AMURAL ARACHNOPHYLLID CORALS FROM THE SILURIAN OF THE NORTH ATLANTIC AREA

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ABSTRACT. Species previously assigned to *Arachnophyllum* and related genera from the Silurian of north-west Europe and North America are revised and their phylogeny and biogeography are discussed. Intraspecific variation, particularly in the English sample of *Arachnophyllum murchisoni*, is described in detail. The genera *Arachnophyllum* and *Prodarwinia* are redefined on the basis of redescriptions of their type species, *A. murchisoni* and *P. speciosa*. In addition the species *A. sinemurum*, *A. separatum*, *A. pentagonum*, *A. striatum*, *A. pygmaeum*, *P. striata*, *P. mamillaris*, and *P. distans* are accepted as senior synonyms and revised. A new species of *Prodarwinia* is described and comments are made on species of doubtful status. Species removed from this group are assigned to *Iowaphyllum*, ?*Zenophila*, *Radiastraea*, and ?*Mazaphyllum*.

ARACHNOPHYLLIDS are the only common amural rugose corals in the Llandovery to Ludlow of north-west Europe and eastern North America, amural Rugosa being defined as massive colonies in which no epitheca is present between constituent corallites (Scrutton 1988). They play an important role in the development of bioherms in some parts of this North Atlantic area, although much subordinate to the stromatoporoids, with which they can be confused on broken longitudinal surfaces, and tabulate corals. Many species have been erected, often under the generic name *Strombodes*, and the local use of different species names obscures the true distribution of lineages in space and time. The only substantial revision this century was by Lang and Smith (1927) for the English material. Thus, as McLean (1975, p. 54) remarked, revision of *Arachnophyllum* is long overdue.

My original intention was to revise north-west European species of the genus, including the type species, to clarify the septal structure in *A. murchisoni*, and to document the remarkable variability of the English material. This has led to re-establishing the genus *Darwinia* (as *Prodarwinia*), long regarded as a junior synonym of *Arachnophyllum*. The necessity for comparisons with North American species indicated that these would also require at least preliminary revision. I therefore comment on all species known to me in the North Atlantic area based on a re-examination of their type material as far as possible (Table 1). This has allowed initial clarification of the biostratigraphy and biogeography of those species I regard as valid (text-figs. 1 and 2).

The section on Systematic Palaeontology at the end of the paper provides the basis for the sections on Biostratigraphy, Biogeography, and Phylogeny, and Intraspecific Variation and Species Discrimination. Much of the work is based on museum material, but includes extensive new collections from the Much Wenlock Limestone of England (deposited in the British Museum (Natural History)), together with small amounts of material from Gotland, Estonia, and Canada.

BIOSTRATIGRAPHY, BIOGEOGRAPHY, AND PHYLOGENY OF NORTH ATLANTIC AMURAL ARACHNOPHYLLIDS

The earliest member of the *Arachnophyllum–Prodarwinia* group is of late Aeronian age (text-fig. 1). *P. speciosa* from the Rumba Formation of the Adavere Stage in Estonia is certainly of this age but may be little if any older than *P. distans*, from the Waco Member of eastern Kentucky. The Waco Member is referred to the Noland Formation of late Llandovery age and is itself regarded as C_{1-2}, possibly as young as C_3 in age (Rexroad and Kleffner, in press; Rexroad, pers. comm.). Further afield in North America, *P. mamillaris* and members of the *A. pentagonum*

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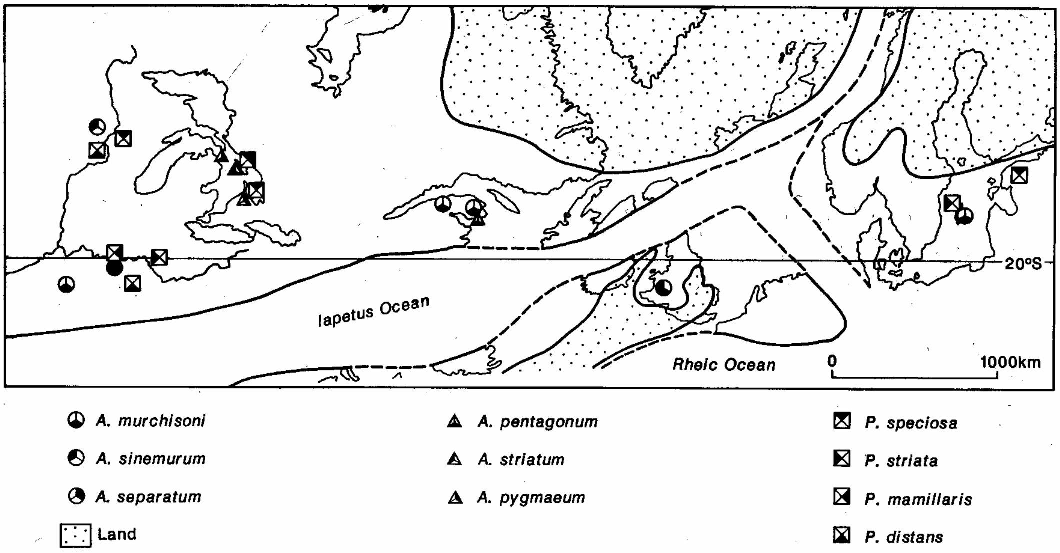
TABLE 1. Revision of North Atlantic species formerly or currently assigned to *Arachnophyllum* or related genera.

