THE SILURIAN RUGOSE CORAL GENUS *ENTELOPHYLLUM* AND RELATED GENERA IN NORTHERN EUROPE

by JOHN S. JELL *and* PATRICK K. SUTHERLAND

ABSTRACT. Restudy of *Entelophyllum* from Gotland (including the type species) and Great Britain indicates restriction of *Entelophyllum* to phaceloid forms with peripheral, parricidal increase. Typical forms also have smooth or carinate septa, well-developed biserial tabularia, and dissepimentaria composed of globose interseptal dissepiments. On Gotland the genus ranges from the late Telychian to the Ludfordian. *Stereoxylodes* Wang and *Carinophyllum* Strelnikov are considered junior synonyms of *Entelophyllum*. Species from Gotland with nonparricidal budding are referred to *Donacophyllum* Dybowski. Cerioid forms internally similar to *Entelophyllum* are referred to *Prohexagonaria* Merriam. *Petrozium* Smith is retained for some Early Silurian forms. Newly described taxa are: *Entelophyllum articulatum anglicum* subsp. nov., *E. dendroides* sp. nov., *E. lauense* sp. nov. *E. hamraense* sp. nov., *E.* sp. A, *Prohexagonaria favia* sp. nov., *P. gotlandica* sp. nov., *Donacophyllum neumani* sp. nov., and *D. wallstenense* sp. nov.

ENTELOPHYLLUM was proposed by Wedekind in September 1927, and Lang and Smith described *Xylodes* in October of the same year, both for Silurian rugose corals similar to *Cyathophyllum articulatum* Wahlenberg, 1821. Since 1927, many forms worldwide have been referred to *Entelophyllum* and other genera have been based on species referred to it at one time or another. Several of the early species were based on unsectioned specimens, some of which have since been lost or destroyed. Variation and stratigraphic distribution of most species were unknown. Consequently, many of the species have been misinterpreted and some identifications away from the type areas are clearly inaccurate.

The Silurian sequence on Gotland, Sweden (Text-fig. 1A) is the type area for several species and provides the best succession of entelophylloid corals worldwide. This restudy is based on collections in the Riksmuseet, Stockholm, Dr B. Neuman's collection in Bergen, Professor D. Hill's collection in the University of Queensland, and on large collections made by the authors in 1972. We have studied the available English and Scottish material in the collections of various British museums and have collected from many of the British sections. Our descriptions and interpretations of other northwestern European occurrences of entelophylloid corals are based on the published data and photographs of type meterial sent to us by various colleagues. It is hoped that this study will provide a significant basis for the re-evaluation of such corals from other regions in the world.

STRATIGRAPHY AND DISTRIBUTION

Great Britain

The earliest known occurrence of entelophylloid corals in Britain is *Petrozium dewari* Smith in the Llandovery (possibly late Rhuddanian: based on correlations by Cocks and Toghill 1973), of southwestern Scotland. In Shropshire, it occurs in the Pentamerus Beds, the graptolites of which are attributable to the early Telychian *turriculatus* Biozone, and in the overlying Hughley Shale (Ziegler *et al.* 1968) (Text-figs 2 and 3).

Entelophyllum has not been recorded from the Sheinwoodian Stage in Britain as this interval is generally noncalcareous but as the sequence becomes more calcareous, *E. articulatum anglicum*

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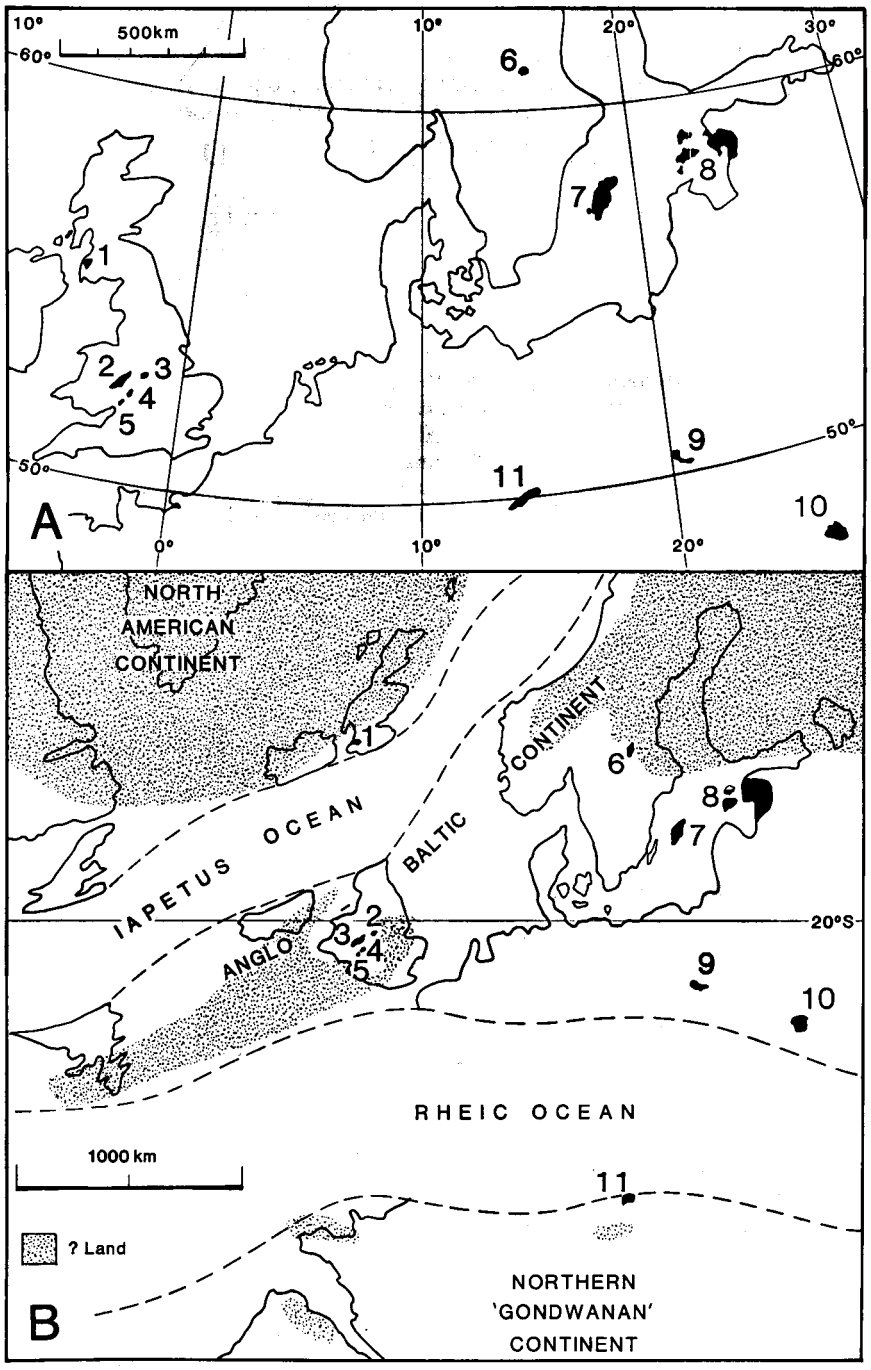
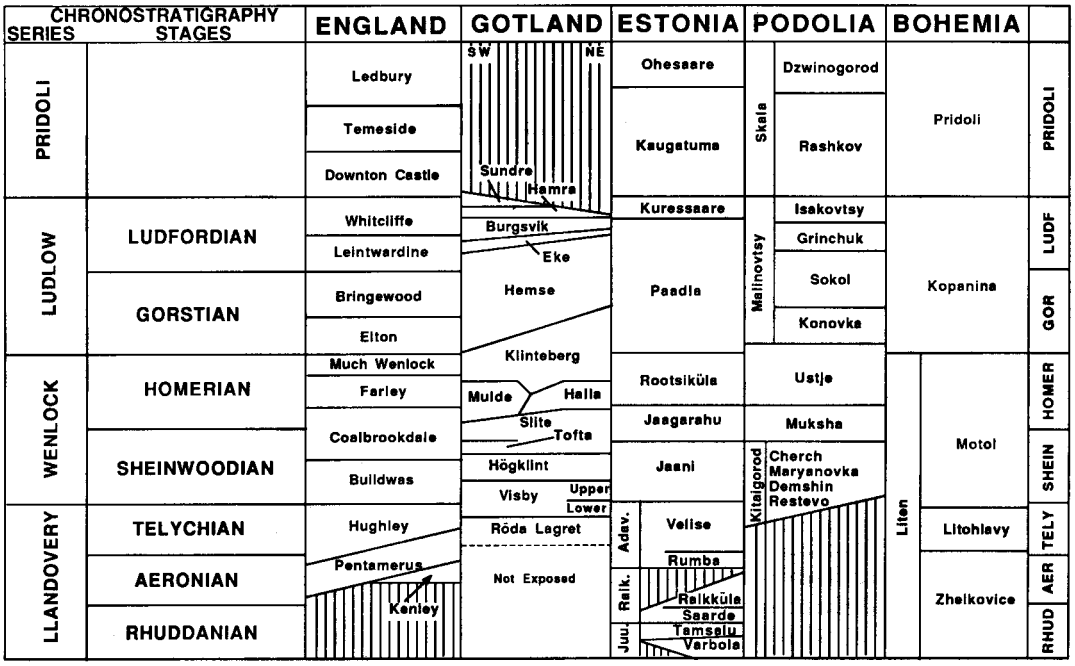


TEXT-FIG. 1. A, Distribution of entelophylloid corals in northern Europe. B, Palaeogeography for mid-Silurian times based mainly on Cocks and Fortey (1982) and McKerrow (1988). Localities: 1, Girvan; 2, Wenlock Edge; 3, Dudley; 4, Malverns; 5, May Hill; 6, Dalecarlia; 7, Gotland; 8, Estonia; 9, Holy Cross Mountains; 10, Podolia; 11, Bohemia.

subsp. nov. and *E. pseudodianthus* (Weissermel) appear together in the Homerian Much Wenlock Limestone at Dudley, Worcestershire. In Shropshire, specimens from the middle Homerian Farley Member of the Coalbrookdale Formation have been referred to both of the above species. The overlying Much Wenlock Limestone, which along Wenlock Edge is late Homerian (Bassett *et al.* 1975), yields both species. Both *E. articulatum anglicum* and *E. pseudodianthus* are known from the lower Elton Beds of early Gorstian age (Holland *et al.* 1980).



TEXT-FIG. 2. Correlation of standard Silurian chronostratigraphic units and the principal entelophylloid bearing sequences of northern Europe; correlations based on Holland and Bassett (1989).

Gotland

Where possible, Gotland collections are related to localities of Laufeld (1974) and to geological mapping of Hede (1960). The earliest occurrence is *Entelophyllum dendroides* sp. nov. (Text-fig. 3) from the Telychian Röda Lagret, which crops out just below sea level north of Visby.

Prohexagonaria favia sp. nov. occurs in the Sheinwoodian Upper Visby Beds. Wedekind (1927) described *E. visbyense* and *E. anschutzi* from early Sheinwoodian Högklint Beds at Visby. Neuman and Hanken (1979) listed *E. visbyense* in the top of the Upper Visby Beds southwest of Visby. We consider these two species synonymous and probably not referable to *Entelophyllum* s.s.

The neotype of *E. articulatum* is from an unknown locality and horizon on Gotland but it is closely similar to specimens occurring in the early Homerian Slite Beds at Bogeklint 1. It also occurs in the Homerian Mulde and Klinteberg Beds and its highest occurrence is in the Gorstian lower part of the Hemse Beds at Snoder 1.

Entelophyllum proliferum (Dybowski) was described from the island of Stora Karlsö in the upper part of the Slite Group (late Sheinwoodian to early Homerian age). From the northwestern coast of Stora Karlsö we describe *Donacophyllum neumani* sp. nov. and *D. wallstenense* sp. nov., which are similar to *E. articulatum* except in mode of increase and in development of lonsdaleoid dissepiments.

E. fasciculatum Wedekind, which descended from *E. articulatum*, is common in the upper Hemse and Eke Beds, the shelly faunas of which suggest an early Ludfordian age (Bassett and Cocks 1974). Of heavily carinate forms, *E. lauense* sp. nov. appears in the Eke Beds and *E. hamraense* sp. nov. occurs in the late Ludfordian Hamra and Sundre Beds.

Central Sweden

The only suggestion of *Entelophyllum* from mainland Sweden is one specimen described by Lindström (1880) as *Cyathophyllum dalecarlicum*. No further material has been found and its assignment is questionable. It is from the Telychian (based on graptolites listed by Hede 1958) in central Sweden.

Estonia

Petrozium losseni (Dybowski) from the late Rhuddanian, upper Juuru Horizon is the oldest known entelophylloid from Estonia (Text-fig. 3). Kaljo (1970) listed *E. articulatum* in the Telychian Adavere Horizon, *E. articulatum* and *E. pseudodianthus* in the late Ludfordian Kuressaare Horizon and in the Pridoli Ohesaare Horizon (Text-fig. 2). These forms are almost certainly not conspecific with English and Gotland species. Fedorowski and Gorianov (1973) referred one specimen from Gorstian-Ludfordian Paadla Horizon and two specimens from the late Ludfordian Kuressaare Horizon to *E. confusum* (Počta).

Podolia

Bulvanker (1952) described *Xylodes nikiforovae* sp. nov. from the Malinovsty and Skala Horizons but this was later referred to *Spongophylloides* by Sytova (1968). We have compared specimens from the Gorstian lower part of the Malinovtsy Horizon to *E. fasciculatum* Wedekind.

Poland

Rozkowska (1962) described *E. pseudodianthus* (Weissermel) from the upper part of the greywacke sequence of the lower Rzepin Beds in the Lezyce-Belczoross section in the Holy Cross Mountains. This unit equates with the lower Pridoli (Bassett *et al.* 1982), lowermost part of the Podlasie Horizon (Tomczyk 1970). The form may well belong to *Entelophyllum* but positive identification from available line drawings is not possible.

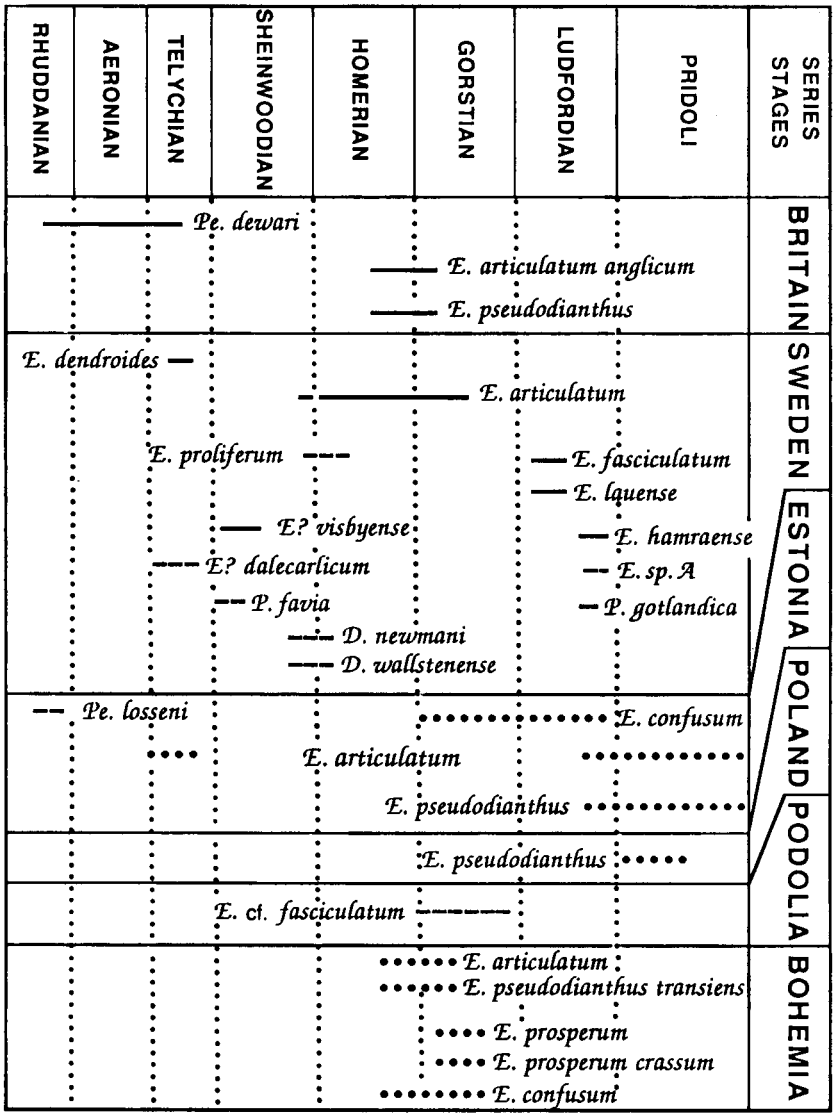
Czechoslovakia

Entelophylloid corals from Bohemia, first described by Počta (1902) and revised by Prantl (1940), are similar to the English *E. articulatum anglicum* – *E. pseudodianthus* forms and became even more carinate. Prantl (1940) recorded the less carinate *E. articulatum* and *E. pseudodianthus transiens* from the upper Motol Formation (Homerian) extending into the lower Kopanina Formation (Gorstian); specimens from the 'Amerika' quarries are now thought to be from the Kopanina Formation (Galle pers. comm.). *E. prosperum* and *E. prosperum crassum* are common in the Kopanina Formation. Prantl's material was from Tachlovice but today the precise locality is not known and it is thought to have been in a mine (Galle pers. comm.). *E. confusum* is known from the upper Motol and Kopanina Formations.

PHYLOGENY

In northern Europe, the earliest members of this group are referred to *Petrozium* (Text-fig. 3) and are characterized by a less well developed biserial tabularium than in later forms, and by stout straight long septa, and a relatively narrow dissepimentarium. The first species with a well-developed biserial tabularium occurs in the Telychian of Gotland but it still shows simple septa and a narrow dissepimentarium. Typical *Entelophyllum* is not known from the early Sheinwoodian of northern Europe.

E. articulatum with well developed long septa, biserial tabularium, and wide uniform



TEXT-FIG. 3. Stratigraphic distribution of species of *Entelophyllum* and related genera in northern Europe. Bold solid lines indicate confirmed identifications and stratigraphic ranges; bold dashed lines indicate confirmed identifications but stratigraphic ranges doubtful; dotted lines indicate identifications and stratigraphic ranges not confirmed by the authors.

dissepimentarium appears in the early Homerian in Gotland. It continues through the Gorstian and is thought to give rise to *E. fasciculatum* in the early Ludfordian, with the withdrawal of the septa from the axis, a reduction in the width of the dissepimentarium, an increase in the size of dissepiments, and a less well defined separation of axial and periaxial tabellae. The middle to late Ludfordian *E. lauense* and *E. hamraense*, with heavily carinate septa, possibly evolved from this stock. In England, *E. articulatum anglicum*, with light carination of some septa, occurs later in the Homerian than *E. articulatum articulatum* in Gotland. The English subspecies also dies out earlier

and again this may be related to changes in facies. In England, forms with different colony shapes and with strongly carinate septa, referred to *E. pseudodianthus* occur throughout the range of *E. articulatum anglicum*. Similar variation is found in the Bohemian forms of the *E. articulatum* – *E. pseudodianthus transiens* – *E. prosperum* – *E. prosperum crassum* group. Here they have a range slightly longer than the English forms but within the range of *E. articulatum* in Gotland. In contrast, the latter species is recorded in Estonia in Telychian as well as late Ludfordian and Pridoli intervals (Text-fig. 3). These presumed occurrences and others from elsewhere in the world may have had the name *E. articulatum* loosely applied.

Cerioid species with typical entelophylloid internal features (*Prohexagonaria favia* and *P. gotlandica*) occur at widely separated horizons on Gotland (Text-fig. 3). Whether these represent iterative evolution from the Baltic entelophylloid stock or successive migrations from an evolving *Prohexagonaria* lineage elsewhere, must await detailed study of *Prohexagonaria*.

Two new species of *Donacophyllum* in Gotland (Text-fig. 3) have similar internal features to *E. articulatum* but show non-parricidal rather than parricidal increase and commonly have well developed lonsdaleoid dissepiments. This generic similarity suggests affinities between Entelophyllidae and Kyphophyllidae.

PALAEOBIOGEOGRAPHY

The first occurrences of entelophylloid forms are from opposite sides of the Iapetus Ocean. In Llandovery times *Petrozium dewari*, from Girvan, Scotland, would have been on the southeastern seaboard of the North American Continent, and *P. losseni*, from Estonia, on the Anglo-Baltic Plate (Text-fig. 1B; Cocks and Fortey 1982). In later Llandovery times as the Iapetus Ocean closed *P. dewari* is known from England and the first species of *Entelophyllum* occurs in Gotland. Although on the same plate, England and Gotland were separated by a broad sea on the site of the earlier deep Tornquist's Sea. This probably led to differentiation of subspecies in *E. articulatum*, earlier development of carinate forms in Britain, and evolution of *E. fasciculatum* in Gotland. Bohemian and English forms show a similar development, reflecting the closer proximity of England to the northern Gondwanan Continent in the Llandovery as the Rheic Ocean opened.

SYSTEMATIC PALAEONTOLOGY

Terminology and suprageneric classification follow Hill (1981). Measurements are standard, with the diameters of corallites being the mean of the diameters of the circumscribed and inscribed circles in transverse section.

Septal microstructure is similar in all species described. Septa are monacanthate with the monacanths arranged in broad half fans over the dissepimentarial floors and inclined upwards and inwards towards the axis in the tabularium. Monacanths vary from 0·01 to 0·02 mm in diameter and the fibres appear to diverge only slightly from the axis of the trabeculae. Thus axes of trabeculae and junctions between trabeculae are not obvious so that in median longitudinal section septa have a fibrous appearance (Pl. 1, fig. 2; Pl. 5, fig. 20).

Variation and taxa discrimination

Large samples of *E. articulatum anglicum* subsp. nov. and of *E. yassensis* (Etheridge) from Australia, to be described in a future paper, indicate considerable intra-colony and intra-specific variation. Previously, characters showing intra-colony variation have been used to differentiate species and even genera by some authors.

In *E. articulatum anglicum*, variation in colony form appears to be dependent on environmental conditions. Flattened colonies are most common in bedded limestones and marls, whereas tall globular heads are found in more massive biohermal limestones. Ranges of variation in corallite diameter and septal number are almost as great for the holotype (10–19 mm, 21–32 major septa) as for the populations from Dudley (twenty-four specimens: 8–19 mm, 21–32 major septa) and Wenlock Edge (forty specimens: 9–20 mm, 20–32 major septa). Mean colony corallite diameters are likewise variable but mean colony tabularium diameters remain fairly constant. There seems to be no relationship between corallite diameter or septal number and corallum form. Major septa are generally long, straight, smooth and extend to the axis, but within one corallum they may tend

to withdraw from the axis, become discontinuous at the periphery, and carry zigzag carinae. Discontinuity in the dissepimentarium appears to be connected with widening of the dissepimentarium associated with connecting processes. In several sections of one corallum, septal carination is confined to the oldest part of the corallite just before budding. However, in other specimens development of carinae is spasmodic throughout the corallite. In contrast, septal microstructure, tabularial characters, and dissepimentarium apart from its width, all show little variation.

E. pseudodianthus (Weissermel), which occurs with and resembles *E. articulatum anglicum* typically but not invariably has heavily carinate septa. Similarly, on Gotland, most specimens of *E. fasciculatum* are readily distinguished from *E. articulatum* but in some colonies a few corallites show characters typical of the other species. The ranges of variation of these stratigraphically separated forms also show considerable overlap.

It is tempting, after admitting such considerable variation, to lump together all the above mentioned forms into one species. This would obscure the biostratigraphic and palaeogeographic usefulness of these groups of corals in northern Europe. Assignments are subjective and may well need future modification but they will provide a basis for the careful description of forms from elsewhere. Diagnoses formulated are for typical coralla and corallites within coralla, and the exceptions are noted but not included.

At generic level, the fasciculate and cerioid forms are differentiated, as are those with parricidal and nonparricidal colony increase. But even at this level intracolony variation has produced exceptions with some cerioid forms becoming locally fasciculate and some colonies with typical parricidal increase having one or two corallites that produced lateral nonparricidal offsets. *Petrozium* is retained for the simpler early forms without well-developed biserial tabularia and dissepimentaria, since it appears to have stratigraphic significance.

Synonymy

We have used many of the symbols proposed by Matthews (1973) to indicate degree of confidence in synonymy listings. These lists include only the most important previous citations, all of which we have examined and evaluated.

