoantharia Rugosa in the light of their minute skeletal structures. *Phil. Trans.*, ser. B, **234**, 175-246, pls. 4-9.

F. J. W. HOLWILL,  
Department of Geology,  
Imperial College,  
London, S.W. 7

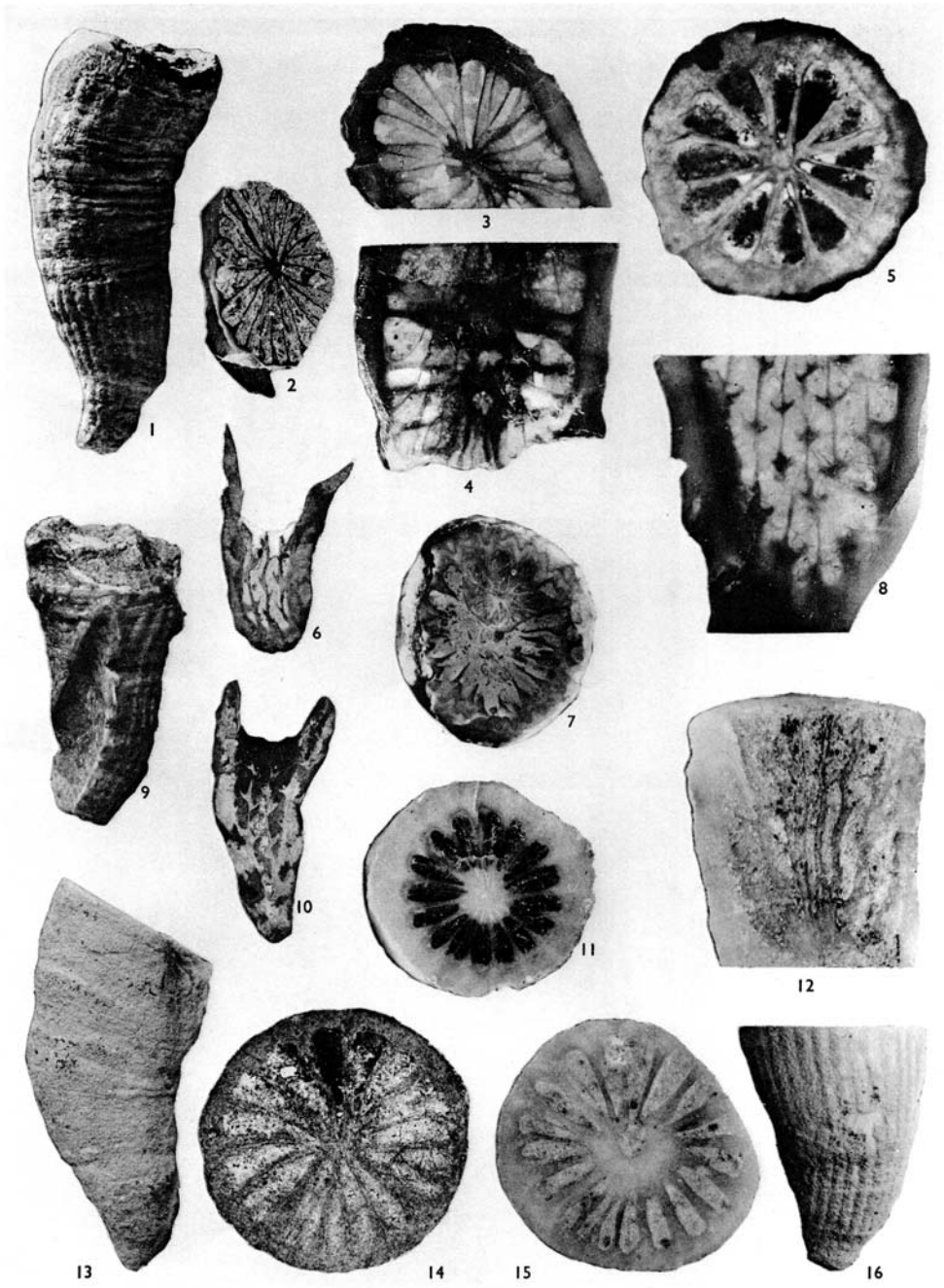
Manuscript received 20 May 1963.