Species and author	Original genus	Assignment herein
alpenensis Rominger	*Strombodes*	*Iowaphyllum alpenensis*
approximatus Parks	*Strombodes*	?*Mazaphyllum approximatum*
diffluens Edwards and Haime	*Strombodes*	*Arachnophyllum murchisoni*
eximius Billings	*Strombodes*	?*Prodarwinia gigas*
gigas Owen	*Astrea?*	?*P. gigas*
gracile Nicholson and Hinde	*Astraeophyllum*	*A. pygmaeum*
granulosum Foerste	*Arach.* (*Strombodes*)	?*P. granulosa*
incertus Davis	*Strombodes*	*A. murchisoni*
infundibularia Owen	*Lamellopora*	indet.
kayi Merriam	*Arachnophyllum*	?*Zenophila kayi*
mamillaris Owen	*Astrea*	*P. mamillaris*
mamillare-distans Foerste	*Arachnophyllum*	*P. distans*
mamillare-wilmingtonensis Foerste	*Arachnophyllum*	*P. striata*
murchisoni Edwards and Haime	*Strombodes*	*A. murchisoni*
pentagonus Goldfuss	*Strombodes*	*A. pentagonum*
phillipsii d'Orbigny	*Actinocyathus*	*A. murchisoni*
pygmaeus Rominger	*Strombodes*	*A. pygmaeum*
quadrangularis Davis	*Strombodes*	*A. sinemurum*
richardsoni Salter	*Arachnophyllum*	*Radiastraea richardsoni*
separatus Ulrich	*Strombodes*	*A. separatum*
sinemurus Davis	*Strombodes*	*A. sinemurum*
speciosa Dybowski	*Darwinia*	*P. speciosa*
striata d'Orbigny	*Favastraea*	*A. striatum*
striata James	*Lyellia*	*P. striata*
typus M'Coy	*Arachnophyllum*	*A. murchisoni*
unicus Davis	*Strombodes*	*A. separatum*
verneuili Edwards and Haime	*Phillipsastrea*	?*P. verneuili*

group appear in the later Telychian, e.g. in the Fossil Hill Formation of Manitoulin Island, Ontario in which the coral biostromes are regarded as of C_3-C_4 age (Copper 1978). *P. striata* appears slightly later in the Dayton Formation of southern Ohio where it is no older than $C_{5\text{-}6}$ (Kleffner *via* Rexroad, pers. comm.).

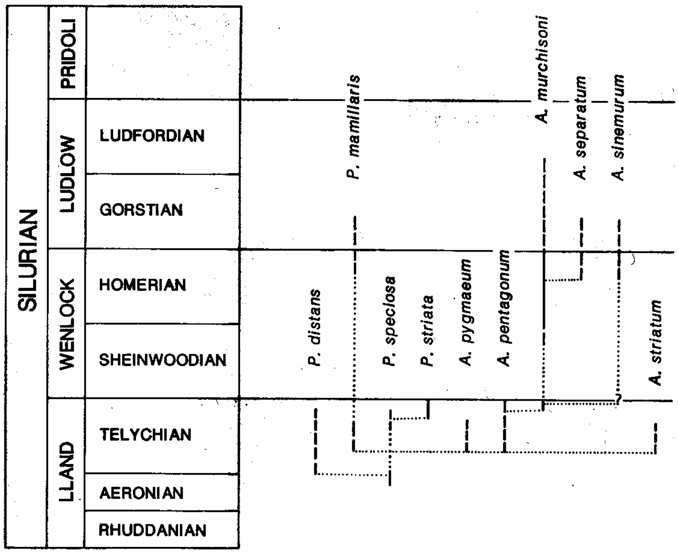
P. speciosa, *P. distans*, *P. mamillaris*, and *P. striata* could have shared a common ancestor or have had a more direct relationship. A possible phylogeny for this lineage is given in text-fig. 1. *P. speciosa* appears to have migrated from Europe to North America, where it appeared at least by mid-Telychian times (text-fig. 2). Current knowledge of species distributions suggests that *P. distans* is confined to North America (Kentucky and Iowa) and its appearance may predate this event. Even so, its evolution from *P. speciosa* seems most likely. *P. mamillaris* is also known only from North America and it may have evolved from either *P. speciosa*, to which it is similar in dimensions and calical form, or less likely from *P. distans*. *P. striata* is confined to more or less coeval levels in the late Telychian of both North America (Ohio) and Gotland. It is very similar to *P. speciosa*, from which it is distinguished by little more than dimensions and calical form, and undoubtedly arose from that species. Some Ontario material of *P. speciosa* shows transition to *P. striata* and the reverse is true in Ohio. If *P. striata* evolved in North America, then the species appears to have migrated back to Europe. Thus trans-Iapetus migration in both directions may have been possible in the Telychian.

The origin of the *A. pentagonum* group is more cryptic. The most likely evolutionary sequence is from smaller forms of *P. speciosa* through *A. pygmaeum* to *A. pentagonum* and *A. striatum*. All

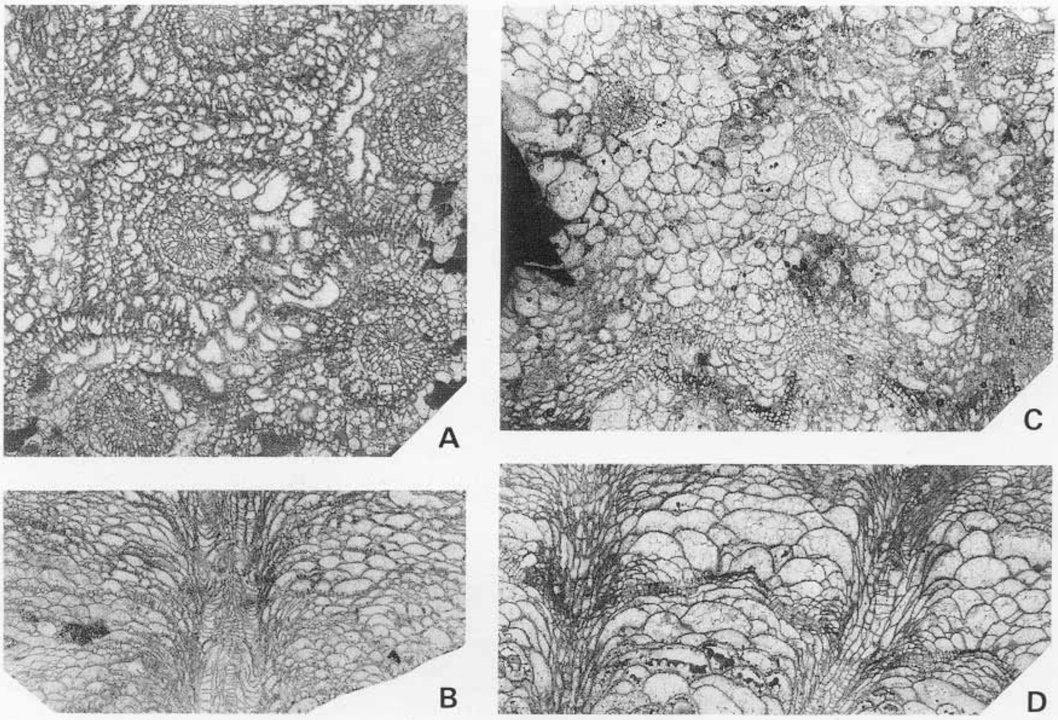


TEXT-FIG. 1. Distribution of species of *Arachnophyllum* and *Prodarwinia* in the North Atlantic area. Continental distributions in the early Silurian largely based on Cocks and Fortey (1982) and McKerrow (1988).