Collections

The repositories in which the material described herein is housed are indicated by the following prefixes: BMNH, British Museum (Natural History), London; BU, University of Bristol, Bristol; EGM, Eesti NSV Teaduste Akadeemia, Geoloogia Instituudi, Tallinn; GSM, Institute of Geological Sciences, Keyworth; NM, Narodní Museum, Prague; OU, University of Oklahoma, Norman; RM, Paleozoologiska sectionen, Naturhistoriska Riksmuseet, Stockholm; SM, Sedgwick Museum, Cambridge; SMF, Natur-Museum Senckenberg, Frankfurt-am-Main; UB, University of Birmingham, Birmingham; UO, University of Oxford, Oxford; UQ, University of Queensland, Brisbane.

Subclass RUGOSA Milne-Edwards and Haime, 1850
Order STAURIIDA Verrill, 1865
Suborder ARACHNOPHYLLINA Zhavoronkova, 1972
Family ENTELOPHYLLIDAE Hill, 1940
Genus ENTELOPHYLLUM Wedekind, 1927

1927 *Entelophyllum* Wedekind, p. 11.
1927 *Xylodes* Lang and Smith, p. 461 (pre-occupied by *Xylodes* Waterhouse, 1876, a Recent coleopteran).
1944 *Stereoxylodes* Wang, p. 25.
1964 *Carinophyllum* Strelnikov, p. 59.

Type species. Chosen by subsequent designation of Lang *et al.* 1940, p. 57, *Entelophyllum articulatum* (Wahlenberg, 1821) from the Slite, Mulde, Klinteberg, and lower Hemse Beds of Gotland; Homerian to early Ludfordian Stages, late Wenlock to early Ludlow.

Diagnosis. Phaceloid or dendroid rugosans with peripheral parricidal increase; septa long, generally radially arranged, counter-cardinal septa rarely distinguishable, smooth or asymmetrically carinate; major septa slightly withdrawn from axis; minor septa contraclined or contratigent in some; tabularium wide, broadly domed commonly with depressed axial area and marginal periaxial

trough formed by small subhorizontal or concave tabellae; dissepiments numerous, small, globose with lonsdaleoid dissepiments in some.

Remarks. Wedekind placed eight species in *Entelophyllum*, but named no type species. Among these was *E. articulatum*, cited without any author's name or statement that it was new. Lang *et al.* (1940) considered that *Madreporites articulatus* Wahlenberg was implied, and with this we would agree. By selecting *E. articulatum* (Wahlenberg) as type, the invalid homonym *Xylodes* Lang and Smith became an objective synonym of *Entelophyllum*.

Soshkina and Dobrolyubova (1962, p. 333) listed *Evenkiella* Soshkina, 1955, as having *Madreporites articulatus* Wahlenberg as the type species, and gave *Xylodes* as a synonym. Soshkina (1955) had, however, named as type species of *Evenkiella* nom. nov., *Evenkiella helenae* Soshkina, 1955 (p. 126, pl. 13, fig. 1) from the Wenlock of the Stony Tunguska River, Siberia. In a footnote she explained 'name *Evenkiella* for the genus given instead of *Xylodes* Smith and Tremberth, previously used for an insect'. In our opinion the designation of *E. helenae* as type species is of stronger force than the citation 'nom. nov.' instead of 'gen. nov.' and the explanatory footnote, and we uphold *E. helenae* as type in spite of Soshkina and Dobrolyubova's later reference to *M. articulatus* as the type. We consider the cerioid *Evenkiella* distinct from *Entelophyllum* in that it has lonsdaleoid dissepiments, flat complete tabulae, septa composed of fine trabeculae, and we agree with its placement in the Kyphophyllidae by McLean and Pedder (1984, p. 18).

Stereoxylodes was proposed by Wang (1944) as a subgenus of *Entelophyllum*, with type *Cyathophyllum pseudodianthus* Weissermel, 1894, for entelophyllids with dilated and carinate septa. The type specimen of *C. pseudodianthus* chosen by Lang and Smith (1927, p. 473) as the original of Weissermel (1894, pl. 47, fig. 3) from the glacial drift of Lauth, Germany, is lost. Ivanovskii (1976, p. 165) invalidly proposed as a neotype of *E. pseudodianthus*, the holotype of *Stereoxylodes pseudodianthus* var. *sinensis* Wang, 1944 from the 'middle' Silurian of Malung, eastern Yunnan, China. To stabilize this species, we have selected a lectotype from Weissermel's syntypes, see discussion of *E. pseudodianthus*. In England, *E. pseudodianthus* commonly occurs as small loose clumps of ceratoid corallites formed by peripheral parricidal budding and with strongly carinate and commonly thickened septa, quite distinct from the typical phaceloid coralla of *E. articulatum anglicum* with cylindrical corallites and typically little or only light carination of the septa. As described in detail later, some specimens of both species show variation that liken individual corallites or whole coralla to those of the other. Prantl (1940) also recognized a similar tendency and proposed *E. pseudodianthus transiens* for forms showing smooth, slightly carinate, dilated and asymmetrical carinate septa combining characters of *E. articulatum* and *E. pseudodianthus*. Similarly, Strelnikov (1964, p. 59) erected *Carinophyllum* for species that have septa thickened in the inner dissepimentarium and are heavily carinate, and designated *E. confusum* (Počta, 1902) as type species. Like Schouppé (1951), we believe that there is a continuum of variation in the thickening and carination of the septa in the dissepimentarium of such entelophylloid corals and that they all belong to the one group. They may be arbitrarily divided into subgenera but there does not appear to be any biogeographic or stratigraphic significance to such divisions. If such a subdivision was practical, then *Nanshanophyllum* Yu (1956; type *N. typicum* Yu, Middle Silurian, China) might be

EXPLANATION OF PLATE 1

Figs 1–10. *Entelophyllum articulatum* (Wahlenberg). 1–6, RM Cn54823 (neotype), unknown horizon and locality on Gotland; 1, lateral view showing tall corallites, × 1; 2 and 3, longitudinal sections showing typical biserial tabularium and small globose dissepiments, × 4, × 2, respectively; 4–6, transverse sections showing long smooth septa, × 2, × 2, × 4 respectively. 7–10, Slite Beds, Bogeklint 1, 2 km SE of Boge church, Gotland; 7 and 8, UQ F34300; 7, longitudinal section, × 2; 8, transverse section, × 2; 9 and 10, UQ F34298; 9, longitudinal section, × 2; 10, transverse section, × 2.

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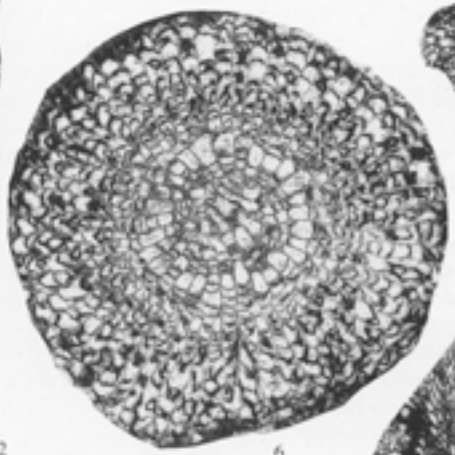

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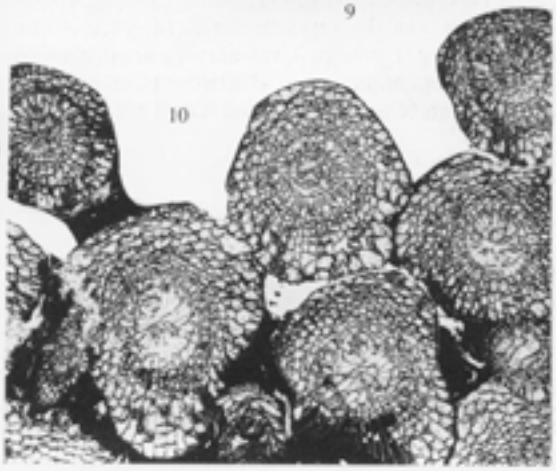

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regarded as another subgenus of the group for solitary forms with thickened and carinate septa, in the same way as Pedder (1976) used it as a subgenus of *Stereoxylodes*.

Although some species contain both cerioid and fasciculate forms (such as *E. polymorphum* Shurygina, 1977, pl. 6, figs 1–3 [= *E. articulatum* of Sytova 1952, p. 140, pl. 4, figs 1–5] from the 'upper' Silurian of the Urals), we refer typical cerioid species to *Prohexagonaria* Merriam, 1973 (see discussion of that genus).

We include in *Entelophyllum* only species that show parricidal budding. One apparent exception is *E. articulatum anglicum*. It almost invariably has obvious parricidal budding but we have observed one corallum, which, in addition to common parricidal budding, includes a single example of lateral budding. Similarly, lonsdaleoid dissepiments are uncommon in most species of *Entelophyllum* but do occur in some corallites in coralla of various species especially in areas of lateral outgrowths and in the late growth stages. Forms showing lateral budding and well-developed lonsdaleoid dissepiments are included in *Donacophyllum* Dybowski, 1874. The two species here included in it are similar to *Entelophyllum* in their septa and tabularia.

Entelophyllum articulatum (Wahlenberg, 1821)

Plate 1, figs 1–10; Plate 2, figs 1–11

(1821) *Madreporites articulatus* Wahlenberg, p. 97.
v*1837 *Cyathophyllum articulatum* (Wahlenberg); Hisinger, p. 102, pl. 29, fig. 4.
1874 *Cyathophyllum articulatum* (Wahlenberg); Dybowski, p. 435, pl. 3, fig. 1, 1*a*, 1*b*.
1927 *Entelophyllum articulatum* (Wahlenberg); Wedekind, p. 22.
v1929 *Xylodes articulatus* (Wahlenberg); Smith and Tremberth, p. 363, text-figs 1 and 2; pl. 7, fig. 5 [*non* figs 1–4, 6].
v1933 *Xylodes articulatus* (Wahlenberg); Smith, p. 513, pl. 1, figs 4 and 5 [*non* figs 1–3].
1940 *Entelophyllum articulatum* (Wahlenberg); Lang *et al.*, p. 57.
(?)1940 *Xylodes articulatus* (Wahlenberg); Prantl, p. 6, pl. 1, figs 1–3; pl. 2, figs 1, 3, 4.

Neotype. Chosen by Smith and Tremberth (1929, p. 363), one of the original specimens of Hisinger labelled '*Cyathophyllum articulatum* e Gottlandia'; RM Cn54823, from an unknown locality and horizon on Gotland.

The exterior side view of the neotype was figured at half size by Smith and Tremberth (1929, p. 365, text-fig. 1). Three thin sections cut from the neotype with the numbers R49348*a*, *b*, and *c* are in the British Museum (Natural History). The two transverse sections, apparently cut from the base of the specimen, include two corallites each and there is a longitudinal cut from a single corallite, apparently from high on the side of the specimen. Smith and Tremberth (1929, p. 365, text-fig. 1) figured one of the four transverse corallites and Smith (1933, pl. 1, figs 4 and 5) refigured that picture and also figured the longitudinal section. At a later time two additional transverse sections were taken from the base of the neotype, which include two corallites each, and a longitudinal section was taken from one of these corallites. These sections carry the same number as the neotype, Cn54823, in the Riksmuseet, Stockholm (Pl. 1, figs 3–6).

Material studied. The neotype; similar material occurring in the Slite Beds at Bogeklint 1, northeast coast of Gotland (6 specimens; figured: UQ F34298, F34300). Other Gotland occurrences: upper Mulde Beds, from Blåhäll 1, on west coast of Gotland (one specimen; figured: RM Cn66044); Klinteberg Beds, from

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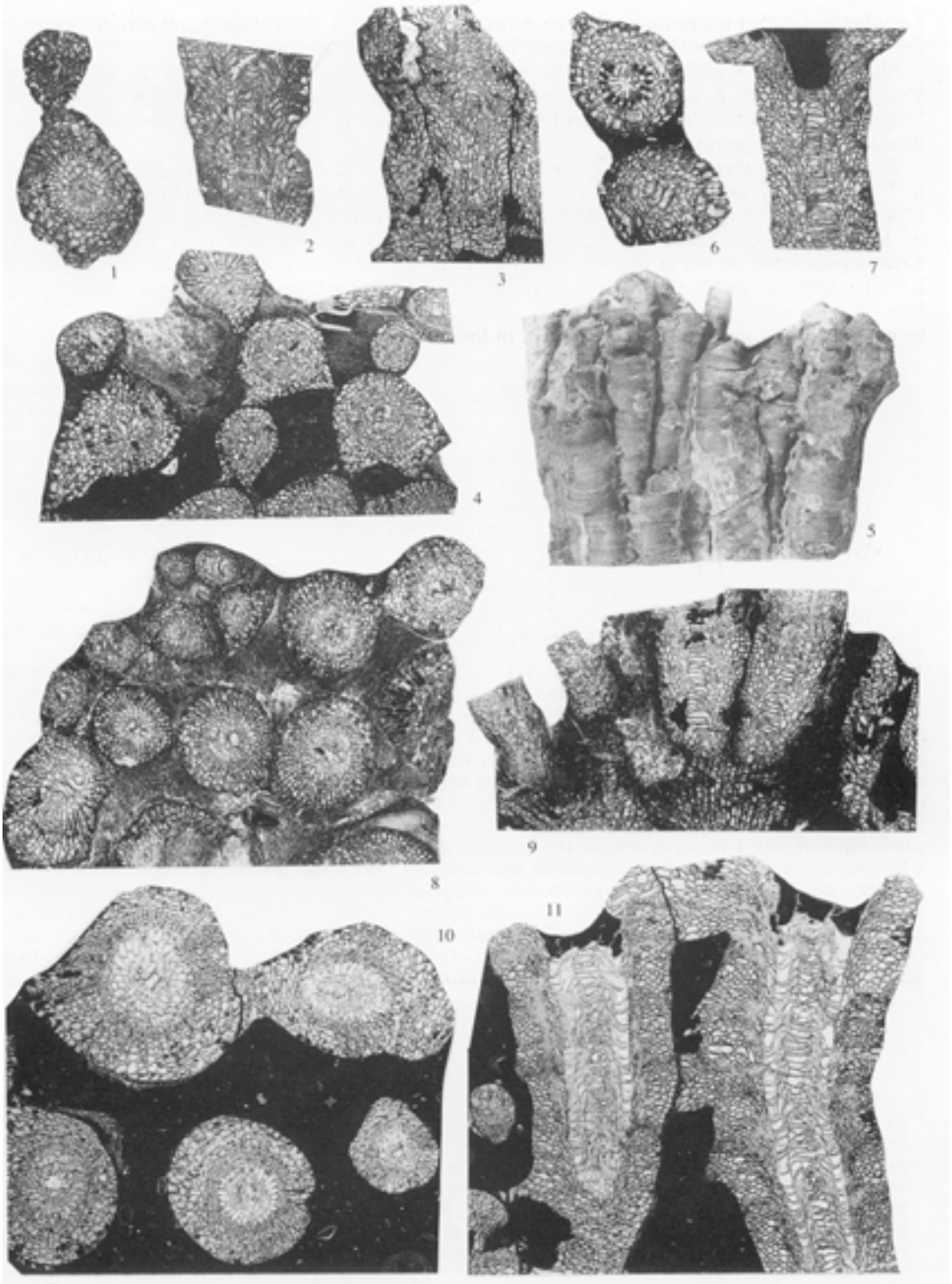
EXPLANATION OF PLATE 2

Figs 1–11. *Entelophyllum articulatum* (Wahlenberg), showing variation in Gotland material. 1 and 2, RM Cn66040, Klinteberg Beds, Klinteberget 1, cliff exposure at Klinte, west coast of Gotland; 1, transverse section, ×2; 2, longitudinal section, ×2. 3–9, lower Hemse Beds, Snoder 1, 2·5 km NW of Slite Church, southwest Gotland; 3–5, RM Cn66041; 3, longitudinal section, ×2; 4, transverse section showing lateral expansions of corallites, ×2; 5, lateral view showing parricidal increase, ×1; 6 and 7, RM Cn66042; 6, transverse section, ×2; 7, longitudinal section, ×2; 8 and 9, RM Cn66043; 8, transverse section, ×2; 9, longitudinal section, ×2. 10 and 11, RM Cn66044, upper Mulde Beds, Blahäll 1, 0·5 km NE of Djupviks fislage, west coast of Gotland; 10, transverse section, ×2; 11, longitudinal section, ×2.



JELL and SUTHERLAND, *Entelophyllum*

Klinteberget 1, central western Gotland (seven specimens; figured: RM Cn66040); Lower Hemse Beds, from Snoder 1, southwest Gotland (four specimens: figured RM Cn66041, Cn66042, Cn66043).

Distribution. Gotland: Homerian and Gorstian; Estonia: ?Telychian to Pridoli; Bohemia: ?late Homerian to early Gorstian.

Diagnosis. Phaceloid, increase peripheral, parricidal; corallite diameter 10–15 mm. Major septa typically 23–28, long, thin, extending to or almost to axis, rarely irregularly zigzag to flexuose in outer dissepimentarium, rarely carinate; minor septa two-thirds the length of major, may be irregularly contratigent, Tabularium one-third to one-half diameter of corallite, distinctly biserial with well developed periaxial trough. Dissepiments small, globose, to medium and irregular in size.

Description. Coralla are typically large, tall and phaceloid. Corallites are subcylindrical, closely packed, subparallel and up to 16 mm in diameter with irregular growth contractions and expansions (Pl. 1, fig. 1). The neotype is a fragment about 130 mm in length and 50 mm in diameter (Pl. 1, fig. 1). It includes parts of four corallites that represent one generation, approximately 100 mm in length. At the top of the fragment ten corallites are to be seen. Increase is peripheral and parricidal with buds extending almost straight up from the dissepimental zone of the parent corallite. Commonly, budding is more frequent than in the neotype and the corallites are less than 100 mm in length.

In transverse section major septa are typically long and thin but are highly variable even in the neotype. Major septa number 23–32 at diameters of 12–16 mm. Septa typically extend to the axial region but do not form an axial structure. A small open axial area about 1 mm in diameter occurs in some corallites. Most septa are thickened in the outer dissepimentarium and taper evenly towards the axis but in some corallites they thin in the tabularium to about half their thickness in the dissepimentarium. Some are irregularly zigzag to sinuous in the dissepimental area and are locally carinate. Some corallites show no carinae at all. Minor septa are about two-thirds the length of the major septa and commonly extend just past the inner margin of the dissepimental zone. However, in two specimens they are four-fifths the length of the major septa and extend into or across that part of the tabularium that forms the outer trough. Some minor septa are irregularly contratingent but they form no pattern. In some corallites, minor septa are discontinuous. In such cases, herringbone dissepiments are generally present. Locally, a few major and minor septa become discontinuous near the periphery and lonsdaleoid dissepiments are developed (Pl. 1, fig. 10). These discontinuous septa coincide with a lateral extension of the margin of the corallite that may represent a lateral outgrowth of attachment and the two developments are presumably related.

The tabularium is typically 4–5 mm in diameter. Longitudinal sections show two series tabellae (Pl. 1, figs 2 and 3; Pl. 2, fig. 11). Those in the axial region are generally flat but sag axially in those corallites with the septa slightly withdrawn from the axis, and have sharply downturned marginal edges. Between this zone and the dissepiments lies a narrow zone occupied by flat, sagging or inclined tabellae that number 5–8 in 5 mm vertical spacing, and form a periaxial trough. Small arched tabellae may be situated at the margins of the flat central region, forming levy-like margins to the central platform (Pl. 1, fig. 9). Dissepiments are small, globose, and form a wide peripheral zone that varies considerably in relative width as a result of rejuvenescence, from about one half to two-thirds the corallite radius. The number of rows of dissepiments varies from 3 to 12 and dissepiments are uniform in size and distribution and number 13–14 in 5 mm vertically.

Remarks. In Gotland, *E. articulatum* occurs in the Slite, Mulde, Klinteberg and Lower Hemse Beds. Even in the Slite, in comparison with the neotype, some specimens have a comparatively narrower

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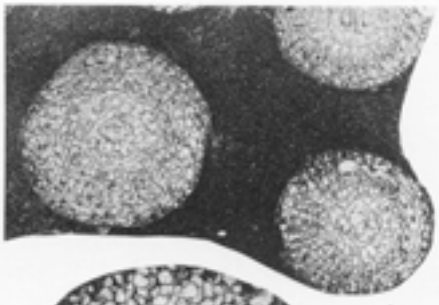
EXPLANATION OF PLATE 3

Figs 1–10. *Entelophyllum articulatum anglicum* subsp. nov., showing variation in holotype, SM A5143, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire. 1, transverse section of typical corallites, ×2. 2 and 3, longitudinal sections, ×4, ×2 respectively. 4, transverse section showing corallite expansion, ×4. 5, transverse section showing some septa slightly thickened and zigzag, ×4. 6, transverse section of an early growth stage, ×4. 7, lateral view of corallum, ×1. 8, transverse section, showing lightly carinate septa, ×4. 9, lateral view showing parricidal increase, ×2. 10, transverse section in the distal part of corallum showing lonsdaleoid dissepiments, ×4.



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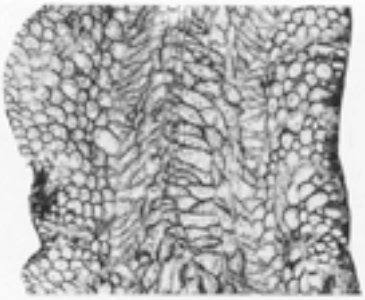

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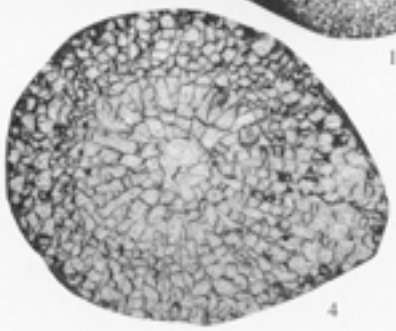

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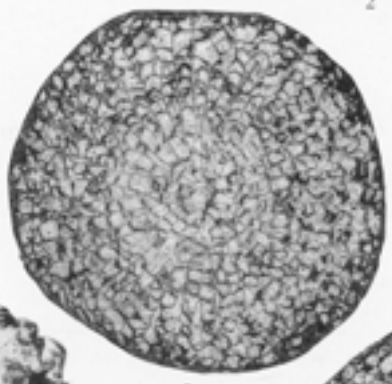

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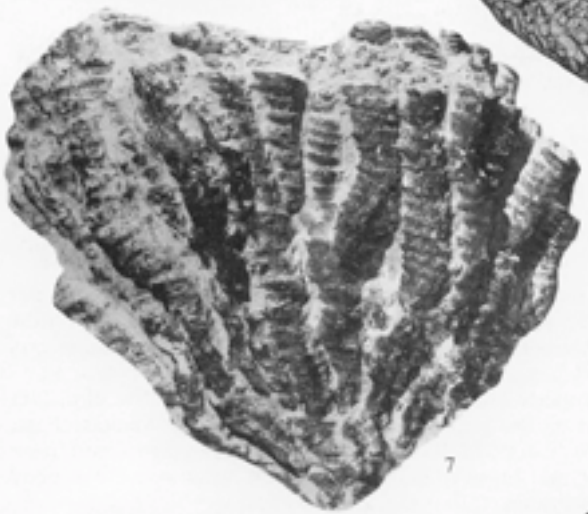

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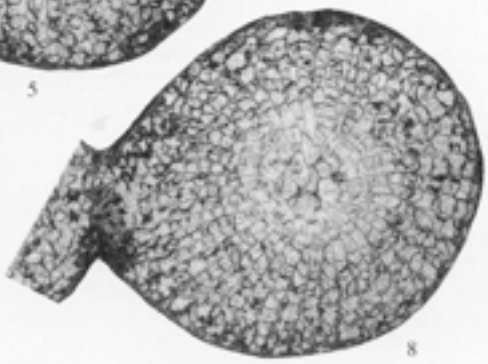

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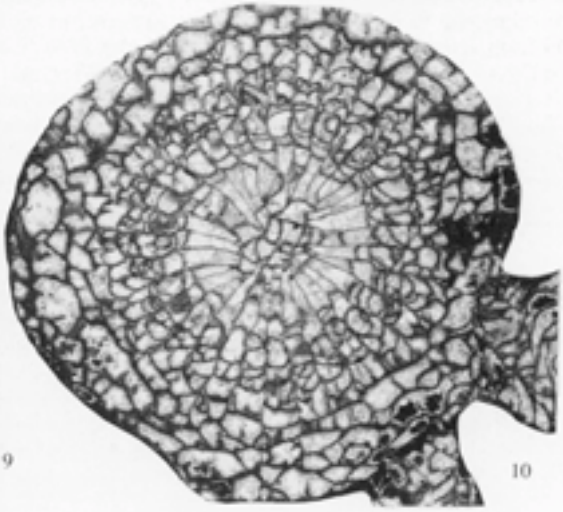

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JELL and SUTHERLAND, *Entelophyllum*

dissepimental zone that includes some larger dissepiments (Pl. 1, fig. 9). Stratigraphically higher, budding patterns are more irregular, offsets are shorter, dissepiments are comparatively larger and more irregular in size, and septa tend to withdraw slightly from the axial region leaving a small open axial area. Beginning in the lower Hemse (Pl. 2, figs 2–4) there is an apparent shift in growth form in that there is a more frequent development of new parricidal offsets but adult corallites remain typical.