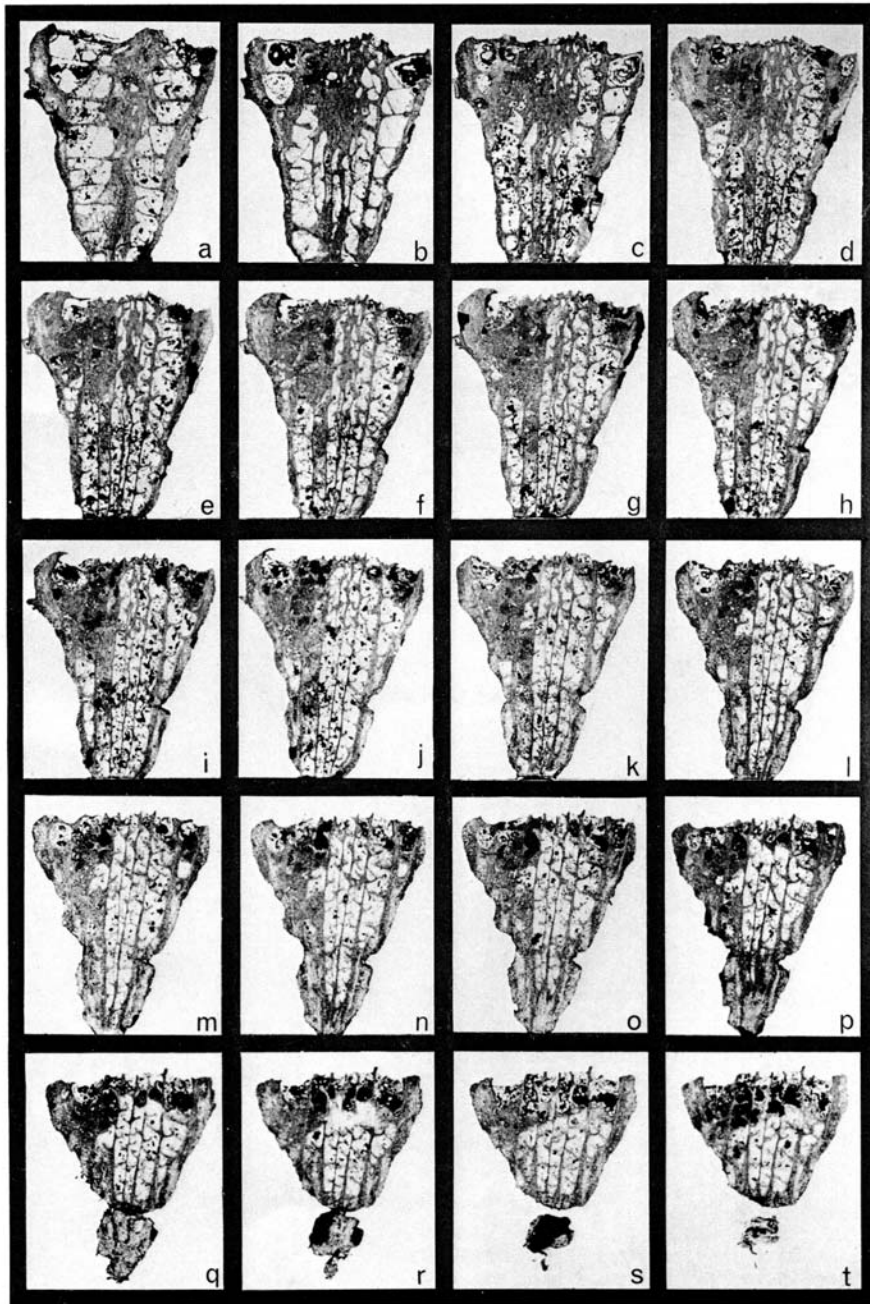
HOLWILL, *Metriophyllum*



HOLWILL, *Metriophyllum*



HOLWILL, *Metriophyllum*



HOLWILL, *Metriophyllum*