TEXT-FIG. 2. Stratigraphical distribution and tentative phylogeny of species of *Prodarwinia* and *Arachnophyllum*. In vertical ranges of species, dots indicate gaps in record and dashes indicate range within which records fall when precise age is uncertain.



are approximately of the same age. The *A. pentagonum* group again has a relatively local distribution in the Telychian of Michigan, Ontario, and Quebec and did not migrate across to Europe. However, *A. murchisoni*, which almost certainly evolved from *A. pentagonum*, also occurs in Quebec, where the two species coexisted in the late Llandovery (although carinae in the specimen of *A. murchisoni* available is slightly abnormal; text-fig. 3). *A. murchisoni* spread widely, reaching England in the latest Llandovery on the basis of a new record in the *Petalocrinus* Limestone.



TEXT-FIG. 3. A, B, *Arachnophyllum murchisoni*; Silurian, late Telychian, La Vieille Formation; Little Port Daniel River, Gaspé, Quebec (GSC 91554). A, cross-section; B, longitudinal section. C, D, *Arachnophyllum pentagonum*; same horizon; railway cut above Anse-à-la-Vieille, east of Port Daniel, Gaspé, Quebec (GSC 91555). C, cross-section; B, longitudinal section. All figs. ×2·5.

This seems to be a clear example of easterly trans-Iapetus migration (in terms of present geography). It is also recorded in the mid- and particularly late Wenlock of England and Gotland and the late Wenlock (?early Ludlow) Louisville Limestone (Rexroad *et al.* 1978; Shaver *et al.* 1985) of the Kentucky area. There is a single record apparently from the English early Wenlock (Woolhope Limestone) in an old collection (SM A5700) but this specimen is almost certainly wrongly labelled. I also have some doubt about a specimen of *A. sp.* cf. *A. sinemurum* recorded from Iowa where it would most likely be from the La Porte City Formation of C_5 to earliest Wenlock age (Witzke 1983 and pers. comm.); its preservation is identical to that of material from the Louisville Limestone. Otherwise, *A. sinemurum* and *A. separatum* are later descendants of *A. murchisoni* in the Louisville Limestone of the Kentucky area, whilst the rare specimens of *A. sinemurum* recorded from the English Wenlock may be independently evolved from *A. murchisoni* rather than the result of migration. The American and English material of *A. sinemurum* is indistinguishable and essentially coeval but the species is of questionable validity (see below). *P. mamillaris* also survived in the Kentucky area until the late Wenlock (?early Ludlow). *A. murchisoni* persisted into the mid-Ludlow Brownsport Formation in Tennessee (Shaver *et al.* 1985), which is the youngest record of *Arachnophyllum* currently known.

The species of *Prodarwinia* and *A. murchisoni* not only clearly demonstrate the possibility of trans-Iapetus migration in the Telychian, but suggest a reversal of direction during that time. Non-migration is more difficult to deal with. For the rarer, local species such as *P. distans*, they may have become extinct before a suitable distribution of environments could facilitate their wider distribution. In the cases of *P. mamillaris* and *A. pentagonum*, one possibility is that these species, most common in the North American dolomite suite (Berry and Boucot 1970), were facies restricted by water temperature and/or salinity. Cocks and Fortey (1982, p. 473 et seq.) suggest a latitudinal difference between England and the American continental interior in the late Llandovery and there is also a significant facies contrast between the American dolomitized pure carbonates and the marls or muddy limestones of England and Gotland. However, *P. mamillaris* coexists with *A. murchisoni* in the Louisville Limestone of late Wenlock (?early Ludlow) times, when it appears that little latitudinal or facies differences existed. Oliver (1977, pp. 95, 96) has shown that by Ludlow times there was 34–36% generic endemism in eastern North America, with the mid-west isolated from the northern Appalachians and Europe by an area of dolomite and clastic deposition. He also considered that migration was from the European area towards eastern North America in the late Silurian. The absence of *P. mamillaris* from the Anglo-Baltic area may reflect the early expression of either or both of these inhibitors to migration towards Europe along the shelf. There is no evidence of a land barrier in this area in the late Silurian.

Finally, the origin of the *Arachnophyllum–Prodarwinia* lineage as a whole is obscure. Iwanowskii (1965, p. 50, fig. 6) proposed descent from *Paleophyllum* (Stauriina) via *Entelophyllum*, whilst Hill (1981, p. 44) suggested derivation from the Streptelasmatina. Another possibility seems to be descent from the Upper Ordovician to Silurian kyphophyllid genus *Donacophyllum* (? = *Strombodes*), in which lonsdaleoid dissepiments had already evolved. This genus is unknown from North America but present in the Upper Ordovician of Estonia, and acceptance of this suggestion would accord with the origin of the lineage in Europe through *P. speciosa*. Of the Ketophyllina (*sensu* Hill 1981) the Kyphophyllidae and Endophyllidae appear to be quite closely related to the Arachnophyllidae and should be merged into the same suborder.

VARIATION AND SPECIES DISCRIMINATION IN *ARACHNOPHYLLUM* AND *PRODARWINIA* SPECIES

Of the species described here, by far the largest single sample is that of *A. murchisoni* from biohermal facies of the late Wenlock Much Wenlock Limestone from the Welsh Borderland. Its intraspecific variation is described together with comparative comments on other species.

Variation in A. murchisoni.