Carinae are lacking in most specimens from Gotland. Where present they occur in the dissepimental zones of only a few septa. None of the specimens from Gotland develops complex vacuolar septa as occur in some corallites of the English subspecies *E. articulatum anglicum*.

In Estonia, Kaljo (1970) listed but did not describe or illustrate *E. articulatum* in coral faunas from the Adavere (Telychian), Kuressaare (late Ludfordian), Kaugatuma (early Prídolí) and Ohesaare (late Prídolí) Horizons (Text-fig. 2).

Smith and Tremberth (1929, p. 366) cited *E. articulatum* in the Upper Silurian of the Island of Bjerköy, Christiania Fjord, Norway, but B. Neuman (pers. comm.) has been unable to find additional specimens in that area.

Smith and Tremberth (1929, p. 363) suggested that many Bohemian specimens (Počta 1902) figured as *Cyathophyllum prosperum* might be synonymous with *E. articulatum*. Prantl (1940) did not include any of Počta's figured material in *E. articulatum* but described *E. articulatum* from the 'Amerika' quarries, near Morina (Budnany). Dr A. Galle (pers. comm., 1989) considers these to be from the Kopanina Formation (Text-fig. 2). Occurrences in the Motol Formation (Prantl 1940) need to be confirmed. The septa are smooth, straight, extending almost to the axis and the tabularium and dissepimentarium are very similar to the Gotland material.

Material from the USSR, China, and Middle East, in Llandovery to Early Devonian strata, previously referred to *E. articulatum*, will now have to be reinterpreted.

Entelophyllum articulatum anglicum subsp. nov.

Plate 3, figs 1–10; Plate 4, figs 1–11

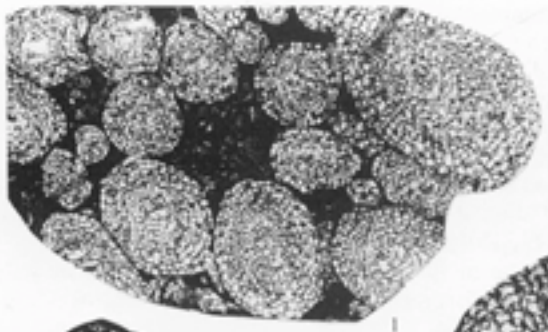
v*1855 *Cyathophyllum articulatum* (Wahlenberg); Milne-Edwards and Haime, p. 282, pl. 67, fig. 1, 1*a*.
v1929 *Xylodes articulatus* (Wahlenberg); Smith and Tremberth, 1929, p. 363, pl. 7, figs 1–4, 6; pl. 8, fig. 2 (*non* pl. 7, fig. 5).

Holotype. Milne-Edwards and Haime, 1855, pl. 62, fig. 1, 1*a*; SM A5134*a* and thin sections SM A5134*b–j* from the Fletcher Collection, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire; Homerian Stage.

Material studied. We examined sixty-four sectioned specimens from the collections of the BMNH, SM, UO, UB, and UQ from the Much Wenlock Limestone at Dudley, Worcestershire, and along Wenlock Edge, Shropshire; figured: SM A5134 (holotype), UQ F35311, F35315, F35319, F36966. Other English occurrences: Farley Member, Coalbrookdale Formation, Wenlock Edge (figured: UQ F41347); lower Elton Beds, Leintwardine, Shropshire; several specimens labelled lower Elton Beds, Wenlock Edge; several specimens labelled lower Ludlow (presumably Elton Beds), Ledbury Quarry, Malverns, Herefordshire.

EXPLANATION OF PLATE 4

Figs 1–11. *Entelophyllum articulatum anglicum* subsp. nov. showing variation in English material. 1–4, UQ F55311, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire; 1–3, transverse sections, ×2, ×4, ×4, respectively; 4, longitudinal section, ×2. 5 and 6, UQ F41347, Farley Member, Coalbrookdale Formation, Presthope tunnel cutting, Wenlock Edge, Shropshire; 5, transverse section showing lateral dissepiments, ×2; 6, longitudinal section, ×2. 7 and 8, UQ F35315, Much Wenlock Limestone, Wenlock Edge, Shropshire; 7, transverse section, ×4; 8, longitudinal section, ×4. 9–11, Much Wenlock Limestone, Lilleshall Quarry, Wenlock Edge, Shropshire; 9 and 10, UQ F36966; 9, transverse section, ×2; 10, longitudinal section, ×2; 11, UQ F35319, transverse section showing thickened and carinate septa, ×4.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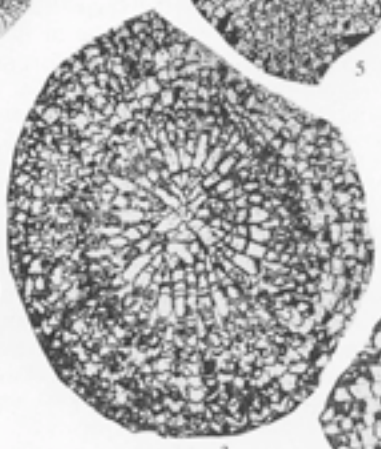
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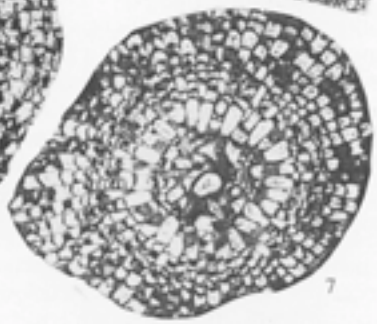
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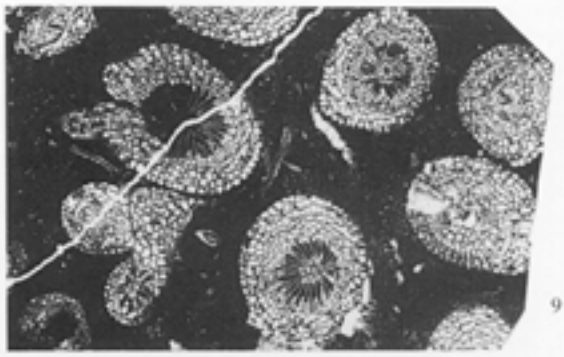
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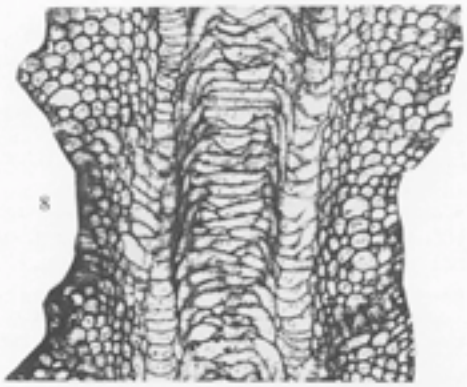
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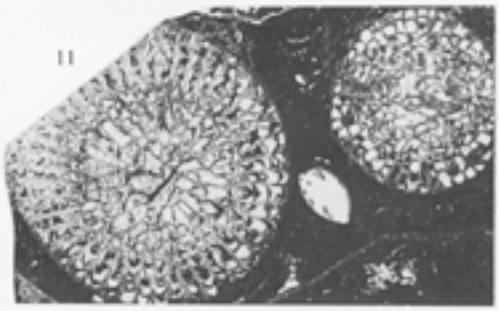
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JELL and SUTHERLAND, *Entelophyllum*

Distribution. England: middle Homerian to early Gorstian.

Diagnosis. Coralla tall phaceloid to squat fasciculate; increase typically peripheral parricidal; corallite diameter typically 10–12 mm, maximum 20 mm; major septa 21–24, maximum 30, straight to flexuose, smooth in tabularium, commonly reaching axis but not confluent; septa vary from straight, smooth or slightly thickened to zigzag and distinctly carinate, becoming very ragged and interrupted by lonsdaleoid dissepiments in the lateral expansions; minor septa commonly contraclined to contratigent around an obscure cardinal-counter plane. Tabularium biserial with well developed periaxial trough; dissepiments small, globose, regularly arranged in 5–8 vertical rows.

Description. Colony form varies from small clump-shaped coralla, 60 mm high and 40–45 mm in diameter showing two generations of budding, to squat or flat cake-shaped coralla several times greater in diameter than in height, up to 300 mm diameter, to tall large globular heads up to 1 m diameter. The holotype is a fragment of a tall, phaceloid colony 160 × 80 mm in cross section and 130 mm in height (Pl. 3, fig. 7).

Protocorallites, where preserved, vary from low petalate, up to 35 mm in diameter, to tall ceratoid corallites, 15 mm in diameter and 80 mm tall. Six to ten buds are generally produced at the first generation. In most coralla, budding occurs at the same level throughout the colony with the corallites in each generation being of the one length. In flattened colonies divergence of daughter corallites from the axis of the parent is rapid. In several flattened colonies growth increases on one side of the corallum. Budding is parricidal but in two cases, UB 42 of Holcroft Collection and UQ F36996, it is nonparricidal. Corallum increase appears to be peripheral, with one to six daughter corallites originating in the peripheral parts of the parent corallite generally at an expansion. The buds abruptly expand so as to occupy most of the calyx of the parent. Thin sections show buds originating at or just axial to the dissepimentarium/tabularium boundary.

Corallites are long, slender, cylindrical, and closely spaced, up to 10 mm. Corallites show regular contractions and expansions (Pl. 3, fig. 11). At intervals, a corallite may expand laterally to abut onto an adjacent corallite forming a connecting process 5–10 mm high. This pattern of outgrowths is not regularly spaced or level specific within a colony. Thus in transverse section the corallites show considerable variation in diameter (8–20 mm) but are commonly 10–13 mm. In the holotype first generation corallites are 20–30 mm long, those of the second 50–60 mm, and of the third 50–80 mm.

Septa are typically long and radially arranged in two orders (Pl. 3, fig. 1); one order commonly has 21–24 septa in adult stages at diameters 10–13 mm. At diameters 17–20 mm, major septa number 28–32. Major septa typically almost reach the axis; in some corallites an open axial area may be 1–2 mm in diameter (Pl. 3, figs 4–6). In a few corallites axial ends of the major septa deflect towards the cardinal-counter plane and the counter-cardinal septa may bisect the axial space. In others axial ends may be irregularly twisted. Minor septa are 0·6–0·8 of major septa and extend a short distance into the tabularium. Some minor septa may be contraclined and even contratigent. Septa are smooth and straight, curved or flexuose in the tabularium but are rather variable in the dissepimentarium even within one corallite. They may be straight or flexuose with smooth, rough or ragged sides (Pl. 3, fig. 8); slightly thickened at the junction of the septa with the curved dissepimental plates and carrying irregular zigzag carinae (Pl. 3, fig. 5); thickened in the inner dissepimentarium and outer tabularium so that they are fusiform (Pl. 4, fig. 11); or uncommonly discontinuous with irregular segments being interrupted by lonsdaleoid dissepiments (Pl. 3, fig. 10). Discontinuity of septa in the peripheral parts occurs in areas of broad expansion of the dissepimentarium (i.e. in a connecting process or just before budding). Septa may become more ragged or carinate in the expansions (Pl. 4, fig. 2).

The tabularium is relatively constant in diameter in adult stages, being 0·6 the corallite diameter. It shows an irregular separation into an axial series and a periaxial series of tabellae (Pl. 3, fig. 2). The axial series forms tabularial floors that are flat or slightly sagged axially and with steep downturned marginal slopes. Between this zone and the dissepimentarium is a periaxial series of flat, slightly sagging, or inclined tabellae (up to 30 per 10 mm vertically) forming a periaxial trough of the tabularial floors. The dissepimentarium varies in width as a result of the contractions and expansions of the corallite. Dissepiments are small, globose, and uniform in size and distribution (20–28 in 10 mm vertically and 6–8 total rows horizontally).

New offsets arise (BMNH R267) from the outer half of the periaxial series of tabellae and the axial edge of the dissepimentarium. The buds arise within the interseptal loculii between major and minor septa and thus budding is marginal and not truly tabularial. Having developed in the inner part of the marginarium they diverge towards the periphery and increase rapidly occupying the total dissepimentarium.

The twenty-five peels from UQ F36996 show close relationship between carinae and stages of parricidal

increase. In this corallum, growth of a corallite stops when offsets develop. The septa are simple during growth but, near the base of the calice, just before budding occurs, septa become thickened, develop rough margins, become zigzag, and develop rudimentary, short carinae. New offsets almost invariably have simple thin septa in their early stages of growth. Earlier development of carinae is seen in some corallites in other coralla where they are not related to the development of offsets. In UQ F8388B, an individual corallite 50 mm in length has simple septa in the earliest stage, then carinate septa in a section 10 mm higher, then simple septa still higher, followed in the highest growth stages by the development of carinate and complex septa with vacuoles. Most of the other corallites in this same corallum have simple septa throughout their growth.

Remarks. Entelophyllum articulatum anglicum subsp. nov. is close to *E. articulatum* (Wahlenberg, 1821) from Gotland and many corallites cannot be differentiated. With sufficient material *anglicum* is seen to have more commonly carinate septa. Both subspecies show parricidal budding but in *anglicum* tabularia of the offsets may originate from the peripheral trough of the parent as illustrated by Smith and Tremberth (1929, text-fig. 2*a*), whereas in *articulatum* the indications are that offsets arise from wholly within the dissepimentarium. Minor differences are the more frequent occurrence among the English specimens of contratigent minor septa, development of an obscure cardinal-counter plane and less frequent development of discontinuous minor septa and lonsdaleoid dissepiments. Sections of *E. articulatum anglicum* showing more carinate septa resemble *E. pseudodianthus* (Weissermel, 1894).

Entelophyllum fasciculatum Wedekind, 1927

Plate 5, figs 1–21

v1927 *Entelophyllum fasciculatum* Wedekind, p. 24, pl. 2, figs 11 and 12; pl. 29, figs 30, 31, 50; ?pl. 29, figs 34–49, 51 [not sectioned]; ?pl. 30, figs 1–8 [not sectioned].

v1927 *Entelophyllum proliferum typus* Wedekind, p. 23, pl. 29, figs 21 and 22 [*non Cyathophyllum proliferum* Dybowski, 1874, p. 445, pl. 3, fig 2*a*, *b*].

v1927 *Entelophyllum proliferum* var. *elongata* Wedekind, p. 23, pl. 29, fig. 23; ?pl. 29, figs 24, 25, 33 [not sectioned].

v1927 *Entelophyllum proliferum* var. *brevis* Wedekind, p. 23, pl. 29, figs 27 and ?28; ?pl. 29, figs 26 and 29 [not sectioned].

non 1927 *Entelophyllum culmiforme* Wedekind, p. 23, pl. 29, fig. 32 [= tryplasmid coral].

vp1927 *Entelophyllum roemeri* Wedekind, p. 23, pl. 30, fig. 15; ?pl. 30, figs 9–12, 16 [not sectioned] [*non* pl. 30, figs 13 (= holotype of *E. roemeri*) or 14 (both specimens = tryplasmid corals)].

?1927 *Entelophyllum rhizophorum* Wedekind, p. 23, pl. 30, fig. 17.

?1927 *Entelophyllum confer rhizophorum* Wedekind, p. 23, pl. 29, figs 18–20 [not sectioned].

?1973 *Entelophyllum articulatum* (Wahlenberg); Fedorowski and Gorianov, p. 19, pl. 4, figs 1–4.

Lectotype. Here chosen, original of Wedekind, 1927, pl. 29, fig. 30; RM Cn54855, *Rhizophyllum* limestone, lower Eke Beds, Lau Backar 1, southeast Gotland; middle Ludfordian Stage.

Material studied. All of Wedekind's (1927) original specimens of *E. fasciculatum* were from Lau Backar 1, southeast Gotland. Additional material examined by us from this locality are in the RM, UQ, OU, and Dr B. Neuman's collections. Sectioned specimens examined from Lau Backar number about thirty-five (figured specimens: RM Cn54855 (lectotype); RM Cn54847, Cn54849, Cn54850, Cn54852, Cn54856, Cn54880, Cn54881). The species also occurs at the same approximate horizon at Hallsarve 1, 0·4 km east of Lau Backar (figured RM Cn66045); Kauparvegård 1, inland cliff north of Kauparve farmhouse, southern Gotland; and possibly from an unknown locality, Östergarn parish, central east coast of Gotland.

Distribution. Gotland: middle Ludfordian.

Diagnosis. Phaceloid, increase peripheral, parricidal; corallite diameters 10–12 mm. Major septa typically 20–22, extending into tabularium but not reaching axis, leaving distinct open area in axial region. Septa typically straight throughout, not zigzag or carinate. Tabularium about one-half diameter, flat axially, sharply downturned to margin of dissepimentarium producing irregular periaxial trough. Dissepiments variable in size, width of zone medium.

Description. Specimens available include fragments of loosely dendroid to phaceloid coralla and numerous loose broken offsets. The latter are 30–70 mm long and ceratoid to cylindrical. Narrow distal ends of some loose offsets are turned abruptly laterally representing areas of attachment to parent. Increase is peripheral and parricidal with 4–6 offsets in each generation but 7 have been observed. Calices are shallow consisting primarily of a flat-bottomed axial pit coinciding with the tabularium and a marginal platform.

Septa typically number 20–22 of each order at diameters of 10–11·5 mm. Septa are relatively thin being thicker in the dissepimentarium compared to the tabularium. Septa are variable in the dissepimentarium. Most are straight and smooth, others are zigzag to sinuose. Isolated carinae are rarely developed in the zigzag septa of some specimens. Septa become discontinuous in the dissepimental zone only near a lateral extension (Pl. 5, fig. 5). Major septa are irregular in length and are 0·7–0·8 corallite radius in length leaving an open axial space up to 2 mm in diameter. Protosepta are not distinguishable and fossulae are not present. Minor septa are irregular in length and extend past the inner margin of the dissepimental zone.

The tabularium occupies half the corallite diameter. It consists of a broad axial region in which the tabulae are flat or with a wide, shallow median depression and a narrow periaxial region where edges of the tabulae are irregularly turned sharply down and in some cases back up again. Thus, an irregular periaxial trough may be developed that may contain a few horizontal tabellae (Pl. 5, fig. 20). Axial tabulae are irregularly spaced (12–16 vertically in 5 mm). The dissepimentarium is irregular due to variation in size and convexity of medium to large globose dissepiments that develop between the septa. There are 4–6 rows of dissepiments in a zone typically 3–4 mm in diameter and there are 8–10 in 5 mm vertically.

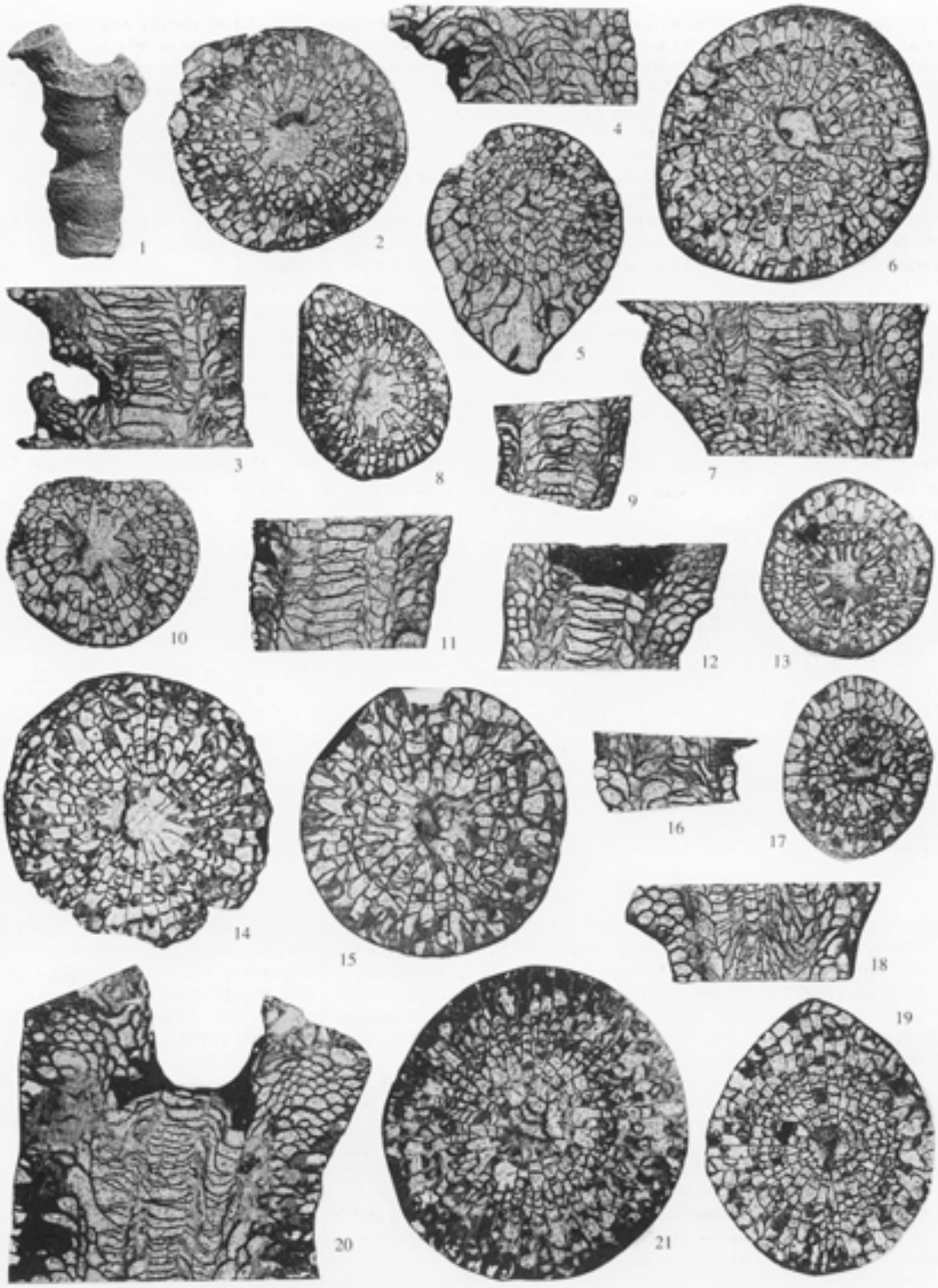
Remarks. *E. fasciculatum* apparently evolved in the Gotland area from *E. articulatum*. The former, in its common occurrences in the Upper Hemse/Lower Eke differs from forms similar to the neotype of *E. articulatum* in the Slite Beds in having a distinctly narrower dissepimental zone of relatively larger and more irregular globose dissepiments, in having septa withdrawn from the axial region, and in having a poorly defined separation of the tabularium into two zones with a less distinctly developed periaxial trough. However, *E. articulatum* in the Klinteberg and lower Hemse is similar to *E. fasciculatum* with which it could be considered to be gradational, but it has distinctly more open axial area and less well defined periaxial tabular trough.