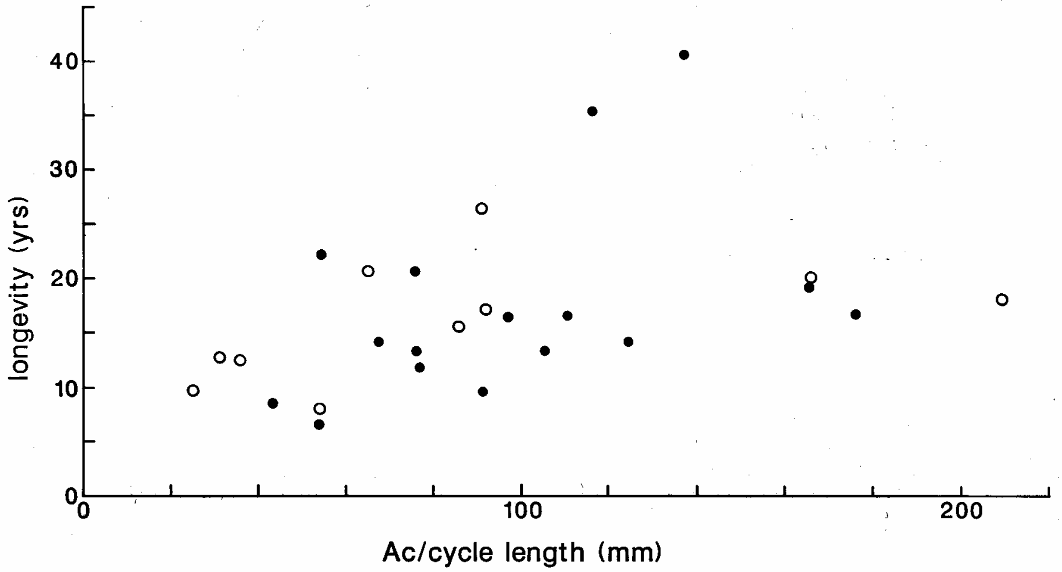
A. murchisoni, is a highly variable species, reflected to some extent by the fact that five different species names have been erected for its subsets. However, fundamental internal structure, such as the typical septal carination, the form of dissepiments and tabulae, microstructure and increase are all relatively uniform. In addition, the principal variable characters, viz. growth form of the calicular surface, corallite size, and the degree of septal development, all show more or less continuous variation within the population samples available, and support the recognition of a single species.

In the British Wenlock as a whole, colony mean tabularium diameter (dt) ranges from 1·85 to 4·63 mm, corallite area (Ac) from 0·70 to 6·33 cm^2, and major septa (n) from 15·3 to 22. Both Ac and n are loosely correlated with dt and the sample plots as a single but rather dispersed group (text-fig. 5). However, both dt and n are difficult to measure accurately, tabularium definition often being vague in cross-section and septa sometimes irregularly developed, with breakdown of a clear major and minor distinction, and more rarely very weak and only partial development (e.g. Pl. 3, fig. 3). The data are regarded as imprecise although the likely degree of error is not greater than 10%. The range of variation is similar for material from a single locality, the biohermal facies of the Farley Dingle road cutting, which has yielded the largest single collection in the present study (text-fig. 6).

Early species discrimination within *A. murchisoni* as defined here largely depended on external features (Pl. 1). The principal calicular surface form end members can conveniently be termed the *murchisoni* morph and the *diffluens* morph. The *murchisoni* morph has distinct intercorallite ridges (Pl. 1, figs. 1, 2, 4) whereas they are completely suppressed in the *diffluens* morph (Pl. 1, figs. 3 and 7). The latter has more or less prominent peritabularial swellings (mamelons bearing the tabularia). Variation between these extremes is expressed by the recognition of a *sub-diffluens* morph in which the swellings coexist with intercorallite walls that vary from very weak to absent across the calicular surface (Pl. 1, figs. 5 and 6). Both in the total sample and in the Farley Dingle sample all gradations exist from colony to colony between the two extremes. In both cases, the *diffluens* plus *sub-diffluens* morphs account for approximately 25% of the samples. These morphs tend to have smaller tabularium and corallite size and septal number ranges (1·85–2·96 mm, 1·1–2·55 cm^2, and 15·8–19, respectively), than the total sample, although it is covariate with the lower end of the *murchisoni* morph range (text-fig. 5). In terms of the cyclicity of dissepiment size in the dissepimentarium (dense bands; see below), the morphs are essentially covariate in the ranges of cycle thickness and number. Furthermore, there is no known disjunct distribution data for the morphs in the English Wenlock that suggest a sharply defined ecological significance for the differences in growth form. In the biohermal facies of Farley Dingle, all variants coexist, suggesting that any ecological control operated on a microenvironmental scale. The rare, isolated colonies in the bedded interbiohermal sediments of the Much Wenlock Limestone tend to be tabular masses of rather weak walled *murchisoni* morph type. Elsewhere, colonies from the argillaceous Mulde Marl on Gotland are broadly conical with domed calicular surfaces and *subdiffluens* morph corallites (Pl. 1, fig. 6); North American material is exclusively of *murchisoni* morph type (Pl. 3, figs. 7 and 8). Both cases may reflect regional genetic variation in local populations, with the *sub-diffluens* and *diffluens* morphs arising in the European area after migration of the species from North America.

In longitudinal section, there is a tendency for the intercorallite ridges to show signs of sharper definition in association with zones of smaller dissepiments which bear the septal crests. In some cases, the ridge is enhanced at these levels by short vertical series of very small, globose dissepiments (Pl. 3, figs. 2, 6, 8). These periodic levels of denser tissue in the skeleton are similar to the 'dense bands' described in Silurian favositid corals from the same beds by Scrutton and Powell (1981), and in other corals by many previous authors, and are interpreted in the same way as annual growth increments. Colonies with ragged margins show the death of peripheral tissue with sediment cover to occur always immediately above dense bands (e.g. Pl. 2, fig. 7). They are thus interpreted as autumn and/or winter growth with notching due to sediment movement by winter storms. The implication is thus that stronger intercorallite ridge development is associated with winter growth and probably with increased turbidity and local sediment settling rates. Ridges may be an adaptation to inhibit sediment encroachment across the colony surface, or may be associated with increased polypal activity to shift smothering sediment (see below). Furthermore, where *diffluens* morph colonies do show a tendency to intercorallite wall development, it occurs at the margins of the colony, sometimes with evidence of sediment interference with growth. The predominance of the *murchisoni* morph may in part reflect the winter period as the most common time of colony death due to sediment burial. However, there is also evidence of *diffluens* morph colonies that have suffered at least minor peripheral sediment encroachment but show no significant signs of intercorallite ridge formation. Ultimately, the full range of variation may have a genetic component that is not apparently subject to strong selection pressure. A parallel may be drawn with the pattern of ecomorph development in scleractinian coral species (Veron and Pichon 1976).

Considering size variation, correlation between mean corallite area and mean tabularium diameter is relatively weak (text-fig. 5B). Corallite area varies widely within some colonies and little in others, whilst tabularium diameter shows relatively little intracolonial variation. Corallite area of apparently mature corallites in the sample as a whole varies by an order of magnitude, as does the volume of corallite skeletal material added annually (from 200 mm^3 to 2021 mm^3). The relationship between colony longevity, rate of growth, and corallite area is also very weak (text-fig. 4). There is considerable scatter in the data but some tendency for enhanced survivorship to



TEXT-FIG. 4. Longevity (in years) plotted against mean corallite area (Ac) divided by mean length of annual growth cycle (result in mm) for colonies of *Arachnophyllum murchisoni* from the Much Wenlock Limestone Formation. Farley Dingle sample indicated by open circles.

be associated with larger corallite areas and slower growth rates. There is no evidence of differential survivorship between the calicular surface morphs.

A priori, a correlation between larger corallite area (and strong corallite walls) and the ability to survive periodic burial by a thin layer of sediment might be expected. Such a relationship has been demonstrated for some living scleractinians (Marshall and Orr 1931) and confirmed by Hubbard and Pocock (1972), who also conclude that more active polyps have greater calical relief and V-shaped calical floors (as here in the *murchisoni* morph). The weak correlation found here may reflect the importance of microenvironmental variation within these bioherms (essentially isolated patches of dense colonization with minor relief on the sea-floor which are persistent in time) and the survivorship value of settlement site. The inverse correlation between survivorship and growth rate may be no more than a reflection of a link between growth rate and sedimentation, periodic (annual) higher rates of sediment accumulation stimulating faster vertical rather than lateral growth, and also increasing the likelihood of death by burial. On the other hand, persistent turbidity resulting from repeated sediment resuspension correlates with decreased growth rates in living scleractinian corals (Dodge *et al.* 1974), possibly due to the deflection of metabolic effort into constant cleaning activity and the effect of decreased light intensity.

Variation in other species of Arachnophyllum

Other species in this group and members of the *A. pentagonum* group all possess very similar internal structure. In particular, they all develop the characteristic reticulate septal structure of *A. murchisoni*, identical in form and dimensions (text-fig. 7A, B, E). The features used to discriminate these species here appear relatively minor when compared with the variation described in the English sample of *A. murchisoni*. In each case, however, variation in these features appears to be discontinuous between species on the basis of previous descriptions and the material available here.

A. sinemurum and *A. separatum* are both discriminated on growth form and calicular size alone (see systematic descriptions). Their retention as distinct species may be questionable and they are undoubtedly closely related to *A. murchisoni*. They occur mainly in argillaceous facies of the Louisville Limestone and if growth form alone was involved, an ecophenotypic explanation of their distinct form might be acceptable. Nevertheless, they are also characterized by large corallite area, the two species appear to coexist without intermediaries and specimens of typical *A. murchisoni* are known from similar facies, e.g. the Mulde Marl. However, some of the latter specimens show a tendency for occasional peripheral corallites to vary towards the form found in *A. sinemurum*. The presence of roughly contemporary *sinemurum* morphs in England and North America could be due to migration, but might also represent independent evolutionary events (if specific distinction is accepted) or simply extreme variants in large samples (if this material is assigned to *A. murchisoni*). In any event, there is no morphological basis for separating the English and North American *sinemurum*.

Members of the *A. pentagonum* group appear to be more securely distinguished from the *A. murchisoni* group on their significantly coarser dissepiments. However, the former is almost restricted in distribution to the North American dolomite belt of Berry and Boucot (1970), whereas the latter is similarly characteristic of limestone and marly facies. The two groups overlap in distribution only in Quebec, where *A. murchisoni* is considered to have evolved from *A. pentagonum*. The possibility has to be considered that the distinct dissepimentaria may be a reflection of contrasting environmental and latitudinal distribution, but their sequential ranges and individually consistent internal structure suggests that this is a case of punctuated phyletic speciation. Indirect evidence from the distribution of *P. mamillaris* supports this conclusion. Within the *A. pentagonum* group, all three species display only *murchisoni*-morph calicular surfaces, least well developed in *A. pygmaeum*. This latter species is more clearly distinct from the other two, whereas *A. pentagonum* itself and *A. striatum* appear to differ only in the much greater mean calicular area of the latter. Both species may show enhanced intercorallite ridge height at dense bands (even though these are less clearly developed), often involving short supplementary colums of small globular dissepiments, as in *A. murchisoni* (Pl. 5, figs. 2, 4, 8). Although only a small sample is quoted here, the disjunct corallite size ranges of *A. pentagonum* and *A. striatum* are supported by large samples from the Fossil Hill Formation of Fossil Hill, Manitoulin Island (Dr Paul Copper, pers. comm.). The three species appear to show low intraspecific variability, although variation in *A. pygmaeum* is insufficiently known.

Variation in species of Prodarwinia

Species of *Prodarwinia* never develop intercorallite walls and show little variation in the development but more in the spacing of mamelons bearing the tabularia. This is most pronounced in *P. speciosa*, less in *P. striata* and *P. distans*, and least in *P. mamillaris*, which always has crowded, prominent, rounded mamelons. Mamelon form is particularly distinctive in *P. distans*.

P. mamillaris and *P. distans* appear to show relatively limited intraspecific variation and differ in several, if individually minor, details. This is despite the fact *P. mamillaris* bridges the distributions of *A. murchisoni* and *A. pentagonum* in time and space in North America, maintaining consistency of internal structure, particularly characteristics of the dissepimentarium, over a range of carbonate facies. This suggests that the contrast in dissepimentaria between *A. murchisoni* and *A. pentagonum* is a valid specific criterion.