Wedekind (1927) confused his definition of *E. fasciculatum* by basing the species primarily on the growth form of unsectioned broken offsets. He illustrated only two transverse sections. Also, he named as new (from the same locality, Lau Backar 1) an additional five species and varieties, all based on unsectioned broken offsets. The holotype or at least one syntype of each of these has been subsequently sectioned. Each of the following specimens is here named lectotype of the listed subspecies or variety of Wedekind (1927) and placed in the synonomy of *E. fasciculatum*:

EXPLANATION OF PLATE 5

Figs 1–21. *Entelophyllum fasciculatum* Wedekind. 1–19, *Rhizophyllum* limestone, Eke Beds, Lau Backar 1, 1·0 km NE of Lau, southeast Gotland; 1–3, RM Cn54855 (lectotype), original of Wedekind (1927, pl. 29, fig. 30); 1, lateral view; 2, transverse section; 3, longitudinal section; 4 and 5, RM Cn54852, original of Wedekind (1927, pl. 29, fig. 50); 4, longitudinal section; 5, transverse section; 6 and 7, RM Cn54857, original of Wedekind (1927, pl. 30, fig. 17), holotype of *E. rhizophorum* Wedekind; 6, transverse section; 7, longitudinal section; 8 and 9, RM Cn54853, original of *E. roemeri* Wedekind (1927, pl. 30, fig. 15); 8, transverse section; 9, longitudinal section; 10 and 11, RM Cn54856, original of Wedekind (1927, pl. 29, fig. 3); 10, transverse section; 11, longitudinal section; 12 and 13, RM Cn54849, original of Wedekind (1927, pl. 29, fig. 23), lectotype of *E. proliferum elongata* Wedekind; 12, longitudinal section; 13, transverse section; 14, RM Cn54881, original of Wedekind (1927, pl. 2, fig. 12), transverse section; 15, RM Cn54880, original of Wedekind (1927, pl. 2, fig. 11), transverse section; 16 and 17, RM Cn54850, original of Wedekind (1927, pl. 29, fig. 27), lectotype of *E. proliferum brevis* Wedekind; 16, longitudinal section; 17, transverse section; 18 and 19, RM Cn54847, original of Wedekind (1927, pl. 29, fig. 21), lectotype of *E. proliferum typus* Wedekind; 18, longitudinal section; 19, transverse section. 20 and 21, RM Cn66045, Eke Beds, Hallsarve 1, 1·35 km NE of Lau, Gotland; 20, longitudinal section; 21, transverse section.

All ×4, except Fig. 1 which is ×1.



JELL and SUTHERLAND, *Entelophyllum*

1. *Entelophyllum proliferum typus* Wedekind, 1927, pl. 29, fig. 21 (RM Cn54847) (= Pl. 5, figs 18 and 17).
2. *E. proliferum* var. *elongata* Wedekind, 1927, pl. 29, fig. 23 (RM Cn54849) (= Pl. 5, figs 12 and 13).
3. *E. proliferum* var. *brevis* Wedekind, 1927, pl. 29, fig. 27 (RM Cn54850, = Pl. 5, figs 16 and 17).

The following specimens are tryplasmid corals and they must be transferred from *Entelophyllum*:
1. *Entelophyllum culmiforme* Wedekind, 1927, pl. 29, fig. 32 (RM Cn54854, holotype).
2. *E. roemeri* Wedekind, 1927, pl. 30, fig. 13 (RM Cn54858, holotype), fig. 14 (RM Cn54859).
Specimen RM Cn54853, the original of *E. roemeri* Wedekind, 1927, pl. 30, fig. 15, is referable to *E. fasciculatum* (= Pl. 5, figs 8 and 9).

The holotype of *E. rhizophorum* Wedekind (1927, pl. 30, fig. 17; RM Cn54857, = Pl. 5, figs 6 and 7) is questionably placed in the synonomy of *E. fasciculatum* as it is slightly larger and has some carinae. It is from Östergarn but the exact stratigraphic horizon is not known in the Hemse Beds and could be equivalent to or slightly older than Lau Backar 1. Wedekind (1927, pl. 29, figs 8–20) compared three specimens from Lau Backar to this species but the internal structures of these are still unknown.

Eichwald (1861) described but did not illustrate specimens from Estonia that he referred to *E. articulatum*. In their revision of Eichwald's collection, Fedorowski and Gorianov (1973) listed twenty-two specimens as *E. articulatum* (Wahlenberg) and figured two from the Paadla Horizon (Gorstian to early Ludfordian), one from the Kuressare Horizon (late Ludfordian) and one from the Kaugatuma Horizon (Prídolí), all from the Island of Saaremaa. From their description and illustrations (Fedorowski and Gorianov 1973, pl. 4, figs 1–4) these Eichwald specimens appear to compare more closely with *E. fasciculatum* in the smaller corallite size, smaller average number of septa, the development of a small open axial area, and the more common development of lonsdaleoid dissepiments that are larger and more irregular in size. The two figured longitudinal sections (Federowski and Gorianov, pl. 4, figs 3*b* and 4*b*) are not median and it is difficult to compare their tabularia with those of the Gotland material.

Entelophyllum cf. *fasciculatum* Wedekind, 1927

Text-fig. 4A–F

Material studied. Material given to us at the Geological Institute in Kiev collected from the lower part of the Malinovtsy Horizon, Grate Sloboda, Dnister River, Podolia (four specimens; figured: OU 10668–10671).

Distribution. Podolia: Gorstian Stage.

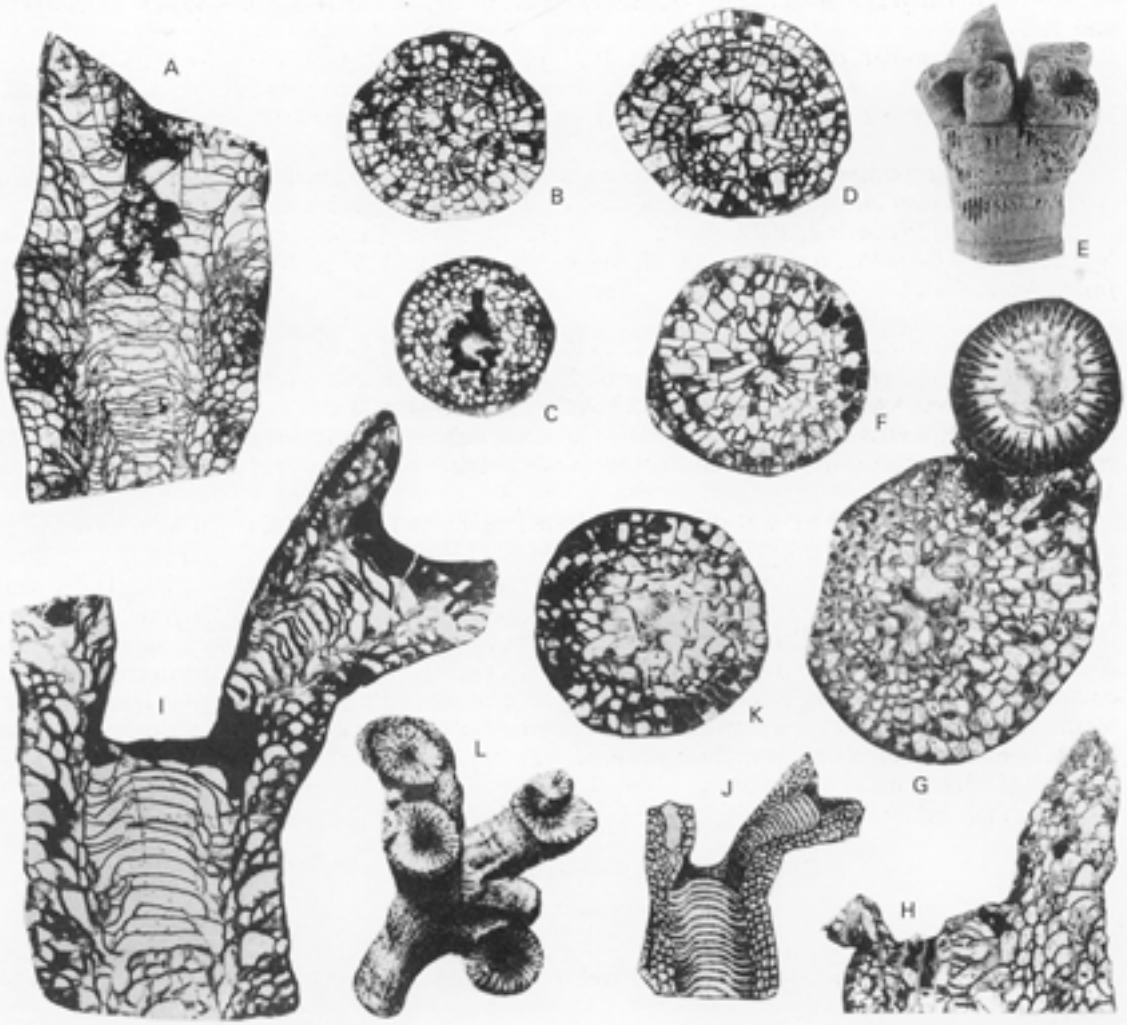
Description. Cylindrical corallites 6–8 mm in diameter and up to 25 mm in length. Two show peripheral parricidal increase with four and five offsets arising from the calical platform of the parent (Text-fig. 4E).

Septa are radially arranged with 22–24 in each order. Major septa are irregularly withdrawn from the axis leaving a distinct axial space. In the tabularium septa are thin, smooth and typically straight. They thicken in the dissepimentarium where they may be zigzag and carry rare carinae. Minor septa are typically 0·6–0·8 as long as the major but may be less than 0·3 or may be discontinuous being interrupted by larger interseptal dissepiments.

The tabularium is half corallite diameter. It consists of either complete tabulae that are strongly arched with flattened axial region and upturned peripheral edges, or more commonly closely spaced flat axial tabellae downturned sharply at their margins to rest on the ones below or supplemented by globose tabellae, with the space between the downturned edges and the dissepimentarium spanned by flat or concave tabellae.

Dissepiments are globose, vary from small to large, and are not arranged in vertical rows (Text-fig. 4A). In longitudinal section, offsets appear to be initiated in the periaxial trough of the tabularium and then expand with the dissepimentarium of the parent being reduced and the tabularium of the offset expanding outwards (Text-fig. 4A).

Remarks. Material from Podolia resembles *E. fasciculatum* from Gotland in having relatively simple



TEXT-FIG. 4. A–F, *Entelophyllum* cf. *fasciculatum* Wedekind, lower part of Malinovtsy Horizon, Grate Sloboda, Dnister River, Podolia; A and B, OU 10668; A, longitudinal section showing offset in top left corner, ×4; B, transverse section, ×4; C, OU 10669, transverse section, ×4; D, OU 10670, transverse section ×4; E and F, OU 10671; E, lateral view showing peripheral parricidal increase, ×2; F, transverse section, ×4. G and H, *Entelophyllum* sp. *A*., Hamra Beds, Kättelviken 3, coast below the road at Kättelviken, 3·5 km N of Hoburgen, southern tip of Gotland; G, transverse section abutting a tryplasmid corallite, ×4; H, longitudinal section, ×4. I–L, *Entelophyllum proliferum* (Dybowski), EGM Co1352 (lectotype), Slite Beds, Stora Karlsö, Gotland; I, longitudinal section showing offset, ×4; J, reproduction of Dybowski (1874, pl. 3, fig. 2*a*), line drawing of longitudinal section, ×2; K, transverse section, ×4; L, reproduction of Dybowski (1874, pl. 3, fig. 2), showing corallum, ×2.

septa withdrawn from the axis, a wide tabularium with a moderately developed periaxial trough, and irregular sized dissepiments. It differs in that the corallites are slightly narrower, more cylindrical, and the offsets do not diverge outwards from the lip of the parent calice as abruptly as in *E. fasciculatum*. Our material closely resembles material from Podolia in Dr V. A. Sytova's collection, which we examined in Leningrad, which she had tentatively referred to *E. proliferum* (Dybowski). Her material showed slightly more variation with one corallite having 30 major septa, and the septa slightly more thickened. The material from Podolia is certainly like the holotype of

E. proliferum (Text-figs 4I–L) but the latter species is known only from the one specimen from the Slite Beds of Stora Karlsö, Gotland and its range of variation is unknown. *E. proliferum* may be a senior synonym of *E. fasciculatum*.

Material from Podolia is similar to *Petrozium losseniformis* Zheltonogova (1965, p. 41, pl. 8, fig. 2) from the Gorstian Chagyr Formation in northwest Altaya, central Asia. We examined six topotypes lent to Dr V. A. Sytova by Dr V. A. Zheltonogova and these are referable to *Entelophyllum* and may well be conspecific with the European *E. fasciculatum*.

Entelophyllum sp. A

Text-fig. 4G–H

Material studied. RM Cn66046 from the Hamra Beds at Kättelviken 3, southern tip of Gotland.

Distribution. Gotland: late Ludfordian Stage.

Description. Small ceratoid corallite 20 mm tall and 11 mm in diameter immediately below the calice. With the proximal tip broken off, it does not indicate whether it is colonial or not.

Septa are radially arranged in two orders with 22 in each. Major septa are slightly withdrawn leaving an axial space 2 mm by 1 mm. Minor septa are one-half to three-fifths the length of the major. The septa of both orders are variable in the dissepimentarium, from slightly flexuose to straight. They are thickened and moderately cardinate in the cardinal quadrants only.

The longitudinal section is not median but indicates that the tabularium is a third to a half the diameter of the corallite wide and has a centrally raised area and probably a periaxial trough. The tabellae are globose and moderately spaced. The dissepiments are globose, up to 1 mm across, and not arranged in regular series.

Remarks. In growth form, size, septal number, open axial space, and longitudinal section, it resembles *E. fasciculatum* Wedekind, 1927, from the Eke Beds. It differs only in that the septa in the cardinal quadrants are thicker and more carinate than in *E. fasciculatum*.

Entelophyllum proliferum (Dybowski, 1874)

Text-fig. 4I–L

1874 *Cyathophyllum proliferum* Dybowski, p. 445, pl. 3, fig. 2, 2*a*, 2*b*.
non 1927 *Entelophyllum proliferum* (Dybowski); Wedekind, p. 23, pl. 29, figs 21–29, 33.

Lectotype. Chosen Wedekind (1927, p. 23), original of Dybowski, 1874, pl. 3, fig. 2 and 2*a* [*non* 2*b*]; EGM Col352, Slite Beds, Stora Karlsö, Gotland; late Sheinwoodian or early Homerian.

Material. Two specimens (Dybowski 1874, pl. 3, fig. 2, 2*a*, 2*b*) from Stora Karlsö and that of fig. 2*b* are only questionably assigned to this species as thin sections are not available.

Distribution. Gotland: late Sheinwoodian or early Homerian.

Diagnosis. Small bushy fasciculate corallum, increase peripheral parricidal; corallites up to 10 mm in diameter, major septa smooth, straight, number 20–22, leave an open axial space; minor septa weak; tabularium not distinctly biserial and periaxial trough not well developed; dissepiments variable in size, not regularly arranged.

Description. The lectotype is a small bushy corallum with a lower ceratoid to subcylindrical corallite producing five offsets one of which has a small bud in its calice. Budding in this mode is peripheral parricidal. The longitudinal thin section (Text-fig. 4I) suggests that the tabularium of the offset commenced as an extension of the periaxial trough of the parent and the neo-wall or part of it was inserted within the tabularium of the parent. The corallites vary from 8–9·5 mm in diameter before budding and the early corallite is 1·7 cm high and those of the second generation 1·2–1·3 cm. The epitheca is thin and shows very fine growth lines on slightly expanded growth bands. The second specimen figured by Dybowski is a tall tapering corallite 33 mm tall and

8 mm in diameter at the calice with four offsets developed in the calice. Dybowski's drawing shows concentric growth constrictions and low longitudinal ridges and furrows.

The septa are radially arranged, straight, thin and smooth. There are 20–22 major septa that extend three-quarters of the way to the axis leaving an open axial space almost 2 mm wide. Minor septa are weakly developed or discontinuous within the dissepimentarium.

The longitudinal section shows a well developed tabularium 0·6 the corallite diameter. In places it is not well delineated from the dissepimentarium. It consists of broad tabulae and supporting tabellae spanning the tabularium forming a raised flat axial area strongly downturned 1 mm from the tabularium boundary and then outturned to meet the dissepimentarium almost horizontally. There are twelve tabulae in 5 mm vertically. Dissepiments are highly variable in size and are irregularly arranged. They are globose with some three times the size of others. Some are horizontally based while others slope downward and inward.

Remarks. Dybowski (1874) gave the locality of his two specimens as Stora Karlsö on which is exposed the Slite Beds. In searching previous collections and in collecting from Stora Karlsö and other outcrops of the Slite Beds on Gotland, we have been unable to obtain further material. The possibility must be considered that Dybowski's specimens may not have come from Stora Karlsö. Of the Gotland species Dybowski's specimens of *E. proliferum* most closely resemble *E. fasciculatum* from the much higher upper Hemse and lower Eke Beds. Both forms have a wide axial area depleted of septa, a generally similar tabularium with a poorly defined periaxial trough, and a peripheral zone of irregularly distributed medium and large dissepiments. In the longitudinal section of *E. proliferum* the tabularium of the offset appears to originate as an extension of the periaxial trough of the parent (Text-fig. 4I), while in *E. fasciculatum* offsets originate from the dissepimental zone only. *E. proliferum* differs from *E. articulatum*, which also occurs in the Slite Beds, in having larger more irregular dissepiments and a tabularium that is much less well defined into two series.

Description and interpretation of this species are based on Dybowski's description and drawings, and photographs of the longitudinal section figured by Dybowski (1874, pl. 3, fig. 2*a*) and a transverse section on the same slide, kindly sent to us by Dr D. Kaljo. Wedekind (1927, p. 23) designated Dybowski's figures 2 and 2*a* as the lectotype, regarding the thin section 2*a* as being from part of 2. The thin longitudinal section is on the same slide as the transverse section but it is not known which specimen the transverse is from (D. Kaljo pers. comm. 1972). If the thin sections are from different specimens and are different from that figured as figure 2 by Dybowski, we select the longitudinal section as the primary type.

Entelophyllum dendroides sp. nov.

Text-fig. 5A–F

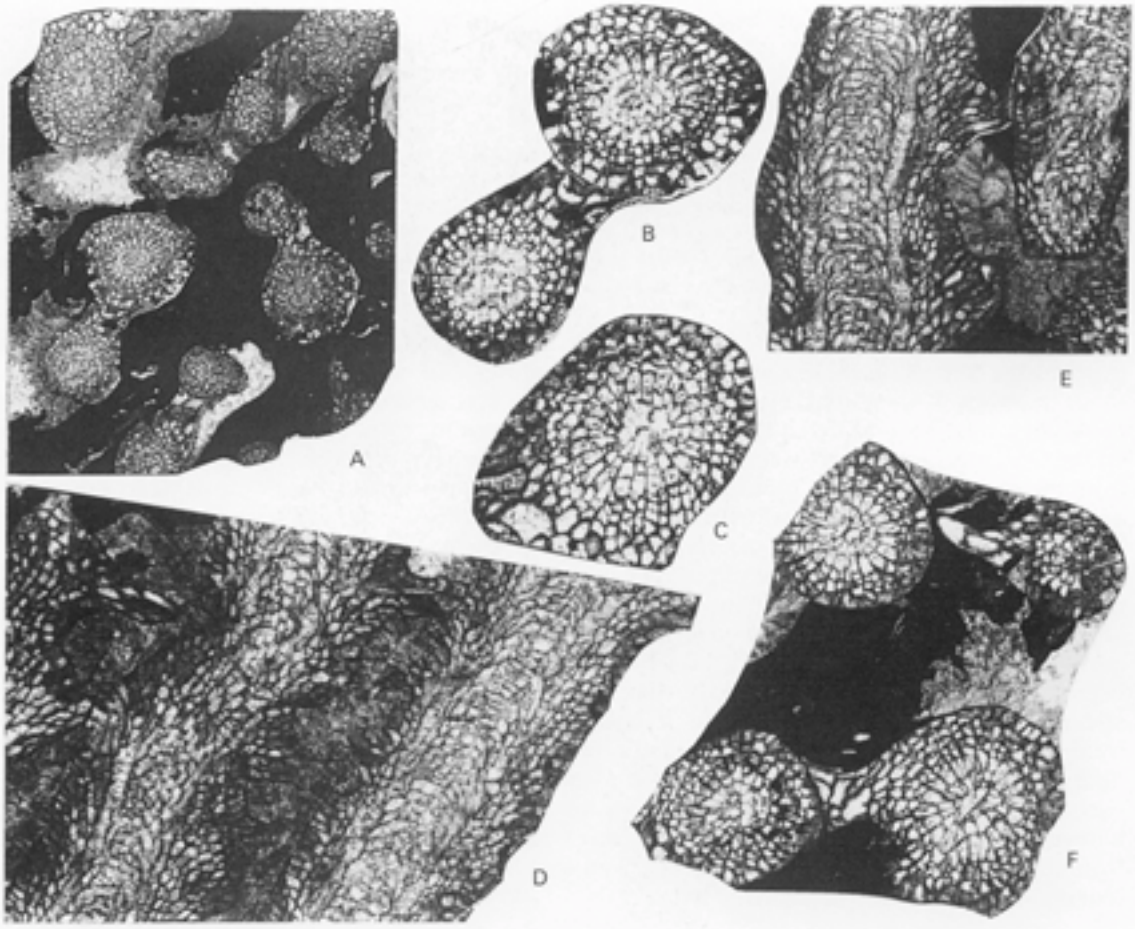
Holotype. RM Cn2560, Röda Lagret, Visby coast, Gotland; Telychian.

Material studied. Holotype (RM Cn2560, including two thin sections), and a paratype of four thin sections (RM Cn55554–Cn55557); both are given as from the Röda Lagret (probably from pebbles on the beach), Visby, west coast of Gotland (both figured).

Distribution. Gotland: Telychian.

Diagnosis. Dendroid colonies of closely-spaced small corallites 4–7 mm in diameter; septa typically straight, noncarinate; major septa number 20–23; 1 mm axial space into which some septa may extend; tabularium biserial with prominent periaxial trough; dissepiments small, globose; increase peripheral parricidal.

Description. The holotype is part of a dendroid colony and measures 30 × 40 mm in cross-section at its widest part and is 75 mm long. It is composed of small subcylindrical corallites 4–7 mm in diameter, typically separated by less than 5 mm. The corallites arise mainly in groups of four from the dissepimentarium of the parent by parricidal increase. They diverge rapidly outward soon after separation from each other and expand in diameter. They then tend to turn vertically and produce lateral extensions that abut adjacent corallites.



TEXT-FIG. 5. *Entelophyllum dendroides* sp. nov., Röda Lagret, from pebbles on the beach at Visby, Gotland. A–D, RM Cn2560 (holotype); A–C, transverse sections, ×2, ×4, ×4 respectively; D, longitudinal section, ×4. E, RM Cn55555, longitudinal section, ×4. F, RM C55556, transverse section, ×4.

Budding across the colony appears irregular; one corallite is 30 mm tall before budding, another is in excess of 60 mm. Lateral expansions are not produced at the same level across the corallum.

The figured transverse section (Text-fig. 5F) shows the initial stages of increase where the neo-walls form as four scallops at the inner dissepimentarium, slightly expanding into the tabularium. A dissepiment is based on the neo-wall, and neo-septa project inwards from the dissepiment towards the atavo-septa. In the longitudinal section (text-fig. 5E) there is a suggestion of one offset being produced by nonparricidal increase but this cannot be definitely established.

Septa are typically long, radially arranged in two orders. The major septa number 20–23 in mature corallites and leave a narrow axial space (Text-fig. 5B and C). The septal ends are typically irregularly bunched near the axis in groups of two to three but two or more septa may extend irregularly to the axis. In immature corallites many of the major septa are confluent at the axis. Minor septa are half major septa in length and variously developed. They may be straight, slightly thinner than the major septa, projecting radially a short distance into the tabularium, and discontinuous.

Longitudinal sections are typically entelophylloid with the tabularium and dissepimentarium distinctly delineated and the tabularium separated into an axial and a periaxial series of tabellae (Text-fig. 5D). The tabularium is typically 0·6 the diameter of the corallite, and the axial series of tabellae 0·75 to 0·8 the diameter of the tabularium. The axial series consists of flat-topped tabellae that have steeply downturned edges and

TEXT-FIG. 6. *Entelophyllum pseudodianthus* (Weissermel), Much Wenlock Limestone, Wenlock Edge, Shropshire; GSM 6575 (neolectotype). A, longitudinal section, ×4. B, transverse section, ×4.

number 10–15 in 5 mm vertically. The periaxial series are flat or slightly concave upwards producing a pronounced periaxial trough with 20–22 tabellae in 5 mm vertically. The dissepiments are small, globose or slightly elongated and sloping downward and inward.

Remarks. This species is distinguished by its relatively small sized corallites and dendroid habit. It differs from the Llandovery *Petrozium dewari* Smith, 1930 and *P. losseni* (Dybowski 1874) by the more marked separation of the tabularium into axial and periaxial series and wider dissepimentarium.