Septal crests are only very weakly developed in *P. mamillaris* and *P. distans* (Pl. 6, fig. 10; Pl. 8, figs. 2, 5, 7). In *P. speciosa* and *P. striata*, the degree of development of solid septal crests shows considerable variation, particularly in the former where in some colonies they may be no better developed than in *P. mamillaris* (Pl. 6, figs. 3, 5, 7, 10, 12; text-fig. 11C). Throughout this genus, however, their structural characteristics, particularly the peculiar pseudorhabdacanthine appearance of trabeculae in the dissepimentarium (text-fig. 7C, D), appear to be consistent.

SYSTEMATIC PALAEONTOLOGY

Terminology follows the standard usage of Hill (1981) and others. In addition, to save repetition, the distinctive structure produced by the fusion of carinae from adjacent septa in *A. murchisoni* and other species is referred to as *murchisoni*-type carination or *murchisoni*-type reticulate septal structure. It is fully described under *A. murchisoni.* The characteristic trabecular structure of *Prodarwinia*, described under *P. speciosa*, is described here as pseudorhabdacanthine.

Measurements are also standard except that corallite area has been measured for a group of representative corallites and averaged for each colony using the method described by Scrutton (1981). In addition, the coarseness of dissepiment sections in cross-section had been measured as sections intersected along a line between adjacent corallite centres 10 mm long, or scaled up to 10 mm.

Horizon and locality for specimens from old collections have been given as registered with the specimen with clarification in parentheses. Interpretation of this information will be clear from the range quoted for the species. Ranges are based only on specimens studied here or sufficiently well illustrated for their identity to be certain. Information from species lists is suspect because of the confusion over the identity of North American species.

For convenience, closely related species of *Arachnophyllum* are placed in two species groups, the *A. murchisoni* and *A. pentagonum* groups. Brief notes are given for species probably referable to either *Arachnophyllum* or *Prodarwinia* but not suitable for revision in detail for some reason. Finally, species removed from these two genera are considered briefly and redescribed if appropriate.

Abbreviations. BMNH—British Museum (Natural History), London; BGS—British Geological Survey, Keyworth; SM—Sedgwick Museum, Cambridge; BMAG—City Museum and Art Gallery, Bristol; UAGC—Geological Collections, University of Aberdeen; MNHN IP—Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris; UCBL—Université Claude Bernard, Lyon; RM—Riksmuseet, Stockholm; SGU—Swedish Geological Survey, Uppsala; IGT—Institute of Geology, A.N. Est. SSR, Tallinn; USNM—National Museum of Natural History, Washington; AMNH—American Museum of Natural History, New York; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; UMMP—Museum of Paleontology, University of Michigan, Ann Arbor; GSC—Geological Survey of Canada, Ottawa.

Subclass RUGOSA Edwards and Haime, 1850
Order STAURIIDA Verrill, 1865
Suborder ARACHNOPHYLLINA Zhavoronkova, 1972

e.p. 1981 Arachnophyllina; Hill, p. 206.
e.p. 1981 Ketophyllina; Hill, p. 217.

Diagnosis. Mainly colonial stauriids in which septa usually become multitrabecular and discontinuous in the dissepimentarium, either lonsdaleoid or as septal crests. Tabularia well defined, with or without peripherally dished tabellae which may rise to meet septal sections in the axis, or with an axial series of arched or mesa-shaped tabellae, or with simple flat to gently depressed more or less complete tabulae. Dissepiments variable in form but usually elongate, poorly inflated.

Discussion. A full revision of this suborder is beyond the scope of this paper. In general terms, this revision of *Arachnophyllum* suggests that the Arachnophyllidae have more in common with the Kyphophyllidae and Endophyllidae of Hill (1981), which constitute the Arachnophyllina as here defined, than with the Entelophyllidae, which I suggest should be removed to the Columnariina.

Family ARACHNOPHYLLIDAE Dybowski, 1873

1873 Arachnophyllidae Dybowski, p. 339.
? 1887 Chonophyllidae Holmes, p. 25.
1949 Chonophyllidae; Stumm, p. 48.
1956 Arachnophyllidae; Hill, p. 274.
e.p. 1965 Arachnophyllidae; Iwanowskii, p. 114.
e.p. 1965 Arachnophyllidae; Stumm, p. 30.
e.p. 1971 Chonophyllidae; Oliver and Galle, p. 67.
1981 Arachnophyllidae; Hill, p. 214.
non 1977 Arachnophyllinae; Pedder, p. 173.

Discussion. Considerable divergence of opinion on the interpretation of the Arachnophyllidae exists. Pedder (1976, p. 133; 1977, p. 175) and McLean (1976*a*, p. 185) regard this group of corals as very close to the Cyathophyllidae, to the extent that Pedder made the Arachnophyllinae a subfamily of the Cyathophyllidae. The predominant characteristic of *Arachnophyllum* is the development of septa in the dissepimentarium only as crests on discrete dissepimental surfaces. I agree with Hill (1981, p. 214) that affinities are probably closer to the chonophyllids. In addition to the genera included in the family by Hill, I add *Iowaphyllum*.

Genus ARACHNOPHYLLUM Dana, 1846

1839 *Acervularia*; Lonsdale, p. 691.
? 1844 *Lamellopora* Owen, p. 70.
1846 *Arachnophyllum* Dana, p. 186.
1850 *Strombodes*; Edwards and Haime, p. lxx.
1851 *Strombodes*; Edwards and Haime, pp. 172, 426.
1855 *Strombodes*; Edwards and Haime, p. 293
1874 *Astraeophyllum* Nicholson and Hinde, p. 152.
1876 *Strombodes*; Rominger, p. 130.
1927 *Arachnophyllum*; Lang and Smith, p. 452.
1940 *Arachniophyllum*; Lang, Smith and Thomas, p. 19.
1956 *Arachnophyllum*; Hill, p. 274.
e.p. 1965 *Arachnophyllum*; Iwanowskii, p. 114.
e.p. 1975 *Arachnophyllum*; McLean, p. 54.
1981 *Arachnophyllum*; Hill, p. 215.

non 1819 *Acervularia* Schweigger, tab. 6.
non 1819 *Strombodes* Schweigger, tab. 6.

Diagnosis. Astraeoid, thamnasterioid colonial corals. Septa in tabularium thin, usually solid blades but rarely may be almost completely suppressed. Major and minor septa usually distinguished, often irregularly developed. In dissepimentarium, septa reduced to crests on discrete dissepimental surfaces, weakly to strongly developed, carinate, more rarely naotic. Dissepiments small, poorly inflated to coarse, irregular, moderately inflated, usually more or less clearly zoned by size, with septal crests on surfaces of smaller dissepiments. Intercorallite wall, if present, formed by arching of dissepimental surface, with or without supplementary vertical series of more globose dissepiments. Tabulae complete or incomplete, with or without dished tabellae in narrow peripheral zone, usually with axial arched or mesa-shaped tabellae. Increase peripheral, non-parricidal. Septal microstructure of monacanthine trabeculae.

Type species (by subsequent designation of Lang and Smith 1927, p. 452). *Acervularia baltica* Schweigger; Lonsdale 1839, pl. 16, fig. 8*b–e* (*non* fig. 8, 8*a*; *non* Schweigger 1819, tab. 6) = *Strombodes murchisoni* Edwards and Haime 1851, p. 428; 1855, p. 293, pl. 70, figs. 1 and 1*a–d*.

Discussion. Contrary to Laub (1979, p. 193), whilst Lonsdale's *A. baltica* was deemed to contain two different species, Lang and Smith's (1927, p. 452) selection of one of them, *A. murchisoni*, as type species was necessary and valid. In fact I show the second species, *A. diffluens*, to be a junior subjective synonym of *A. murchisoni* and thus all of Lonsdale's material is regarded as conspecific.

Edwards and Haime (1850, p. lxx) wrongly quoted *Strombodes pentagonus* Goldfuss as type species of *Strombodes* and listed *Arachnophyllum* as a junior synonym of that genus . This usage was widely followed until the early part of this century. *Strombodes*, type species *Madrepora stellaris* Linnaeus (designated by M'Coy 1849, p. 10), is a phaceloid genus quite distinct from *Arachnophyllum* although possibly ancestral to the arachnophyllids. Goldfuss' species is congeneric with *A. murchisoni* and is described below.

Lamellopora Owen is based on *L. infundibularia* Owen, 1844 which is shown below to be unrecognizable. It could be an *Arachnophyllum* but equally likely it could be a stromatoporoid. The genus should be set aside.

Astraeophyllum Nicholson and Hinde is based on *A. gracile* Nicholson and Hinde, 1874 which is shown below to be a synonym of *A. pygmaeum*. This species possesses typical *murchisoni*-type septal structure and *Astraeophyllum* is therefore established as a junior synonym of *Arachnophyllum*.

Arachnophyllum is distinguished from *Prodarwinia* principally on the basis of its septal structure. Septa in *Arachnophyllum* are only thickened to contiguity in a very thin veneer on dissepimental surfaces, if at all, and possess distinctive *murchisoni*-type carination. In *Prodarwinia*, on the other hand, septa are weakly and irregularly carinate, or non-carinate, and are present in the dissepimentarium of some species as solid septal crests, which may be quite thick. Septa may be multitrabecular in both but in *Arachnophyllum* trabeculae are monacanths, whilst in *Prodarwinia* they appear to be pseudorhabdacanths, at least in the outer dissepimentarium where the trabeculae are set in lamellar sclerenchyme.

Zenophila, tentatively placed in synonymy with *Arachnophyllum* by McLean (1975, p. 55), has unthickened, more continuous septa composed of very long trabeculae. I regard it as a distinct genus, although provisionally retaining it in the Arachnophyllidae.

Range. Silurian, Llandovery (?Aeronian, Telychian)—Ludlow; England, Gotland, USA, Canada, ?USSR, ?Australia.

Arachnophyllum murchisoni group

Arachnophyllum murchisoni (Edwards and Haime, 1851)

Plate 1, figs. 1–7; Plate 2, figs. 1–11; Plate 3, figs. 1–8;
text-figs. 3A, B, 4–6, 7A, B, E

1839 *Acervularia baltica* Schweigger; Lonsdale, p. 689, pl. 16, fig. 8, 8a–e.
1841 *Acervularia baltica* Phillips, p. 13, pl. 7, fig. 18E, *a*, *b*, *c*.
1850 *Actinocyathus balticus* d'Orbigny, p. 48.
1850 *Actinocyathus phillipsii* d'Orbigny, p. 107.
1850 *Arachnophyllum typus* M'Coy, p. 278.
1851 *Arachnophyllum typus* M'Coy; M'Coy, p. 38, pl. 1B, fig. 27 and 27*a*.
1851 *Strombodes labechii* Edwards and Haime, p. 427.
1851 *Strombodes murchisoni* Edwards and Haime, p. 428.
1851 *Strombodes phillipsi* (d'Orbigny) Edwards and Haime, p. 429.
1851 *Strombodes diffluens* Edwards and Haime, p. 431.
1855 *Strombodes typus* (M'Coy) Edwards and Haime, p. 293, pl. 71, fig. 1, 1*a*, *b*.
1855 *Strombodes murchisoni* Edwards and Haime; Edwards and Haime, p. 293, pl. 70, fig. 1 and 1*a–d*.
1855 *Strombodes phillipsi* (d'Orbigny); Edwards and Haime, p. 294, pl. 70, fig. 2 and 2*a*.
1855 *Strombodes diffluens* Edwards and Haime; Edwards and Haime, p. 294, pl. 71, fig. 2 and 2*a*.
1887 *Strombodes striatus* (d'Orbigny); Davis, pl. 121, fig. 1; pl. 122, figs. 1 and 2.
1887 *Strombodes pentagonus* Goldfuss; Davis, pl. 121, figs. 2 and 3.
1887 *Strombodes pygmaeus* Rominger; Davis, pl. 123, fig. 1.
1887 *Strombodes incertus* Davis, pl. 123, fig. 2.
1927 *Arachnophyllum murchisoni* (Edwards and Haime); Lang and Smith, p. 467, pl. 34, figs. 2 and 3.
e.p. 1927 *Arachnophyllum diffluens* (Edwards and Haime); Lang and Smith, p. 468, pl. 34, fig. 4.
1927 *Arachnophyllum typus* M'Coy; Lang and Smith, p. 469.
1949 *Arachnophyllum pentagonum* (Goldfuss); Amsden, p. 104, pl. 26, figs. 1–6.
1965 *Arachnophyllum pentagonum* (Goldfuss); Stumm, p. 30, pl. 20, figs. 1–3; pl. 21, fig. 1.
1965 *Arachnophyllum striatum* (d'Orbigny) Stumm, p. 30, pl. 20, figs. 4–6.

non 1819 *Astrea baltica* Schweigger, tab 6.