Entelophyllum pseudodianthus (Weissermel, 1894)

Text-figs 6A, B and 7A–E

v1839 *Cyathophyllum dianthus* Goldfuss; Lonsdale, p. 690, pl. 16, figs 12*b*, 12*c*, 12*d* [*non Cyathophyllum dianthus* Goldfuss, 1826].
1894 *Cyathophyllum* (*Heliophyllum*) *pseudodianthus* Weissermel, p. 591, pl. 47, figs 2 and 3.
v1927 *Xylodes pseudodianthus* (Weissermel); Lang and Smith, p. 475, pl. 35, fig. 9.
v1929 *Xylodes pseudodianthus* (Weissermel); Smith and Tremberth, p. 366, pl. 8, figs 3 and 4.

Neolectotype. Here chosen, original of Lonsdale, 1839, pl. 26, fig. 12*b*, *c*, *d*; GSM 6575 and thin section PF 4617 from the Geological Society Collection, Much Wenlock Limestone, Wenlock Edge, Shropshire, England; Homerian.

Type material. Weissermel (1894, p. 591) described *Cyathophyllum* (*Heliophyllum*) *pseudodianthus* as a new name for a species represented by the four specimens which had been figured as *Cyathophyllum dianthus* by Lonsdale (1839, pl. 16, fig. 12, 12*a–e*). Lang and Smith (1927, p. 473) stated that one of Lonsdale's four specimens (fig. 12*e*) is lost and that the other three represent three distinct species, each belonging to a different genus. They state that only Lonsdale's figures 12*b–d* (all from the one specimen: GSM 6575) represents the species described by Weissermel as *C.* (*H.*) *pseudodianthus* and selected as lectotype the specimen figured by Weissermel (1894, pl. 47, fig. 3) from a boulder in the glacial drift of Lauth, Germany. That specimen, in the East Prussian Provincial Museum at Konigsberg (now Kaliningrad), was never sectioned and was destroyed during the Second World War (Dr V. A. Sytova pers. comm.).

We have thus selected one of Weissermel's original syntypes as the neolectotype, the specimen figured by Lonsdale (1839, p. 16, fig. 12*b–d*); GSM 6575, and herein refigured (Text-figs 6A, B and 7E).

Material studied. Neolectotype (GSM 6575) and twenty-four specimens from the collections of the GSM, BMNH, UO, SM, UB, and UQ from the Much Wenlock Limestone, Wenlock Edge, Shropshire; figured: GSM 6575 (neolectotype), BMNH R2022. Farley Member, Coalbrookdale Formation; Much Wenlock Limestone of Dudley, Worcestershire, including Wren's Nest (numerous specimens from same collections as the Wenlock Edge material above; figured: UB 124); Much Wenlock Limestone of May Hill, Gloucestershire (figured BU 8715); and lower Elton Beds, from Ledbury Quarry, Malverns, Herefordshire.

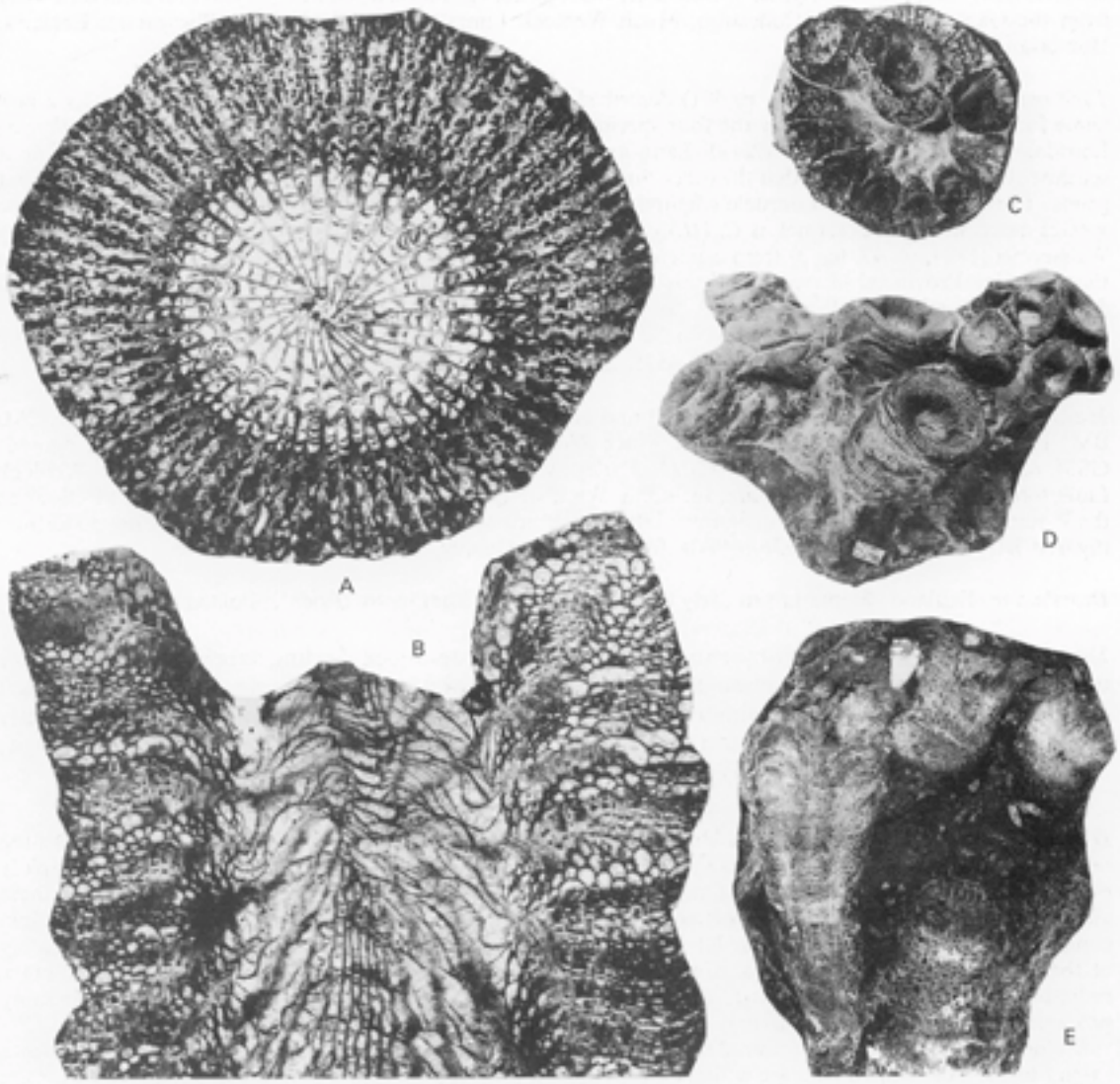
Distribution. England: Homerian to early Gorstian; Estonia: Ludlow to ?Prídolí; Poland: ?early Pridoli.

Diagnosis. Typically small bushy coralla of turbinate to rapidly expanding subcylindrical corallites up to 25 mm in diameter; increase peripheral parricidal with up to 10 offsets. Septa 20–33 in each order, long, thickened in dissepimentarium and heavily carinate to aerolate; major septa slightly withdrawn from axis; minor septa rarely contratigent. Tabularium biserial with periaxial trough; dissepiments globose, horizontally based at periphery and steeply inclined axially.

Description. The coralla are small and bushy, up to 200 mm in diameter and 150–200 mm in height, consisting of two to five generations of corallites (Text-fig. 7D). The coralla are fasciculate, generally formed of rapidly expanding corallites 60 mm in height and 15–20 mm in diameter but in some coralla they may be cylindrical and up to 100 mm in height. The neolectotype is a small bushy clump 20 mm in diameter and 40 mm high, consisting of 8–10 corallites (Text-fig. 7E). Budding is peripheral, parricidal with up to ten corallites originating at the extreme margin of the calyx. Corallites rapidly expand and quickly diverge giving the corallum a radiating appearance (Text-fig. 7D); they have strong contractions and expansions but few connecting processes. Corallite walls are thin and epithecate.

Major septa number 21–33 (mean 27 at diameter 12 mm) in adult stages (Text-fig. 6B). Some major septa extend to the axis while others are withdrawn leaving an axial space up to 3 mm in diameter. Axial ends are commonly turned aside or twisted. Minor septa typically do not project into the tabularium, are commonly 0·6–0·7 the length of the major, and are only rarely contratigent. In the dissepimentarium both orders of septa are thickened, heavily carinate and commonly aerolate, but in parts of some corallites they are relatively smooth. Carinae are zigzag and parallel the trabeculae. In the outer dissepimentarium they diverge at a small angle to the vertical and are fanned over the inner dissepimentarium so that at the dissepimentarium/tabularium boundary they are 30° to the horizontal.

In longitudinal section the dissepimentarium and tabularium are distinctly delineated. The tabularium is 6–7 mm wide and differentiated into two series of tabellae. In forms with septa extending to the axis the axial series are domed and relatively high (Text-fig. 6A), while in those with the septa withdrawn from the axis they are flat or sagging and of low profile (Text-fig. 7B). A narrow series of small, flat or slightly saucered tabellae span the area between the axial series and the dissepimentarium forming a periaxial trough. Dissepiments are small, globose, occurring in almost horizontal rows at the periphery and steeply inclined inwards and downwards at the tabularium boundary. In some specimens broad zones of more globose dissepiments alternate vertically with thinner zones of smaller and slightly thicker dissepiments (Text-fig. 7B). The former correspond to expansions of the corallite diameter and the latter to the contractions.



TEXT-FIG. 7. *Entelophyllum pseudodianthus* (Weissermel). A and B, BU 8715, Much Wenlock Limestone, May Hill, Gloucestershire; A, transverse section showing typical carinate and thickened septa, ×4. C and D, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire; C, UB 124, calical view showing peripheral parricidal increase, ×1; D, UO C17516, oblique view showing typical loose fasciculate corallum, ×1. E, GSM 6575 (neolectotype), Much Wenlock Limestone, Wenlock Edge, Shropshire, polished surface, ×2.

Remarks. In England, *Entelophyllum articulatum anglicum* and *E. pseudodianthus* have the same distribution and commonly occur together. We have included those forms with their septa typically thickened, highly carinate and in some cases aerolate in *E. pseudodianthus*, as did Smith and Tremberth (1929). These specimens generally have squatter coralla, more turbinate corallites, shorter minor septa that are rarely contratigent, and less regular biserial tabularia. However, some have corallites that are slender and cylindrical, minor septa that project into the tabularium and are contratigent, and have regular biserial tabularia. On the other hand corallites in some colonies

referred to *E. articulatum anglicum* are turbinate or have some thickened and carinate septa. Thus some specimens seem to be gradational between the two forms and their specific designation is arbitrary.

Entelophyllum pseudodianthus transiens (Prantl, 1940)

Plate 6, figs 5–7

1940 *Xylodes pseudodianthus transiens* Prantl, p. 13, pl. 1, fig. 4; pl. 3, figs 1, 2, 4.

Holotype. Prantl, 1940, pl. 1, fig. 4, from the Kopanina Formation, 'Amerika' quarries near Morina (Budnany of Prantl 1940), Czechoslovakia; Gorstian.

Material. Interpretation based on photographs of thin sections figured by Prantl (1940, pl. 3, figs 1, 2, 4).

Distribution. Bohemia: ?late Homerian to ?Gorstian.

Diagnosis. Small bushy coralla with ceratoid to subcylindrical corallites 11–17 mm in diameter; increase peripheral, parricidal. Major septa 31–34, withdrawn up to 1 mm from axis, cardinal septum projecting into axial space; septa thin in tabularium; continuous, some thickened and carinate in dissepimentarium. Tabularium distinctly biserial with axial tabellae flat topped; dissepiments small, globose, inclined axially.

Remarks. Prantl (1940) proposed this species for forms that show both long thin smooth septa typical of *E. articulatum* and thickened carinate septa typical of *E. pseudodianthus*. Considering the variation in *E. articulatum anglicum* and *E. pseudodianthus* described previously, the Bohemian form could well belong to this series. The lack of heavily carinate and cavernous septa suggest similarities to *E. articulatum anglicum* rather than *E. pseudodianthus*. In size and septal number, it is more like specimens of the subspecies from the Elton Beds of similar age.

Entelophyllum prosperum (Počta, 1902)

Plate 6, figs 1–4

1902 *Cyathophyllum prosperum* Počta, p. 105, pl. 43, figs 1, 2, 10–19, 23–29, 36–41; pl. 44, figs 1–33; pl. 45, figs 1–5, 18–39; pl. 46, figs 8–24; pl. 103, figs 6–8; pl. 109, fig. 8.
1902 *Cyathophyllum minusculum* Počta, p. 104, pl. 42, figs 1–8.
1940 *Xylodes prosperus prosperus* (Počta); Prantl, p. 8, pl. 1, figs 5 and 6; pl. 2, figs 2, 5, 7.

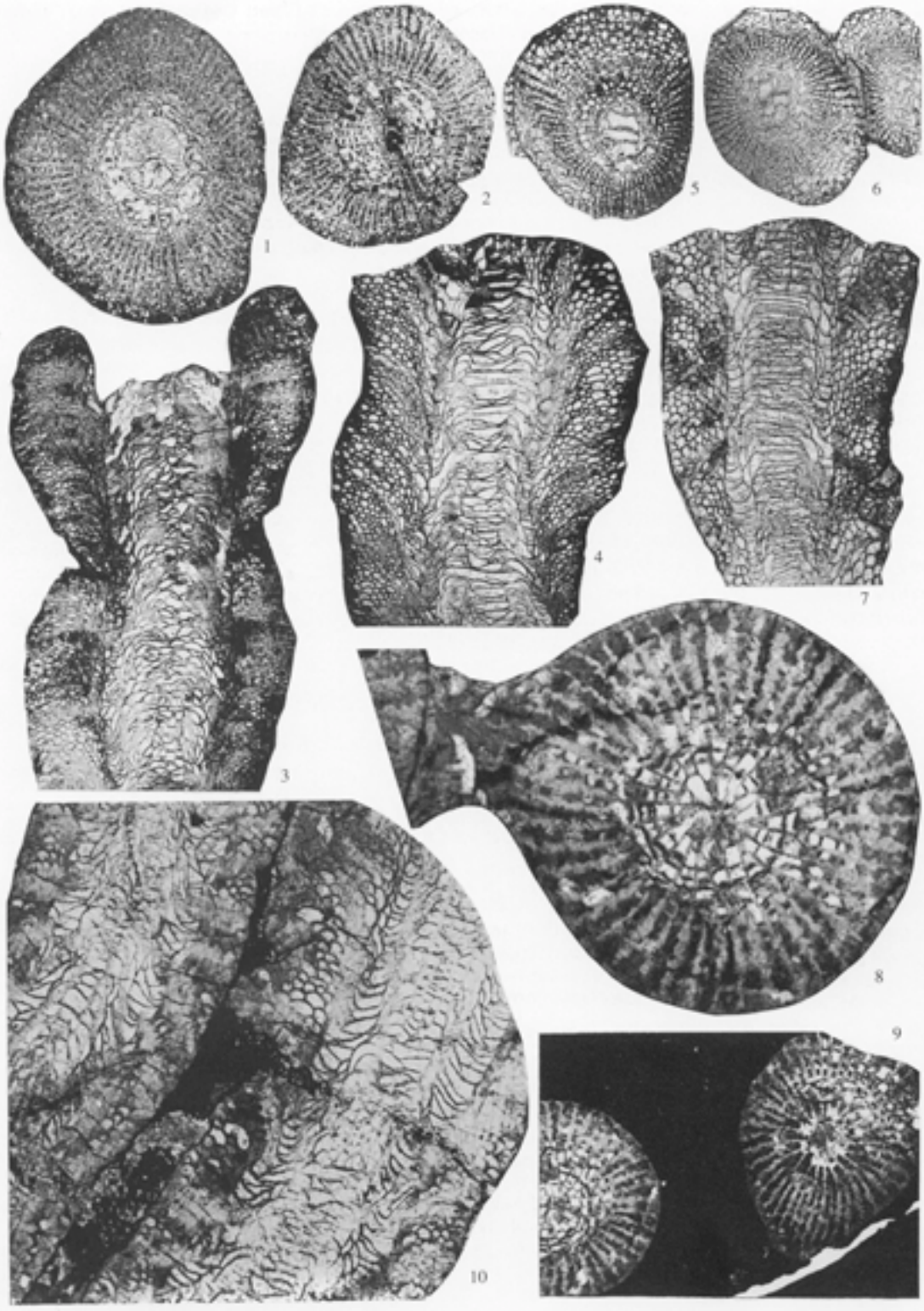
Lectotype. Chosen Prantl (1940, p. 8), original of Počta, 1902, pl. 44, figs 1–4 from Budnaner Kalksteine, Kopanina Formation at Tachlovice, Czechoslovakia; Gorstian.

EXPLANATION OF PLATE 6

Figs 1–4. *Entelophyllum prosperum* (Počta), Kopanina Formation, Tachlovice, Czechoslovakia. 1, NM No. 768, original of Počta (1902, pl. 103, fig. 7), transverse section, ×2. 2, NM unnumbered, original of Prantl (1940, pl. 2, fig. 2), transverse section ×2. 3, NM No. 855, original of Počta (1902, pl. 103, fig. 8), longitudinal section, ×2. 4, NM No. 473, original of Počta (1903, pl. 103, fig. 6), longitudinal section, ×2.

Figs 5–7. *Entelophyllum pseudodianthus transiens* (Prantl), Kopanina Formation, 'Amerika' quarries, near Morina, Czechoslovakia. 5, NM 26329, original of Prantl (1940, pl. 3, fig. 2), transverse section, ×2. 6, NM 26329, original of Prantl (1940, pl. 3, fig. 4), transverse section, ×2. 7, NM 26329, original of Prantl (1940, pl. 3, fig. 1), longitudinal section, ×2.

Figs 8–10. *Entelophyllum confusum* (Počta), Upper Litén Group [Motol Formation], 'V Kozle' between Beroun and Srbsko, Czechoslovakia. 8 and 9, NM unnumbered, transverse sections, ×7·5, ×4, respectively. 10, NM unnumbered, longitudinal section, ×4.



JELL and SUTHERLAND, *Entelophyllum*

Material. Interpretation based on photographs of thin sections figured by Počta (1902, pl. 103, figs 6–8) and Prantl (1940, pl. 2, fig. 2); all from Kopanina Formation at Tachlovice.

Distribution. Bohemia: Gorstian.

Diagnosis. Small bushy coralla with trochoid to subcylindrical corallites 18–19 mm, maximum 35 mm, in diameter; increase peripheral parricidal. Major septa 28–40, withdrawn from axis in the cardinal quadrants leaving axial space elongate in counter-cardinal plane; minor septa 0·6 the length of major; septa considerably thickened, heavily carinate to aerolate, continuous in dissepimentarium. Tabularium biserial; axial series varying from small tabellae forming high domes to large complete tabellae slightly sagged axially; dissepiments small, globose, horizontally based at periphery and steeply inclined axially.

Remarks. Prantl (1940) in redescribing the entelophylloid corals in the collection of Počta (1902), recognized two subspecies for the material described as *Cyathophyllum prosperum* and the synonymy given above is that of the nominate subspecies. *E. prosperum* is characterized by thickened and heavily carinate septa with the outer dissepimentarium appearing reticulate in transverse section and resembling *E. pseudodianthus* from Britain. These two species are very similar, the Bohemian species only differing in its slightly greater size and more numerous septa, and the more noticeable fossula. Offsets arising right at the margin of the parent in the specimen figured by Prantl (1940, pl. 1, fig. 6) are identical to that figured herein for *E. pseudodianthus* (Text-fig. 7c). The Bohemian form might best be considered a subspecies of *E. pseudodianthus*. However, not enough material is available to us and the type locality 'Tachlovice' is today unknown but thought to have been in a mine (A. Galle, pers. comm.).

Entelophyllum prosperum crassum (Prantl, 1940)

1902 *Cyathophyllum prosperum* Počta, p. 105, pl. 43, figs 3–9, 20–22, 30–35; pl. 44, figs 34–40; pl. 45, figs 40–42; pl. 46, figs 1–7.
1940 *Xylodes prosperus crassus* Prantl, p. 11, pl. 1, figs 7–9; pl. 2, fig. 6; pl. 3, fig. 3.

Holotype. Počta, 1902, pl. 44, figs 33–34, from Budnaner Kalksteine, Kopanina Formation at Tachlovice, Czechoslovakia; Gorstian.

Material. No material was available for this study.

Distribution. Bohemia: Gorstian.

Remarks. This subspecies was described by Prantl (1940) for the larger specimens of *E. prosperum* from the same strata. The originals of Prantl (1940, pl. 2, fig. 6; pl. 3, fig. 3) have not been located.

Entelophyllum confusum (Počta, 1902)

Plate 6, figs 8–10

1902 *Cyathophyllum confusum* Počta, p. 103, pl. 99, figs 3–11.
1940 *Xylodes confusus* (Počta); Prantl, p. 16, pl. 3, figs 5 and 6.
1981 *Carinophyllum confusum* (Počta); Hill, fig. 127, 2*d*, *e*.

Lectotype. Chosen Prantl (1940, p. 16), original of Počta, 1902, pl. 99, fig. 3, from the Budnaner Kalksteine, Kopanina Formation of Tachlovice, Czechoslovakia; Gorstian.

Material. Interpretation based on photographs of the thin sections figured by Prantl (1940, pl. 3, figs 5 and 6) from the upper Liten Group (Motol Formation), 'V Kozle' between Beroun and Srbsko (Homerian). Fedorowski and Gorianov (1973) referred three specimens of the Eichwald collection from Estonia to this

species, one from the Gorstian-Ludfordian Paadla Horizon of Pilguse and two from the late Ludfordian Kuressaare Horizon of Lode.

Distribution. Bohemia: Homerian and Gorstian; Estonia: Ludlow.

Diagnosis. Small dendroid to phaceloid coralla; corallites cylindrical, 8–14 mm in diameter; increase peripheral parricidal. Septa fusiform, carinate in dissepimentarium; 22–24 major septa extend almost to axis leaving small axial space; cardinal septum projects slightly into axial space. Tabularium biserial; axial series high, flat topped; dissepimental zone broadly arched; dissepiments small, globose.

Remarks. This species is distinguished by the fusiform and carinate nature of septa, characters Strelnikov (1964, p. 59) used to typify his new genus *Carinophyllum* with *E. confusum* as type species. These features and the corallite size seem to distinguish the Bohemian material as a distinct species but we do not consider the carination and thickening to be of generic significance.

Entelophyllum lauense sp. nov.

Plate 7, figs 1–12

Holotype. RM Cn66047, *Rhizophyllum* limestone, lower Eke Beds, Lau Backar 1, southeast Gotland; middle Ludfordian.

Material studied. E. lauense is known only from the type locality (ten specimens; figured: RM Cn66047 (holotype); UQ F35165, 35169, 35170, 35281 (paratypes)).

Distribution. Gotland: middle Ludfordian.

Diagnosis. Presumably fasciculate, corallites flaring after early trochoid stage, up to 25 mm in diameter and 20 mm high; major septa 30–32, cardinal fossula confluent with axial space; minor septa 0·6–0·7 length of major; septa in dissepimentarium thickened axially and heavily carinate to retiform peripherally. Tabularium biserial with axial tabellae domed typically with axial sag; dissepiments small globose; broad dissepimentarial zone peripherally domed.

Description. Broken isolated corallites are trochoid initially but flare rapidly producing wide, everted calices 14–25 mm in diameter, while the corallites are less than 20 mm high. The dissepimental zone forms a broad calical platform that may show several rejuvenescenes. They surround moderately deep tabularial pits that have a shallow trough about the outside and a central depression which may be connected to the trough by a depressed cardinal fossula (Pl. 7, fig. 3). Early stages of several specimens show either broken early tips or crescent-shaped broken walls that are interpreted as fragments from a parent corallite. Some corallites show a supporting buttress (Pl. 7, fig. 4). One specimen, UQ F35165, shows two generations of budding with one offset arising at a rejuvenescene by peripheral non-parricidal budding and the parent has two small offsets developing in the dissepimentarium 8 mm higher. The holotype has at least three offsets beginning by the development of scalloped neo-walls near the inner margin of the dissepimentarium (Pl. 7, fig. 1).

There are 30–32 major septa arranged pinnately about a long cardinal septum which bisects a distinct fossula (Pl. 7, fig. 11). They are slightly withdrawn abaxially leaving a narrow axial space 1–2 mm in diameter, into which the cardinal fossula opens. The septa in the tabularium are thin, straight or slightly flexuose at their axial extremities. The minor septa are well developed only slightly thinner than the major and 0·6–0·7 their length, projecting a short distance into the tabularium. In the dissepimentarium both orders are variably thickened, zigzag, irregularly carinate to retiform. The thickening is more pronounced in the inner dissepimentarium and the carination increases toward the periphery. Carinae typically alternate, arising from the angles of the zigzag septa but in places they are so numerous and the segments of the septa so short and turned away from the plane of the septum that the carinae appear opposite each other.

The tabularium expands rapidly with growth and is 0·6–0·7 the diameter of the corallite immediately below the calice. The tabularial floors are domed centrally with a slight axial depression, and downturned in the outer tabularium producing a periaxial trough (Pl. 7, fig. 2). The axial tabellae are relatively large and globose, and their downturned edges rest on tabellae below or outturn to the dissepimentarium. Periaxial tabellae are flat or concave upwards. Dissepiments are small, globose, peripherally domed, and not arranged in vertical series.

Septa appear to be composed of a uniserial row of monacanthine trabeculae 0·01–0·02 mm in diameter. Extension of the fibres of the trabeculae form the carinae. Both the trabeculae and carinae show a fanning over the dissepimentarial floor, becoming flatter near the dissepimentarium/tabularium boundary and then becoming steep again axially.

Remarks. All specimens are isolated but they are interpreted as being broken offsets from loosely fasciculate colonies. The colonial nature is also suggested by UQ F35165 which shows two generations of budding.

E. lauense differs from other described Gotland species of *Entelophyllum* by its corallum form, flat flaring nature of the corallites, and heavy carination and thickening of the septa. In the latter regard, it resembles *E. pseudodianthus* but differs from it in that the corallites are much flatter and have well developed fossulae.

There is some reservation in referring *E. lauense* to *Entelophyllum* because it is not clearly as fasciculate, the cardinal septum and fossulae are more pronounced, and the septa more heavily carinate than in the type species. However, as discussed above, it appears to be compound with at least two generations of buds. The development of the cardinal septum is variable in other species of *Entelophyllum* and this is not regarded as a generic character. The carination and retiform nature of the septa are comparable with that of *E. pseudodianthus* and *E. prosperum* which we included in *Entelophyllum* rather than separating out the carinate forms as *Stereoxylodes* Wang, 1944. There are similarities to *Nanshanophyllum typicum* Yu, 1956, a solitary form, heavily carinate in the dissepimentarium, showing a cardinal fossula opening into an axial space. Pedder (1976) considered *Nanshanophyllum* Yu to be a subgenus of *Stereoxylodes*.

Entelophyllum hamraense sp. nov.

Plate 8, figs 1–9

Holotype. RM Cn66048; Hamra Beds, Närs fyr 1, southeast Gotland; late Ludfordian.

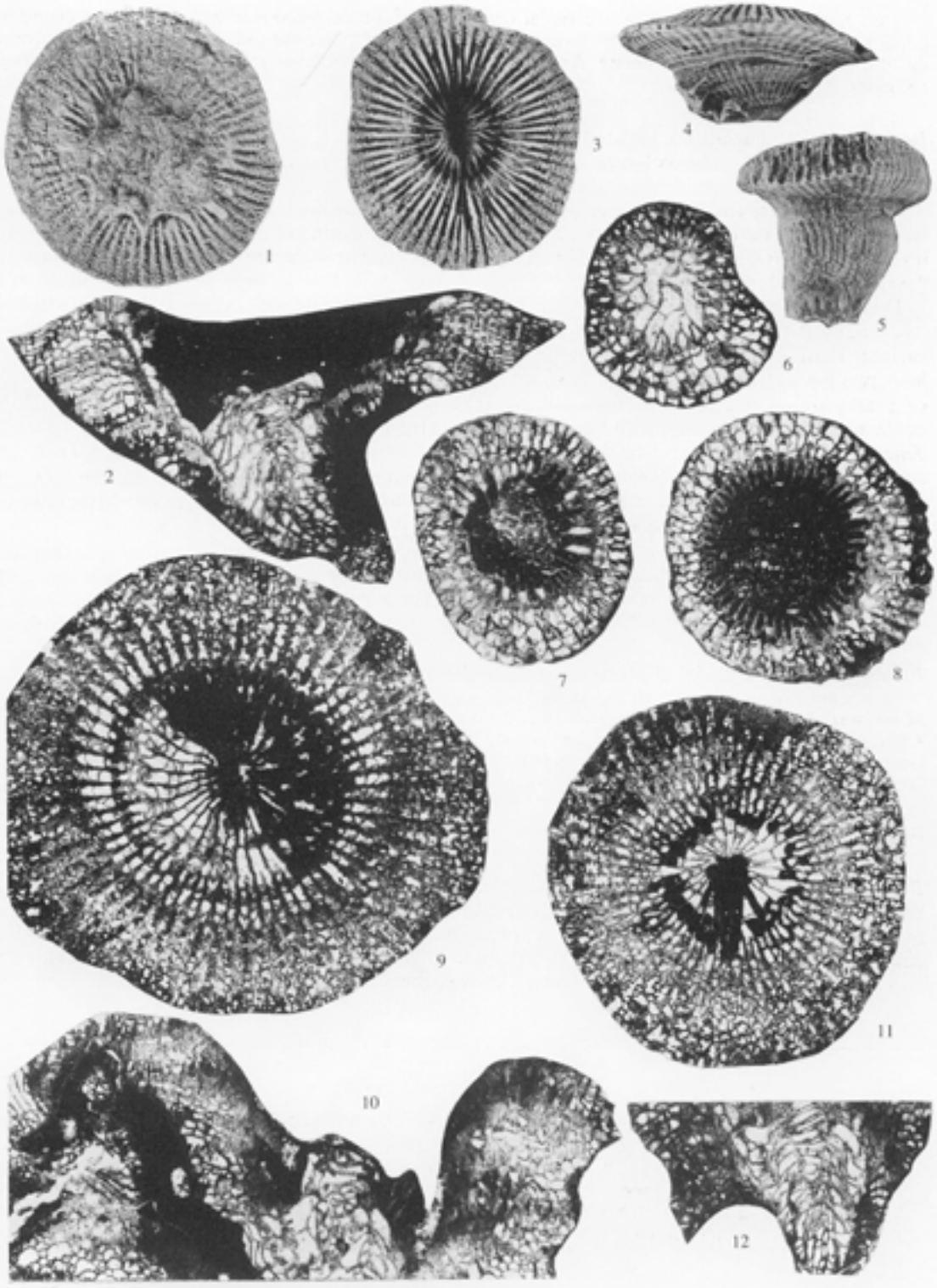
Material studied. Hamra Beds of Gotland: the type locality (one specimen; figured: RM Cn66048 – holotype); Kättelviken 3, southern tip of Gotland (one specimen; figured: UO 10672); Hoburgen 2, southern tip of Gotland (six specimens; figured: UQ F34001); ?Hamra or Lower Sundre Beds at Juves 3, southern tip of Gotland (one specimen; figured: RM Cn66049).

Distribution. Gotland: late Ludfordian.

Diagnosis. Fasciculate corallites trochoid to ceratoid, maximum diameter 25 mm, height 40 mm, peripheral parricidal increase. Major septa number 27–31, withdrawn from axis, axial ends slightly thickened, septal segments and long cardinal septum common in axial space; minor septa commonly contratigent; septa heavily carinate and thickened in inner dissepimentarium; tabularium regularly biserial; dissepimentarium broad, dissepiments small, globose.

EXPLANATION OF PLATE 7

Figs 1–12. *Entelophyllum lauense* sp. nov., *Rhizophyllum* limestone, Eke Beds, Lau Backar 1, 1·0 km NE of Lau, southeast Gotland. 1 and 2, RM Cn66047 (holotype); 1, calical view showing incipient buds, ×2; 2, longitudinal section, ×4. 3 and 4, UQ F35170; 3, calical view, ×2; 4, lateral view, ×2. 5–8, UQ F35281; 5, lateral view, ×2; 6, transverse section from base, ×4; 7, transverse section from central part, ×4; 8, transverse section of calice, ×4. 9 and 10, UQ F35165; 9, transverse section, ×4; 10, longitudinal section showing edge of second corallite, ×4. 11 and 12, UQ F35169; 11, transverse section ×4; 12, longitudinal section, ×4.



JELL and SUTHERLAND, *Entelophyllum*

Description. Corallites are trochoid to ceratoid commonly occurring as isolated broken offsets up to 25 mm in diameter and 40 mm in height. The holotype consists of three offsets, 18, 18 and 20 mm in diameter and 35 mm in height, arising from the weathered edge of a calice. One of the offsets has at least three offsets in its calice. Another specimen, UO 10672, shows three small trochoid corallites arising from the periphery of a corallite 1·7 mm in diameter. Increase is peripheral parricidal.

Major septa number 27–30 and are smooth and straight in the tabularium, commonly withdrawn from the axis leaving an axial space 2–4 mm in diameter (Pl. 8, fig. 6). The cardinal septum and rarely the counter are longer than the others and project well into the axial space. Axial ends of septa are commonly thickened and discrete septal segments are common in the axial space based on the axial tabellae. Minor septa are 0·5–0·75 the length of the major and are commonly contratingent. In the dissepimentarium they are commonly as thick as the major and both are dilated in the inner parts and strongly carinate in the outer parts (Pl. 8, fig. 4). Carinae on the thickened inner parts are short and stout, and in places appear to have short prickles coming off them as though they were extensions of secondary trabeculae. In the outer parts the carinae are longer and more numerous, coming off the angles of the zigzags of the septa. The long carinae give a rather ragged appearance to the septa and only rarely are they retiform or aerolate.

The tabularium is 0·4–0·5 the diameter of the corallite, domed centrally with the tabulae sloping steeply downward peripherally and then turning outwards giving a shallow periaxial trough (Pl. 8, figs 5 and 7). The central area is composed of numerous globose tabellae. In places where the outer globose tabellae do not reach the dissepimentarium, flat periaxial tabellae span the space. Dissepiments are small, globose, not arranged in vertical series, and commonly flat peripherally but inclined axially downward near the tabularium.

Remarks. Specimens from Hoburgen are mainly isolated corallites but have similar internal structures to the holotype. Some may be initial protocorallites while others may be offsets broken from loosely fasciculate colonies.

E. hamraense differs from *E. lauense* from the Eke Beds, which also is heavily carinate, in that the corallites are taller, no fossula is developed, the septa are thicker in the inner dissepimentarium, and the septal ends commonly extend into the axial area. The occurrence of short prickles on the carinae suggests that the trabeculae may bear secondary trabeculae, which is not an entelophylloid character.

This species differs from *E. pseudodianthus* in that its axial space is not as open, the axial ends of the septa are not grouped as in the latter species and there is not as regular a biserial tabularium.

Entelophyllum? visbyense Wedekind, 1927

Plate 9, figs 1–9

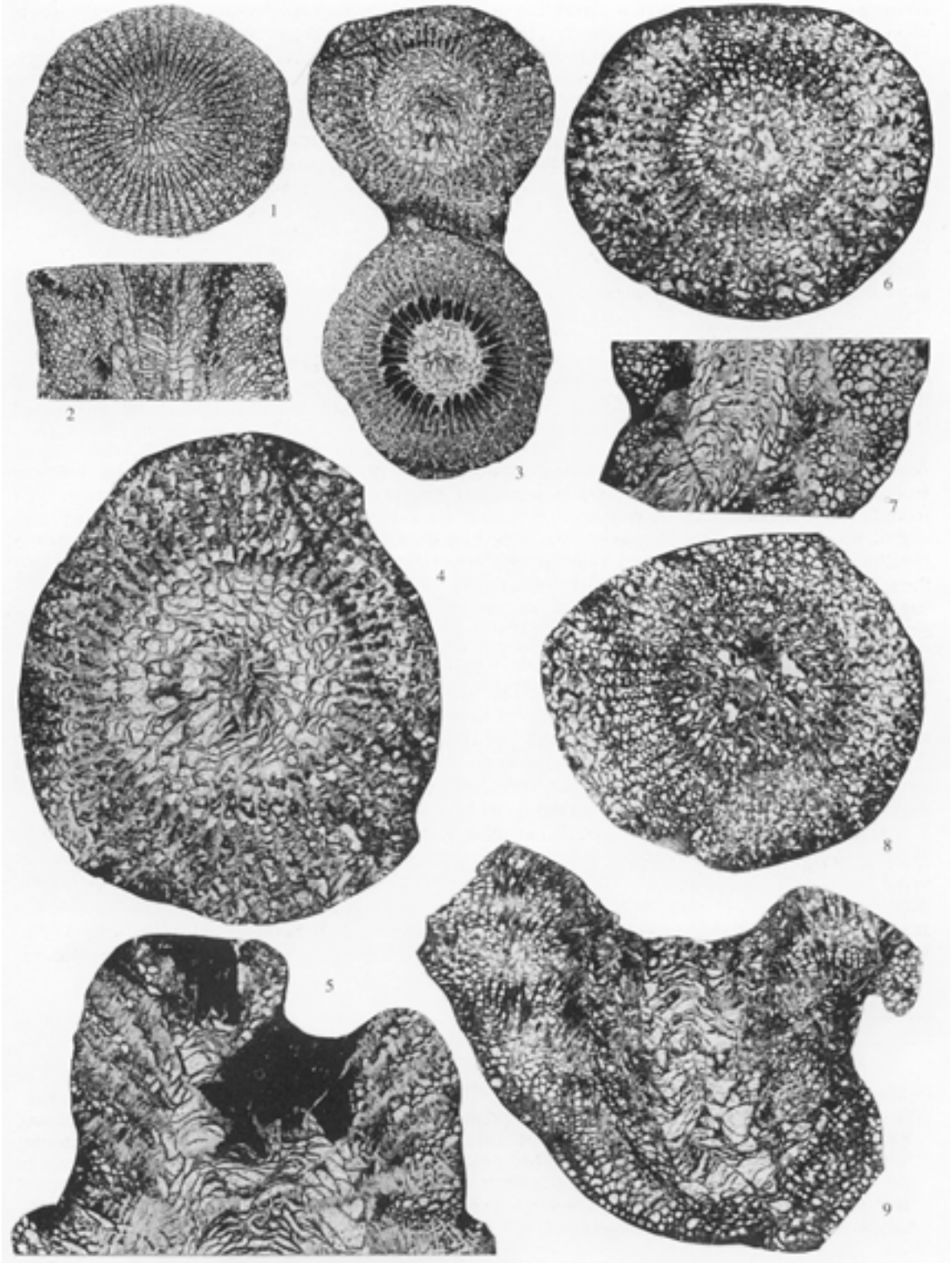
v*1927 *Entelophyllum visbyense* Wedekind, 1927, p. 24, pl. 7, figs 9 and 10.
v*1927 *Entelophyllum anschutzi* Wedekind, 1927, p. 24, pl. 7, figs 7 and 8.

Holotype. Wedekind, 1927, pl. 7, figs 9 and 10; RM Cn54873, Högklint Beds, Gutevägen 3 [= Cement factory], Visby, Gotland; Sheinwoodian.

Material studied. Four specimens from the type locality; figured: RM Cn54873 (holotype), SMF Wdkd. 10308–10309 (holotype of *E. anschutzi*), RM Cn66196, Cn66197. Neuman and Hanken (1979) recorded this

EXPLANATION OF PLATE 8

Figs 1–9. *Entelophyllum hamraense* sp. nov. 1 and 2, UQ F34001, upper Hamra Beds, Hoburgen 2, southern tip of Gotland; 1, transverse section, ×2; 2, longitudinal section, ×2. 3–5, RM Cn66048 (holotype), lower Hamra Beds, Närs fyr 1, coast at När, southeast Gotland; 3 and 4, transverse sections, ×2, ×4, respectively; 5, longitudinal section, ×4. 6 and 7, OU 10672, Hamra Beds, Kättelviken 3, coast below road, 3·5 km N of Hoburgen, southern tip of Gotland; 6, transverse section, ×4; 7, longitudinal section, ×4. 8 and 9, RM Cn66049, Sundre Beds, Juves 3, western side of road at Juves, 2 km E of Hoburgen, southern tip of Gotland; 8, transverse section, ×4; 9, longitudinal section, ×4.



JELL and SUTHERLAND, *Entelophyllum*

species from the Upper Visby and lowermost Högklint Beds in the Vattenfallsprofilen 1, near the ferry harbour of Visby.

Distribution. Gotland: Sheinwoodian.

Diagnosis. Phaceloid, corallites 10–12 mm in diameter, closely spaced, increase parricidal; major septa number 20–23, straight, thickened in inner tabularium, withdrawn from the axis leaving a broad axial space; minor septa very short; tabularium broad, axial tabulae flat-topped or sagging, weakly developed axial trough; dissepimentarium irregularly narrow, in one to four vertical series.

Description. The holotype is of a subcylindrical corallite 11 mm in diameter. Other specimens are fragments of large phaceloid coralla consisting of closely packed cylindrical corallites 10–12 mm in diameter, some are crushed due to later compaction. Calices are moderately deep with inverted conical sides and a wide flat axial floor. Increase is parricidal (Pl. 9, figs 8 and 9) with up to 12 offsets originating in the one calice. The neo-wall is initiated in the tabularium and it appears as though part of the tabularium of the parent is continuous with that of the offset.

In transverse section major septa are prominent, thickened in the outer tabularium and taper axially and some peripherally (Pl. 9, fig. 4). They are 0·6–0·8 the radius of the corallite in length and number 20–23 in mature corallites. In some the cardinal septum is shortened and may lie in a shallow fossula. The counter and counterlateral septa may be slightly extended. In the dissepimentarium major septa become irregular in places with the stereome that thickened them in the tabularium continuous onto the dissepiments. They may be thickened into triangular bases at the wall. Minor septa are short, 0·2–0·3 the length of the major, much thinner than the major, and in places interrupted by interseptal dissepiments.

The tabularium is 0·65–0·75 the diameter of the corallite in width, composed of tabulae that are flat or axially sagged with the edges downturned initially, then turned outward to meet the dissepimentarium nearly horizontally (Pl. 9, fig. 7). There are 8–15 tabulae in 5 mm vertically. Dissepiments are irregular in size and vary from small globose forms to more elongate ones, arranged in one to four rows (Pl. 9, fig. 8), three and rarely four in the holotype (Pl. 9, fig. 2).

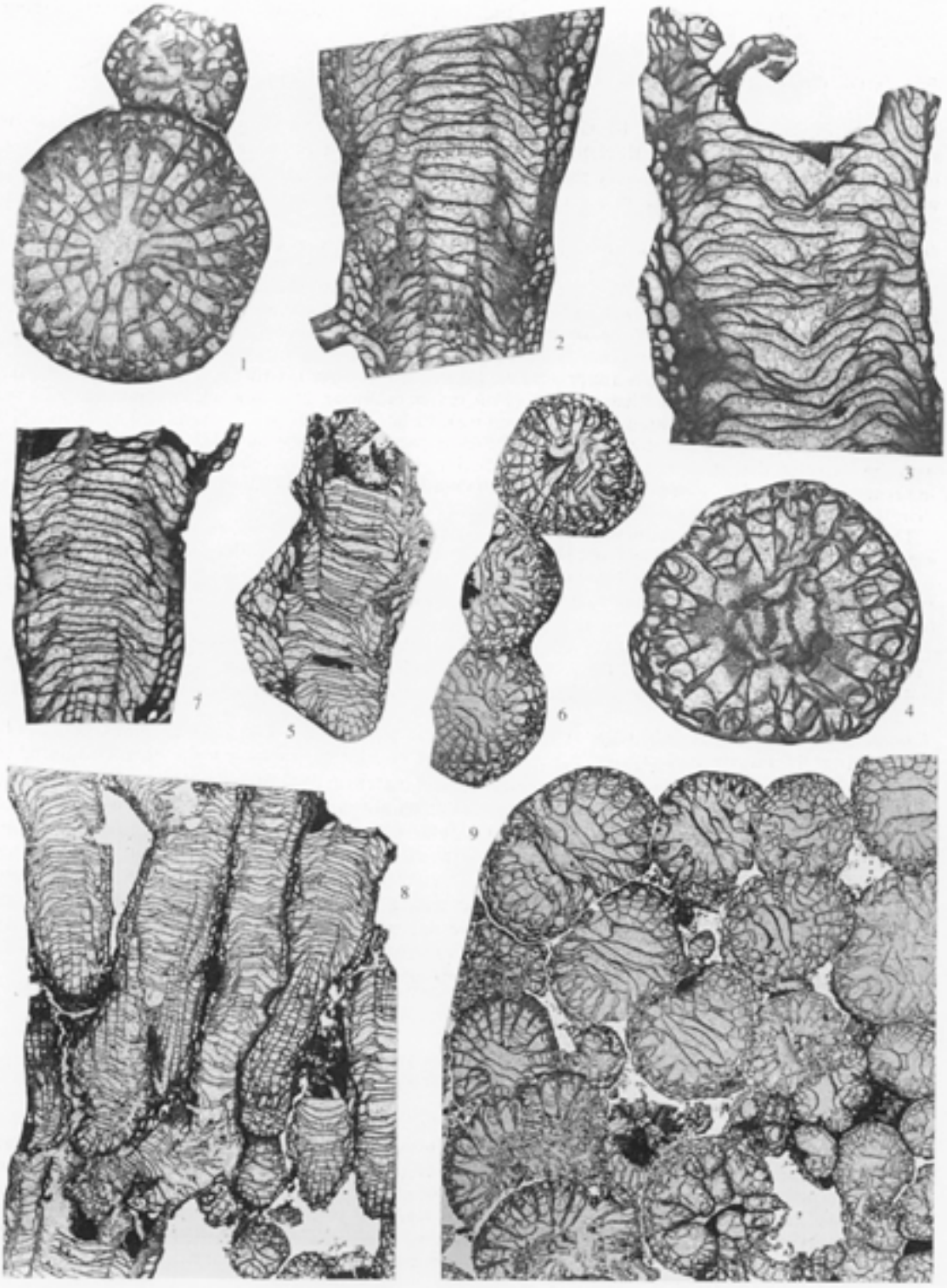
Septa are recrystallized in the holotype but appear to be monacanthate, with the monacanths sloping in and upward toward the axis at about 45° peripherally, and steepening axially to 55°–60°. There are approximately 3 trabeculae per 0·4 mm in vertical section.

Remarks. We consider *E.? visbyense* to belong to some genus other than *Entelophyllum* because of the striking differences in character in both transverse and longitudinal section when compared to *E. articulatum*. The tabularium is not distinctly divided into two series with a well developed periaxial trough, and the septa are much more thickened and more typically withdrawn from the axis. The material at hand, however, is not considered adequate as a basis for defining a new genus.

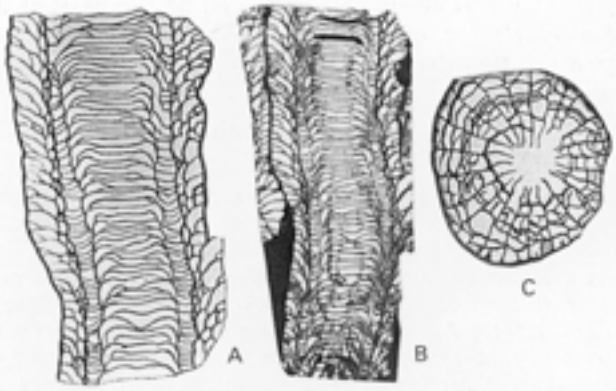
The holotypes of *E.? visbyense* and *E.? anschutzi*, both from the same locality and described by Wedekind (1927), show only minor differences. In transverse section *E.? anschutzi* has thinner major septa that are more withdrawn from the axis, leaving a broader axial space, and in longitudinal section the tabularium sags compared with more flat tabulae in *E.? visbyense*. Sections through many corallites of the one corallum show similar variations (Pl. 9, figs 8 and 9). For these reasons, we are treating them as conspecific as did Neuman and Hanken (1979, p. 89).

EXPLANATION OF PLATE 9

Figs 1–9. *Entelophyllum? visbyense* Wedekind, Högklint Beds, Gutevägen 3, 1·54 km SW of Visby Cathedral, Gotland. 1 and 2, RM Cn54873 (holotype), original of Wedekind (1927, pl. 7, fig. 10); 1, transverse section, ×4; 2, longitudinal section, ×4. 3 and 4, from holotype of *E. anschutzi* Wedekind, (1927, pl. 7, figs 7 and 8); 3, SMF Wdkd. 10308, longitudinal section, ×4; 4, SM Wdkd. 10309, transverse section, ×4. 5 and 6, RM Cn66196; 5, longitudinal section, ×2; 6, transverse section, ×2. 7–9, RM Cn66197; 7 and 8, longitudinal sections, ×4, ×2, respectively; 9, transverse section showing parricidal increase, ×2.



JELL and SUTHERLAND, *Entelophyllum*?



TEXT-FIG. 8. *Entelophyllum*? *dalecarlicum* (Lindström), RM Cn57149 (holotype), Styggforsen Limestone, Styggforsen, Siljan district, Dalecarlia, central Sweden. A, reproduction of Lindström (1880, pl. 2, fig. 8), ×3. B, thin section from which Lindström's figure was drawn, showing accuracy of the drawing, ×2. C, reproduction of Lindström (1880, pl. 1, fig. 22), ×3.

Entelophyllum? *dalecarlicum* (Lindström, 1880)

Text-fig. 8A–C

1880 *Cyathophyllum dalecarlicum* Lindström, p. 34, pl. 1, fig. 22; pl. 2, fig. 8.

Holotype. Lindström, 1880, pl. 2, fig. 8; RM Cn 57149, Styggforsen Limestone, Styggforsen, Siljan district, Dalecarlia, central Sweden; Telychian.

Material studied. The description is based on Lindström's (1880, pl. 1, fig. 22; pl. 2, fig. 8) illustrations of the type specimen and on the longitudinal thin section of the holotype (RM Cn57149); his transverse section is presumed lost. Dr B. Neuman (pers. comm.) has searched for more material in the type area without success.

Distribution. Central Sweden; Telychian.

Diagnosis. Fasiculate, possibly peripheral nonparricidal increase; corallites slender, less than 10 mm in diameter containing 22–23 major septa; prominent axial space; minor septa weakly developed; tabularium regularly arranged broad, flat-topped axial series and narrow, closely spaced, sagging periaxial series of tabellae; dissepiments elongate in one or two rows.

Description. The specimen from which the slide was cut is not available. The longitudinal section has the central corallite abutted on one side by the dissepimentarium of another and on the other side by the apparent margin of an offset (text-fig. 8B). This presumed offset shows the early stage of what is possibly a narrow row of flat tabellae beside the neo-wall, which is inserted on top of a dissepiment and which is not continuous with that of the parent. If these relations are correctly interpreted then the budding is peripheral nonparricidal. Immediately before the budding the corallite is 10 mm wide and at the top of the section it is 9·5 mm.

The transverse section is not available. Lindström (1880, pl. 1, fig. 22) shows 22 or 23 major septa that are smooth, straight and extend 0·8 the corallite radius to the axis where their axial tips may be turned aside, leaving an axial space. Minor septa are poorly developed as segments on the interseptal dissepiments between some major septa.

In longitudinal section the tabularium is very regularly developed and is well differentiated from the dissepimentarium. It shows axial series of broad flat tabellae with strongly downturned peripheral parts that are based on the tabellae below. There are 14–18 in 5 mm vertically. Between this zone and the dissepimentarium is a narrow periaxial series of slightly concave upward tabellae (17–19 per 5 mm) forming an exceptionally regular periaxial trough (Text-fig. 8B). Dissepiments are very irregular in size and shape, some twice as broad as others and varying from globose to elongate. The tabularia are 0·6–0·7 the corallite diameters and the axial series is 0·8 the diameter of the tabularium.

Remarks. E.? dalecarlicum cannot be adequately evaluated on the basis of the single longitudinal section of the holotype available for study. The possible occurrence of nonparricidal budding indicates a generic assignment other than *Entelophyllum*.

Genus PETROZIUM Smith, 1930

1930 *Petrozium* Smith, p. 307.

Type species. By original designation, *P. dewari* Smith, 1930, from the Pentamerus Beds of Shropshire, England; early Telychian.

Diagnosis. Phaceloid, corallites slender, cylindrical; increase presumably peripheral, nonparricidal. Septa long, grouped at axis or slightly withdrawn, thin or slightly thickened, commonly zigzag but rarely carinate in dissepimentarium. Tabularium strongly domed, tabulae complete with central area flattened or sagged and with outturned edges, or commonly incomplete with outermost tabellae forming a distinct series producing a periaxial trough. Dissepimentarium relatively narrow, dissepiments small, interseptal.

Remarks. Smith (1930) introduced *Petrozium* for one species described from a limited number of specimens and no further material has become available (see discussion of *P. dewari*). The genus has been variously interpreted by subsequent revisors. In his description of the type species, Smith (1930, p. 308) recognized the similarity, in longitudinal section, of *Petrozium* to *Entelophyllum* but did not elaborate on how they were to be distinguished and some authors have considered them synonymous.

Smith (1930) described the increase as marginal nonparricidal but we have not been able to confirm this in the material still available. If this is correct, then it contrasts with the typical parricidal mode of increase in *Entelophyllum* and resembles *Donacophyllum* Dybowski, 1876, but lacks the lonsdaleoid dissepiments characteristic of the latter genus.

Kaljo (1958) and Fedorowski and Gorianov (1973) both recognized the similarity between *P. dewari* and *Donacophyllum losseni* Dybowski, 1874, from the Llandovery of Estonia. Kaljo referred the Estonian form to the genus *Petrozium*, and Fedorowski and Gorianov questionably included *P. dewari* in the synonymy of the Estonian species which they referred to *Entelophyllum*. The latter authors described six specimens of *P. losseni* from Eichwald's collection and noted that increase was peripheral nonparricidal. Apart from this, *P. losseni* resembles other species of *Entelophyllum* in which the major septa are thin, straight, and somewhat withdrawn from the axis leaving a conspicuous axial space such as that found in *E. fasciculatum*. In its early growth stages the septa may join at the axis as shown by Fedorowski and Gorianov (1973, fig. 6). The relatively narrow dissepimentarium and the incomplete development of the periaxial series of tabellae separate both *P. dewari* and *P. losseni* from *E. articulatum* but those features are found in varying degrees in other species of *Entelophyllum*.

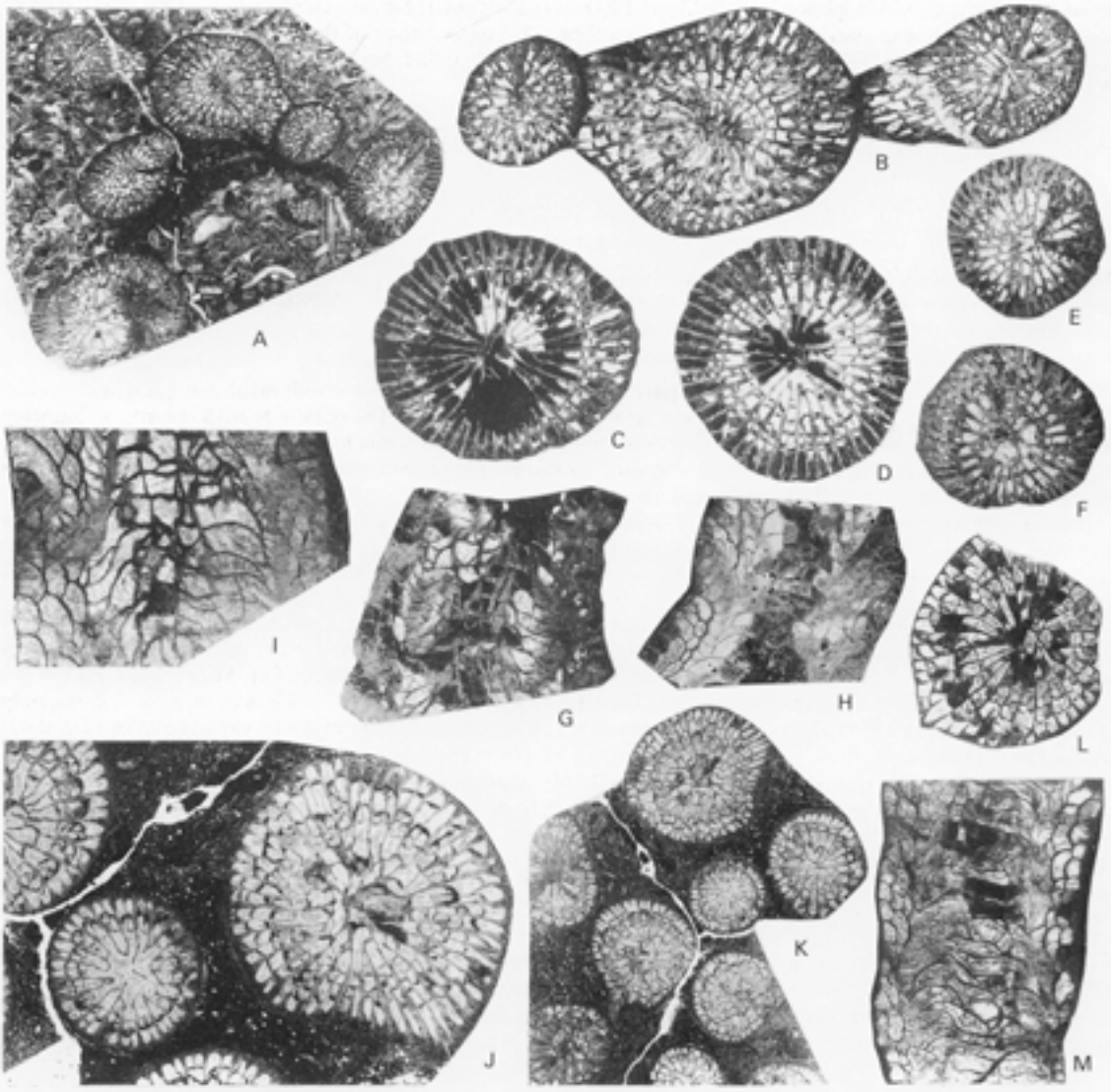
Smith (1930, p. 307) described the development of stereome between the axial ends of the longer major septa as forming with them an axial structure. Merriam (1972, 1973) considered the development of an incipient axial structure as a significant generic character of *Petrozium*. As seen in the Gotland species of *Entelophyllum* the withdrawal of the axial ends of the major septa from the axis is very variable within species as well as between species. Examination of the type material of *P. dewari* shows that the grouping of septa near the axis is common but the development of an incipient axial structure is rare.

Until the type species is better known *Petrozium* is maintained for those species similar to *Entelophyllum* but with nonparricidal increase, relatively narrow dissepimentarium, incomplete development of the periaxial series of tabellae, and lacking lonsdaleoid dissepiments.

Petrozium dewari Smith, 1930

Text-fig. 9A–M

v*1930 *Petrozium dewari* Smith, p. 307, pl. 26, figs 20–28.



TEXT-FIG. 9. *Petrozium dewari* Smith. A–F, Pentamerus Beds, right bank Morrells Wood Brook, 275 m NNE of Morrells Wood Farm, 1·6 km NNW of Buildwas, Shropshire; A and B, GSM PF4618 (holotype); transverse sections; ×2, ×4, respectively; C, GSM PF4622*a*, transverse section in upper part of corallite, ×4; D, GSM PF4622*b*, transverse section, ×4; E, GSM PF4622*d*, transverse section, ×4; F, GSM PF4622*e*, transverse section showing septa slightly thickened in early growth stage, ×4. G, GSM PF4619, longitudinal section, ×4. H, GSM PF4623, longitudinal section, ×4. I–M, Saugh Hill Group, Woodland Point, Girvan, Ayrshire; I–K, SM A15217; I, longitudinal section, ×4; J and K, transverse sections, ×4, ×2 respectively; L and M, SM A15215; L, transverse section, ×4; M, longitudinal section, ×4.

Holotype. Smith, 1930, pl. 26, fig. 22; GSM 48674 (thin section PF4618), Pentamerus Beds, Morrells Wood Brook, 1·6 km NNW of Buildwas, Shropshire, England; early Telychian.

Material studied. The holotype and most of Smith's (1930) material is from the *Calostylis* limestone, a thin 10–15 cm thick bed of limestone in the Pentamerus Beds, at the type locality (seven specimens; figured: GSM

PF4618 (holotype); GSM PF4619, PF4622*a–d*, PF4623 (paratypes)); Smith's collection from the upper part of the Hughley Shale in the north bank of the Severn River, 366 m southeast of the church, Buildwas, Shropshire (one specimen); Saugh Hill Group, Woodland Point, Girvan, Ayrshire, Scotland (two specimens; figured: SM A15215, 15217).

Distribution. England: Telychian; Scotland: Llandovery (?Rhuddanian).

Diagnosis. Dendroid, almost placeloid; corallite diameter typically 8–10 mm; most of the 28–30 major septa meet at the axis or join in groups just short of the axis; minor septa 0·4–0·6 the length of major; septa slightly thickened or lightly carinate in outer dissepimentarium; tabularium biserial, axial tabellae arched, periaxial series incompletely developed; dissepiments globose, irregular in size, in two or three vertical rows.

Description. The holotype is a thin upper part of a dendroid to phaceloid corallum showing eight corallites imbedded in a coarse bioclastic limestone so that no calices are exposed. The corallites are 8–10 mm in diameter and appear to be cylindrical. Adjacent corallites are separated by as much as 5 mm but in section they are touching in places suggesting they have lateral expansions that spread out to support the corallite against adjacent ones. The mode of increase is not evident.

The other specimens are all fragments of isolated cylindrical corallites. Some show slight lateral expansions of the corallite as though they were part of a phaceloid coralla.

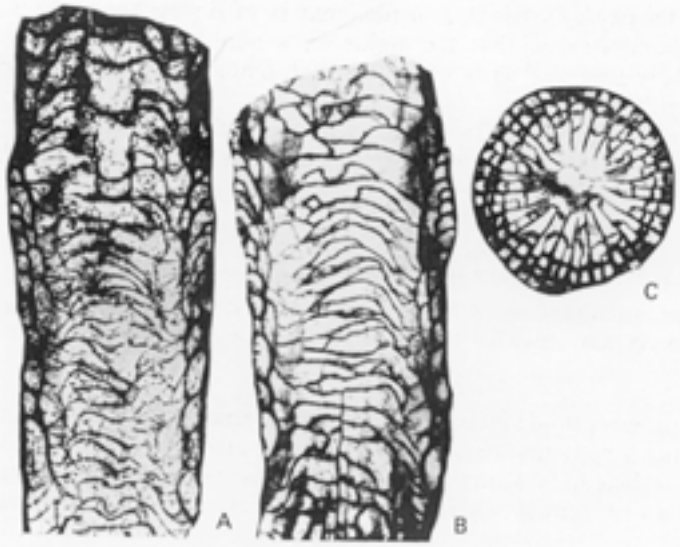
Septa are commonly thin, straight, radially arranged in two orders with 28–30 in each. Major septa extend well into the tabularium and may meet at the axis or join in groups of three or four just short of the axis (Text-fig. 9C, D). In the holotype, an axial plane is evident across which opposing septa join so that the corallite has a bilateral symmetry. Only in the largest corallite of the holotype, the axial ends of the septa are slightly thickened and in places confluent, forming a small open axial structure (Text-fig. 9B). Minor septa are 0·4–0·6 the length of the major with a few contraclined. In the dissepimentarium, both orders of septa are: commonly straight and thin; rarely straight, slightly thickened and noncarinate; or rarely thin, slightly zigzag with short carinae.

The tabularium and dissepimentarium are clearly differentiated with the former consisting of an axial and periaxial series of tabellae. Axial tabellae are domed with the central part flattened or depressed in some and their peripheral edges sharply downturned. A series of horizontal or slightly sagging tabellae, closely spaced with 20–26 per 5 mm vertically, span the space between the downturned peripheral edges of the axial tabellae and the dissepimentarium, forming a periaxial trough (Text-fig. 9H). The dissepimentarium is composed of irregular sized, globose dissepiments, horizontally based at the periphery and steeply declined axially, and arranged in two or three irregular rows with 8–10 in each row per 5 mm vertically.

Septa are composed of fine monacanths arranged in one series. Trabeculae are directed upwards at a small angle to the vertical at the periphery and flatten axially so that at the tabularium/dissepimentarium boundary they are within 20° of the horizontal and then towards the axis they steepen considerably. Thickenings of the septa and the short carinae are only the lengthening of fibres of the trabeculae.

Remarks. Description is based on the same material as described by Smith (1930), excluding specimen GSM 48721. We have twice visited the type locality without finding any additional material referable to this species. Also, we have not recognized this species in our collections from other upper Llandovery localities of Shropshire.

Smith (1930) included in this species specimen GSM 48721 (PF4529–30) from the type locality. It is a fragment of a much larger corallite (20 mm in diameter) and whether or not it is a corallite from a colony or a worn solitary form is not apparent. It seems unlikely that it is conspecific with the smaller cylindrical corallites. A fragment of a phaceloid corallum (Text-fig. 9I–K) and an isolated cylindrical corallite (Text-fig. 9L and M) from the Saugh Hill Group, Woodland Point, Girvan, Ayrshire (SM A5215, A5217) are very similar to the Shropshire material. The Scottish material may be Rhuddanian in age and thus somewhat older than the type material. We have searched the Woodland Point sequence for additional material but without success. Several larger specimens are known from the same collection but whether solitary or from fasciculate coralla is not known and they are not included in the species at this time.



TEXT-FIG. 10. *Petrozium losseni* (Dybowski), EGM Co1282, Tamsalu Formation, Juuru Horizon, Suuremyiza (near Grossenkhof), Isle of Hiiumaa, Estonia. A and B, longitudinal sections, ×4. C, transverse section, ×4.

Petrozium losseni (Dybowski, 1874)

Text-fig. 10A–C

1874 *Donacophyllum lossenii* Dybowski, p. 464, pl. 4, fig. 6, 6*a*, *b*.
1958 *Petrozium losseni* (Dybowski); Kaljo, p. 114, pl. 4, figs 11–17.
1973 *Entelophyllum losseni* (Dybowski); Fedorowski and Gorianov, 1973, p. 20, pl. 4, fig. 5*a*–*c*; text-figs 6 and 7.

Holotype. Dybowski, 1874, pl. 4, fig. 6, 6*a*, *b*; EGM Co1282; Tamsalu Formation, Juuru Horizon, at Suuremyiza (near Grossenkhof), Isle of Hiiumaa, Estonia; Rhuddanian.

Material studied. This species is interpreted from published data and from photographs of the holotype kindly supplied by Dr D. Kaljo (figured: EGM Co1281, holotype). It is known from several localities on Hiiumaa Island. Kaljo (1970) listed it as only occurring in the Juuru Horizon (Rhuddanian) in Estonia. Two specimens in the Eichwald Collection are labelled as from Lode on Saaremaa Island and thus from the Kuressaare Horizon (Ludfordian) but Fedorowski and Gorianov (1973, p. 23) suggest this is an error. The same authors list another of Eichwald's specimens from Viljandi in southern Estonia and suggest it is probably from an erratic boulder.

Distribution. Estonia: Rhuddanian.

Diagnosis. Phaceloid, peripheral nonparricidal increase; corallite diameters 6–7 mm, maximum 9·5 mm; major septa number 23–26, straight, smooth, withdrawn from the axis leaving axial space or extending to or almost to axis, several adjacent septa may be grouped just short of axis; minor septa half length of major, not contratigent. Tabularium broad, biserial with narrow periaxial trough; dissepiments small, globose in one to three rows.

Remarks. *P. losseni* is very similar to *P. dewari*, and Fedorowski and Gorianov (1973) suggested that the two might be synonymous. *P. losseni* is here distinguished from *P. dewari* by the thinner septa, especially in the tabularium, absence of any septal carination, thicker corallite walls, and typically a narrower dissepimentarium. Tabularia of both species are very similar but there appears to be more complete tabellae and less complete development of the periaxial series of tabellae in *P. losseni*. The Estonian *P. losseni* is from slightly older strata (Rhuddanian) than the type material of

P. dewari of England (early Telychian). *P. losseni* may be of similar age to the Scottish form referred to *P. dewari* and resembles it in that the major septa may be withdrawn from the axis and are similarly grouped. However, the septa of the Scottish material are thicker and more like the type material of *P. dewari*.

P. losseni differs from the Llandovery *E. dendroides* from Gotland by its phaceloid habit, withdrawal of septa from the axis, more complete and less densely spaced tabulae, and narrower dissepimentarium.

Genus PROHEXAGONARIA Merriam, 1973

1973 *Entelophylloides* (*Prohexagonaria*) Merriam, p. 50.

Type species. By original designation, *Entelophylloides* (*Prohexagonaria*) *occidentalis* Merriam, 1973, from bottom of unit 3, Roberts Mountains Formation, northwest side Roberts Creek Mountain, Nevada, U.S.A.; ?Prídolí Series.

Diagnosis. Cerioid or subcerioid; increase peripheral nonparricidal; septa thin with inconspicuous asymmetrical carinae, long, some reaching the axis; tabulae closely spaced, complete or typically incomplete, axially arched and outturned at their periphery; dissepiments globose, small, increasing in axial inclination away from the periphery, typically interseptal, rarely lonsdaleoid.

Remarks. Merriam (1973) originally defined *Prohexagonaria* as a subgenus of *Entelophylloides* Rukhin, 1938 (type species *Columnaria inequalis* Hall, 1852), but that genus is a ptenophyllid coral and possibly synonymous with *Xystriphyllum* Hill, 1939. *Prohexagonaria* is generally similar to *Entelophyllum* in internal character but is cerioid and has nonparricidal increase. In the latter feature it shows resemblance to the phaceloid *Donacophyllum* but in *Prohexagonaria* lonsdaleoid dissepiments are rare except in the extended corners of some corallites. Until the modes of increase in all of the cerioid forms with typical entelophylloid internal structure are better known, *Prohexagonaria* is included in the Entelophyllidae.

Prohexagonaria may be congeneric with *Tenuiphyllum* Soshkina, 1937 (type species *T. ornatum* Soshkina, 1937, from the Elkinskii Horizon, right bank of River Vya, near Elkino, eastern slopes of the Urals, USSR; see Ivanovskii and Shurygina 1975, p. 23). Pedder (1976, p. 290) indicates that the two genera may not be synonymous as *T. ornatum* shows significantly expanded septal bases.

Prohexagonaria favia sp. nov.

Plate 10, figs 1–4

v1929 ?*Xylodes* sp. Smith and Tremberth, p. 366, pl. 8, fig. 1.
v1973 *Entelophylloides* (*Prohexagonaria*) sp., Merriam, pl. 9, fig. 5.

Holotype. Original of Smith and Tremberth, 1929, pl. 8, fig. 1; RM Cn57005, two parts of specimen plus three thin sections; two parts of the holotype plus two thin sections are in the BMNH collection (R26168–26171); from upper Visby Beds, Norderstrand, Visby, Gotland; early Sheinwoodian.

Material. The holotype is the only known specimen.

Distribution. Gotland: early Sheinwoodian.

Diagnosis. Cerioid, increase peripheral nonparricidal; corallites 10–15 mm in diameter; major septa number 21–25, long, extending to or almost to axis, only rarely confluent, commonly interrupted at periphery; minor septa weakly developed, discontinuous in places; tabularium weakly biserial with incomplete periaxial trough; dissepiments irregular in shape and size.

Description. The holotype is a fragment of a cerioid corallum and measures 15 × 10 cm in cross section and 5 cm high. Corallites are five- to six-sided and measure 10–15 mm in diameter. Offsets common along

boundaries between corallites especially on corners between three adjacent corallites (Pl. 10, fig. 2) so that it is difficult to determine from which corallite they have arisen. In longitudinal view they appear to arise from the extreme outer edge of the dissepimentarium. Increase is nonparricidal.

Septa are long, thin, radially arranged in two orders. Major septa number 22–25 and extend right to or almost to the axis (Pl. 10, fig. 2). In a few cases one and even two major septa project into axial area further than the others. Major septa thin slightly towards periphery and in extended corners before budding they may be incomplete resting on larger dissepiments. Minor septa may be thin and complete, 0·3–0·4 the length of the major septa, but more commonly they are incomplete and represented as short segments based on herringbone dissepiments and more strongly developed in inner dissepimentarium than in outer parts. The septa are noncarinate. In small offsets some of the septa are discontinuous in the dissepimentarium.

Tabularium is 0·6–0·7 diameter of corallite in width and is well marked from the dissepimentarium. It consists of small globose tabellae arranged in a domed or flattened domed axial series 0·7 diameter of tabularium, and flatter and smaller tabellae forming a periaxial series abutting dissepimentarium (Pl. 10, fig. 4). Periaxial series does not form a continuous periaxial trough. There are up to 12 tabellae in both series in 5 mm vertically. Dissepimentarium is composed of irregular sized dissepiments varying from small globose, less than 0·5 mm across, to elongated moderately inclined up to 3 mm in length spanning the complete dissepimentarium.

Septa are composed of one series of fine trabeculae (5–6 in 1 mm in median longitudinal section) that are inclined upwards and inwards in the dissepimentarium and steepening to near vertical in the tabularium.

Remarks. This species is not similar to any known European entelophylloid ceroid coral. It is similar to the type species of the genus, which is from considerably younger strata in western North America, differing only in that *P. favia* has noncarinate septa and its tabularium is considerably wider.

Prohexagonaria gotlandica sp. nov.

Plate 10, figs 5–8

Holotype. RM Cn66198, Hamra Beds, Storburg 1, Hoburgen, southern tip of Gotland; late Ludfordian.

Material. Only the holotype is known.

Distribution. Gotland: late Ludfordian.

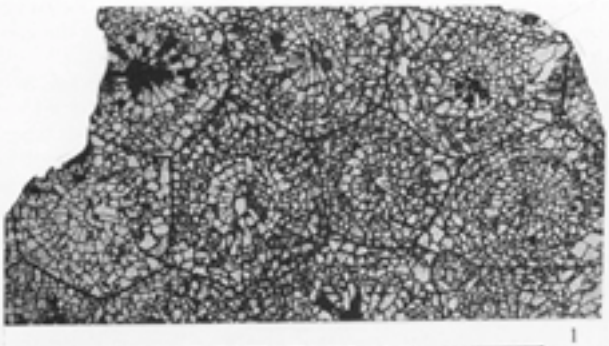
Diagnosis. Cerioid, increase peripheral nonparricidal; corallites 8–12 mm diameter; major septa number 20–25, extending almost to axis, thickened in the inner dissepimentarium, zigzag and carinate in outer dissepimentarium; minor septa well developed, carinate; tabularium biserial with distinct periaxial trough; dissepiments globose, irregularly arranged with outer series horizontally based and inner ones steeply inclined axially.

Description. Holotype is a fragment (8–10 cm in section and up to 5 cm in height) of a larger corallum. Corallites are five-to six-sided and measure 8–12 mm in diameter. Offsets arise in the expanded corners of the corallites (Pl. 10, fig. 6) and quickly expand so that the corallum resumes a regular cerioid form. Twenty calices are preserved and from these and the sections, all increase appears to be peripheral nonparricidal.

EXPLANATION OF PLATE 10

Figs 1–4. *Prohexagonaria favia* sp. nov. RM Cn57005 (holotype), upper Visby Beds, Nordenstrand, Visby, Gotland. 1 and 2, transverse sections, ×2, ×4, respectively. 3 and 4, longitudinal sections, ×2, ×4, respectively.

Figs 5–8. *Prohexagonaria gotlandica* sp. nov. RM Cn66198 (holotype), Hamra Beds, Storburg 1, Hoburgen, southern tip of Gotland. 5 and 6, transverse sections, ×2, ×4, respectively. 7 and 8, longitudinal sections, ×2, ×4, respectively.



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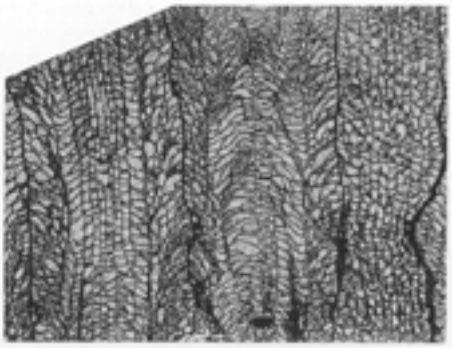

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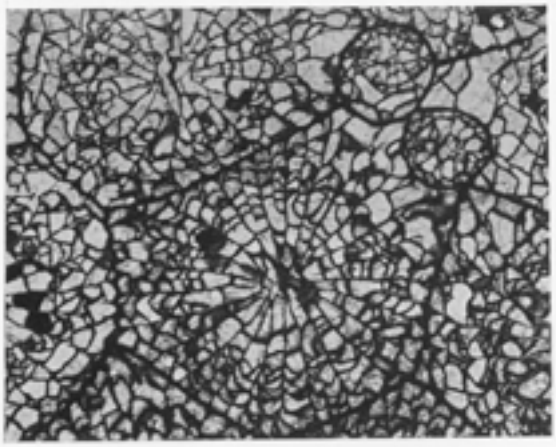

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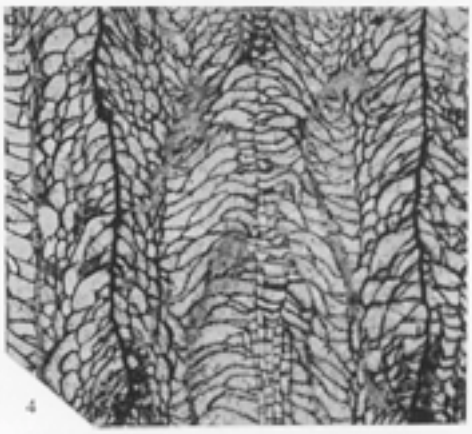

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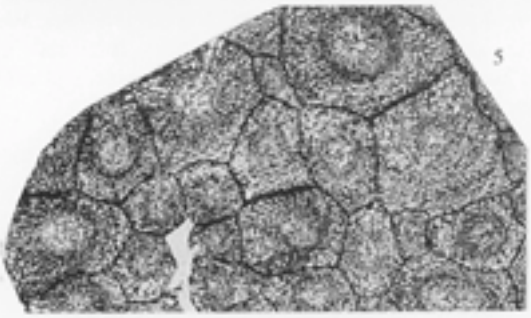

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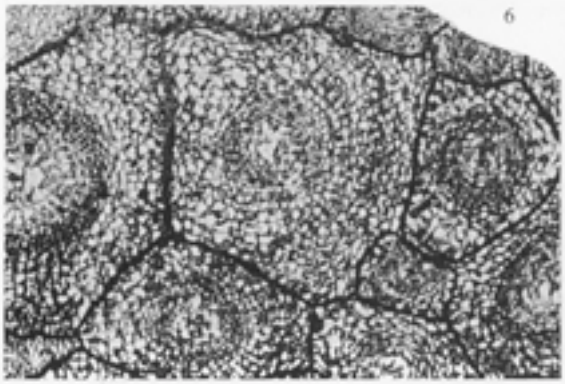

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8

JELL and SUTHERLAND, *Prohexagonaria*

Major septa number 20–25 with one corallite having 30. They are slightly thickened in the inner dissepimentarium and thin in the tabularium where they are straight to flexuose and extend almost to the axis, leaving a narrow axial space (Pl. 10, fig. 6). Minor septa are slightly thinner than the major, 0·7–0·8 the length of major, and project into tabularium a short distance. All septa are zigzag in outer dissepimentarium and may carry short carinae. Carination varies from absent to light in outer dissepimentarium, light to heavy in middle dissepimentarium, and light on thickened parts in the inner dissepimentarium. Only in extended corners where offsets are forming do septa become discontinuous.

The longitudinal section is oblique but locally shows a typical entelophylloid tabularium half the radius of the corallite (Pl. 10, fig. 8). Axial series consists of flattened tabellae strongly downturned at their margins; the downturned edges may flatten out to meet inner dissepimentarium horizontally or they are surrounded by a series of flat to sagging tabellae. A periaxial trough is well-developed. Dissepiments are globose, varying from 0·5–1·0 mm across, not arranged in regular vertical rows.

Remarks. This species differs from *P. favia* in having distinctly smaller corallites, better developed septa that are commonly carinate, and a narrower tabularium with a well developed periaxial trough.

Family KYPHOPHYLLIDAE Wedekind, 1927
Genus DONACOPHYLLUM Dybowski, 1874

1874 *Donacophyllum* Dybowski, p. 460.
1927 *Kyphophyllum* Wedekind, p. 19.

Type species. Chosen by subsequent designation of Wedekind, 1927, p. 34, *Donacophyllum schrenkii* Dybowski, 1874, from Raikküla Horizon of Estonia; Aeronian, middle Llandovery.

Diagnosis. Phaceloid, typically with nonparricidal peripheral increase; periodic rejuvenescence of corallites, reflecting expansions and subsequent contractions of dissepimentarium; major septa long and thin, a little withdrawn from axis, one may be longer; tabularium wide, domed, commonly with depressed axial area and marginal periaxial trough; dissepiments commonly lonsdaleoid.

Remarks. We follow Hill (1981) in placing *Kyphophyllum* in the synonomy of *Donacophyllum*. We have not made a comprehensive study of these genera. Gotland species here included in *Donacophyllum* are close to *Entelophyllum* in septal and tabularial characters but increase is lateral nonparricidal and lonsdaleoid dissepiments are much better developed.

Donacophyllum neumani sp. nov.

Plate 11, figs 1–8

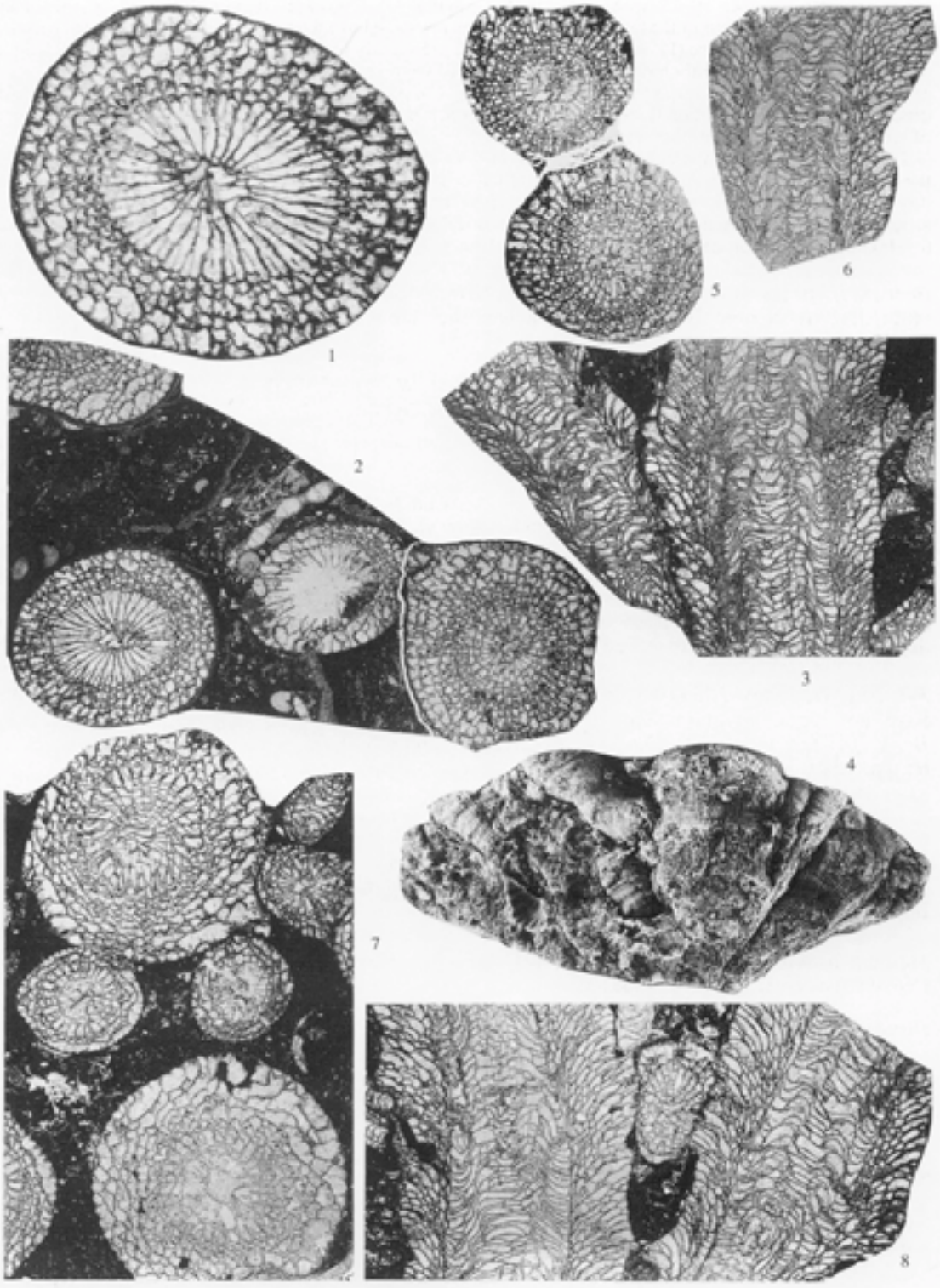
Holotype. RM Cn66199, from a limestone of the Slite Beds, towards top of cliff section of Lerberget 1, Stora Karlsö, Gotland; late Sheinwoodian or early Homerian.

Material studied. This species is known only from the type locality (five specimens; figured: RM Cn66199 (holotype), Cn66200, Cn66201).

Distribution. Gotland: late Sheinwoodian or early Homerian.

EXPLANATION OF PLATE 11

Figs 1–8. *Donacophyllum neumani* sp. nov., Slite Beds, Lerberget 1, south of lighthouse, western shore of Stora Karlsö, Gotland. 1–4, RM Cn66199 (holotype); 1 and 2, transverse sections, ×4, ×2 respectively; 3, longitudinal section, ×2; 4, lateral view of corallum, ×1. 5 and 6, RM Cn66200; 5, transverse section, ×2; 6, longitudinal section ×2. 7 and 8, RM Cn66201; 7, transverse section, ×2; 8, longitudinal section, ×2.



JELL and SUTHERLAND, *Donacophyllum*

Diagnosis. Fasciculate, flat, laterally flaring coralla; increase lateral nonparricidal; corallites up to 20 mm in diameter. Major septa 25–31, long, generally straight, smooth in tabularium, extending to within 1 mm of axis; slightly thickened in outer tabularium and inner dissepimentarium; may be carinate in dissepimentarium, interrupted by lonsdaleoid dissepiments in outer dissepimentarium; minor septa absent to weakly developed. Tabularium half diameter of corallite, biserial with well developed periaxial trough, axial part of domed tabularial floor sagged. Dissepiments medium to large sized, highly irregular, not in regular vertical rows with larger lonsdaleoid dissepiments at periphery.

Description. Holotype is a flat laterally flaring corallum 100 mm in diameter and 70 mm high. Corallites are ceratoid up to 20 mm in diameter and 20–50 mm in height. Increase is lateral, nonparricidal with offsets arising from extreme peripheral rim of the calice (Pl. 11, fig. 3). Offsets turn outwards soon after initiation and diverge up to 30° from parent (Pl. 11, fig. 4). No lateral expansions between corallites have been observed. Other specimens from type locality show same corallum form and corallite shape and size.

Major septa number 25–31, are moderately straight and smooth in tabularium, and extend to within 1 mm of the axis. In a few corallites, a single septum extends into axial space and in some, two or three adjacent septa are confluent giving small groupings of septal ends about the axial space. Some show a slight thickening in outer tabularium and/or inner dissepimentarium. Septa are commonly discontinuous in outer dissepimentarium where they are interrupted by irregular lonsdaleoid dissepiments. They may become zigzag and carry short carinae, especially along their peripheral parts. Minor septa mostly poorly developed, much thinner and more irregular than adjacent major septa and commonly lacking from parts of some corallites. They project only slightly into tabularium. In young, small corallites septa of both orders are smooth, straight and interrupted peripherally by large dissepiments.

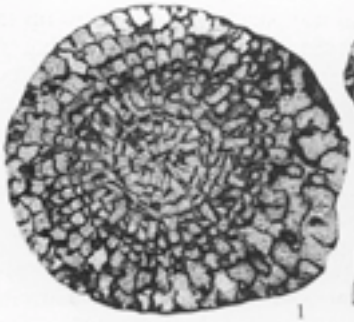
Wide tabularium, 0·4–0·5 corallite diameter in width, is distinctly separate from dissepimentarium. It is biserial with axial tabulae centrally domed but with an axial depression, downturned steeply at margin of this central area and then flattening out or even concave peripherally to give a prominent periaxial trough. Central tabellae are flat or slightly concave upwards and number 8–10 in 5 mm vertically. They are surrounded by more globose tabellae that have steeply downturned outer edges that rest on the ones immediately below. Periaxial tabellae may span interval between domal part of tabularium and dissepimentarium. These are flat or concave upwards and number 10–12 for 5 mm vertically. Dissepiments are mostly elongated, adaxially inclined, variable in size, and not arranged in regular vertical series. Lonsdaleoid dissepiments common in peripheral parts.

Septa consist of one series of monacanthine trabeculae that are directed upwards and inwards across the dissepimentarium at approximately 45°. They tend to flatten to nearly horizontal in periaxial region of tabularium but steepen to within 30° of vertical in axial region. Fibers within trabeculae diverge at only a slight angle from axis so that fibers appear to parallel trabeculae, and boundaries and axes of individual trabeculae cannot be distinguished. Carinae are lateral extensions of the fibers of the trabeculae and, where present, are 0·2–0·5 mm apart, centre to centre.

Remarks. D. neumani is distinguished from *E. articulatum*, also from the Slite Beds, primarily by its lateral nonparricidal increase and flaring growth form of the corallum, and major development of lonsdaleoid dissepiments. It differs from *D. wallstenense* in the flaring growth form of the corallum and much larger size of the corallites.

EXPLANATION OF PLATE 12

Figs 1–11. *Donacophyllum wallstenense* sp. nov. 1–4, RM Cn10637, Slite Beds, Stora Karlsö, Gotland; 1, transverse section, ×4; 2, longitudinal section, ×4; 3 and 4, lateral view of corallite; 3, showing offset arising from expansion of corallite, ×4; 4, showing series of expansions, ×1. 5–8, RM Cn11963 (holotype), Slite Beds, Stumra stenbrott, Wallstena Parish, Gotland; 5 and 6, lateral view of corallum showing lateral nonparricidal increase, ×1, ×2, respectively; 7, longitudinal section, ×2; 8, transverse section, ×2. 9–11, Slite Beds, Stora Karlsö, Gotland; 9, RM Cn10643, showing lateral expansion, ×4; 10 and 11, RM Cn10635; 10, transverse section, ×4; 11, longitudinal section, ×4.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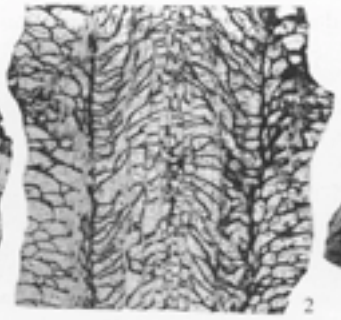
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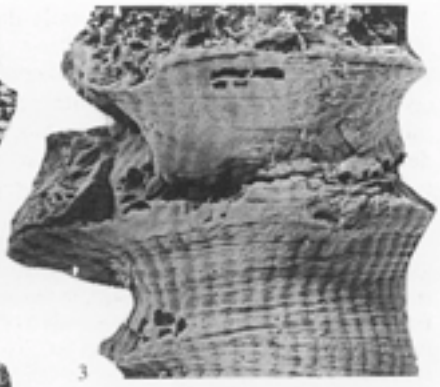
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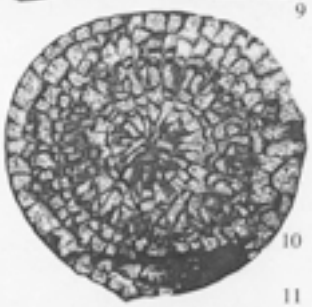
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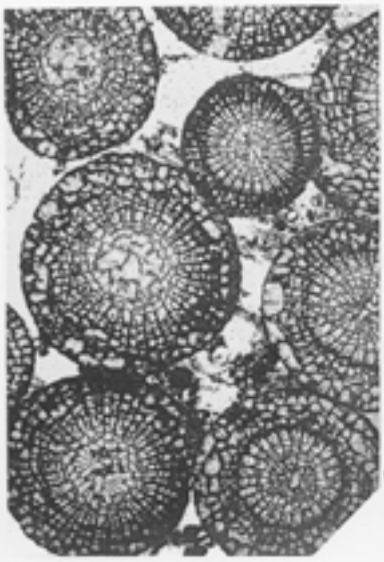

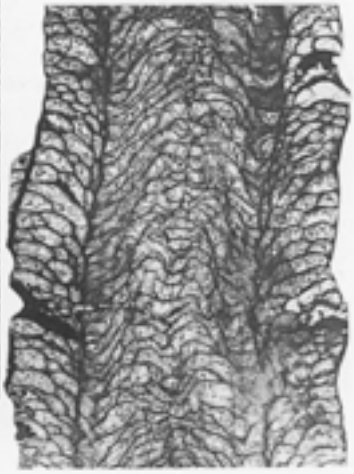

JELL and SUTHERLAND, *Donacophyllum*

Donacophyllum wallstenense sp. nov.

Plate 12, figs 1–11

Holotype. RM Cn11963, Slite Beds, Stumra stenbrott (stone quarry), Wallstena Parish, Gotland; Slite Group; late Sheinwoodian to early Homerian.

Material studied. Holotype (RM Cn11963) is the only specimen from Wallstena. Additional specimens referred to this species are also apparently from the Slite Group, from an unknown locality on the island of Stora Karlsö, Gotland (14 Specimens, RM Cn10635–10647; figured: RM Cn10635, Cn10637, Cn10643). Some of the specimens from Stora Karlsö show small remnants of gray marl and thus they may have come from the lithology of that type observed in the lower part of the Slite Group below the more greenish limestone from which were collected the type specimens of *D. neumani* sp. nov. An additional occurrence is questionable: 2 km southeast of ferry at Broa, Isle of Fårö, Gotland.

Distribution. Gotland: late Sheinwoodian to early Homerian.

Diagnosis. Phaceloid, tall coralla; increase lateral nonparricidal; corallites up to 15 mm in diameter. Major septa number 23–27, typically smooth leaving a small open axial area into which a single septum may extend; may be distinctly thickened in outer tabularium and/or in dissepimentarium; may be interrupted by lonsdaleoid dissepiments in outer dissepimentarium. Tabularium half diameter of corallite, biserial with a well developed periaxial trough. Dissepiments variable in size and distribution.

Description of holotype. Holotype is a fragment of a tall, phaceloid corallum up to 90 mm in height and 75 mm across, consisting of close to 20 corallites. Corallites are long, subcylindrical and closely packed. They show semi-regular expansions and contractions at a spacing of 10–15 mm apart (Pl. 12, fig. 5). Method of increase is lateral and nonparricidal, with the offset diverging at outer lip of expansion but becoming immediately parallel to parent (Pl. 12, fig. 6).

Major septa number 23–27 and they extend to within 1 mm of axis. Commonly one long septum bisects the narrow axial space (Pl. 12, fig. 8). Septa mostly smooth and straight throughout their length but a few are zigzag in dissepimentarium and a few are carinate. In some corallites they are rather markedly thickened in the outer tabularium and less commonly in dissepimentarium. Septa thickening is lacking in some corallites. Peripherally septa may be discontinuous or interrupted locally by lonsdaleoid dissepiments, especially at lateral expansions. Minor septa extend slightly into tabularium and tend to have a similar pattern in dissepimentarium to major septa or they may be more discontinuous.

Tabularium is half diameter of corallite and is distinctly delineated from dissepimentarium. Central highly domed area may or may not have a central depression. Tabulae steeply downturned periaxially to form a distinct periaxial trough (Pl. 12, fig. 7). Axial tabellae number about 8 in 5 mm vertically. Axial part of domal area consists of flat or slightly depressed tabellae bordered by more globose plates whose peripheral edges are steeply downturned. Flat to deeply sagging tabellae span space between central domal area and dissepimentarium. Dissepiments are variable in size and shape and range from globose to more elongate, peripherally lonsdaleoid dissepiments are common. Width of dissepimentarium varies markedly because of expansions and contractions of corallite.

Microstructure is similar to that described in *D. neumani.*

Description of other material. Specimens from the island of Stora Karlsö that are referred to this species consist of 14 broken individual corallites (Pl. 12, figs 1–4, 9–11). They are similar to the smaller corallites of holotype in number of septa, nature of biserial tabularium and variable dissepimentarium. They differ from holotype primarily in lack of pronounced thickening in outer tabularium in some corallites, in greater tendency of septa to extend to axis, and in more common occurrence in dissepimentarium of zigzag septa and carinae.

Remarks. D. wallstenense differs from *D. neumani* in the upright growth form of the corallum, the distinctly smaller size of the corallites, and the greater development of thickening at the outer tabularium and dissepimentarium.

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