Diagnosis. Arachnophyllum of variable external form comprising tabular, discoidal, or low domal colonies with or without more or less sharply defined intercorallite ridges on the calicular surface. Surface flat, or may funnel gently to tabularial pit, or tabularia centred on broad, low mamelons. Tabularia more or less well defined, 1·8–4·7 mm in diameter with fifteen to twenty-two thin major septa usually with weak bilateral arrangement and reaching the axis where they may form a weak columella. In the dissepimentarium, major and minor septa reduced to crests on discrete dissepimental surfaces, occasionally naotic peritabularially and always distinctly carinate. Carinae of adjacent septa normally fuse to form a characteristic box-work structure with dissepimental plates. Dissepiments variable in size but characteristically small on average. Dissepimentarium surface matches colony surface but with no structural modifications at intercorallite boundaries except for intermittent columns of small, globose dissepiments in some specimens. Tabulae usually flat-topped domes. Increase marginarial, non-parricidal.

Type material. Lectotype of *Strombodes murchisoni* Edwards and Haime (chosen by Lang and Smith (1927, p. 467)): BGS GSC6577 (Much) Wenlock Limestone (Formation), Shropshire (= *Acervularia baltica* Schweigger; Lonsdale (1839, pl. 16, fig. 8*e*)). Paralectotypes: BGS GSC6579 and BGS GSC6578, same horizon and locality (= *A. baltica* Schweigger; Lonsdale (1839, pl. 16, fig. 8*b*, *c*, *d* respectively)).

Two other species placed in synonymy with *A. murchisoni* here are also based on one or other of the specimens illustrated as *A. baltica* Schweigger by Lonsdale (1839, pl. 16, figs. 8 and 8*a*–*e*). *S. diffluens* Edwards and Haime was said by them to be the species illustrated by Lonsdale (1839) in pl. 16, figs. 8 and 8*a*. Edwards and Haime (1855, pl. 71, figs. 2 and 2*a*) figured a specimen of their own under this name, which can be construed as a syntype with Lonsdale's material. Lang and Smith (1927, p. 468) reported Lonsdale's specimens as missing and therefore chose the original of Edwards and Haime (1855, pl. 71, figs. 2 and 2*a*), which is MNHN IP S11664, from Wenlock, as the lectotype. *Arachnophyllum typus* M'Coy was said to be *Acervularia baltica* Lonsdale (1839, pl. 16, fig. 8*a*) by M'Coy (1850). However, the figure quoted may have been in error as in the same paper, he noted fig. 8*a* as probably the same as his new species *Strombodes wenlockensis* (M'Coy 1950, p. 274), whilst later (M'Coy 1851, p. 38) he quoted Lonsdale's fig. 8*b* with reference to *A. typus*. As noted above, the original of Lonsdale's fig. 8*a*, a paralectotype of *S. diffluens*, is missing and the original of fig. 8*b* (BGS GSC6579) is a paralectotype of *A. murchisoni*. However, M'Coy in 1850 clearly had in front of him at that time the specimen he figured for the species in 1851 as he refers to it and quotes its locality (M'Coy 1850, p. 278). This figured specimen (M'Coy 1851, pl. 1B, figs. 27, 27*a*) is SM A4828, from the Wenlock Limestone of Aymestry, and is a syntype with Lonsdale's specimen. Lang and Smith (1927, p. 469) quoted SM A4828 as the holotype of the species in error and to avoid any confusion, I hereby designate it as lectotype of *A. typus*.

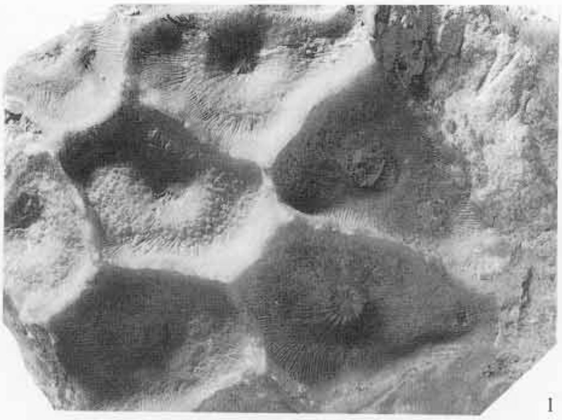
The holotype by monotypy of *A. phillipsii* is the original of Phillips (1841, pl. 7, fig. 18E *a*, *b*, *c*) from an unknown locality in the (Much) Wenlock Limestone (Formation). This appears to be the same specimen as that illustrated by Edwards and Haime (1855, pl. 70, figs. 2 and 2*a*), said to be from 'Wenlock'. MNHN IP S11668 is labelled as probably the original of Edwards and Haime's figures, but I regard this specimen as not convincingly similar to either Phillips' or Edwards and Haime's illustrations. The holotype, therefore, appears to be missing.

An original of *Strombodes labecheii* is MNHN IP S11666 and S11665 may be another syntype (Dr Pierre Semenoff-Tian-Chansky, pers. comm.). I hereby select MNHN IP S11666 as lectotype on his advice. Both specimens are labelled as from Wenlock.

EXPLANATION OF PLATE 1

Figs. 1–7. *Arachnophyllum murchisoni*, calicular surfaces of type and other material, all × 1. 1, lectotype of *A. murchisoni* (BGS GSC6577); Wenlock Limestone; Shropshire. 2, lectotype of *A. typus* (SM A4828); Wenlock Limestone; Aymestry. 3, lectotype of *Strombodes diffluens* (MNHN IP S11664); Wenlock Limestone; Wenlock. 4, lectotype of *Strombodes labecheii* (MNHN IP S11666); Wenlock Limestone; Wenlock. 5, BMNH R46415; Wenlock Limestone; ?Dormington, Hereford and Worcester. 6, RM Cn67213; Mulde Marl; Eksta, Djupvik, Gotland. 7, BMNH R53513; Much Wenlock Limestone Formation; Lea Quarry, north side of B4371, 1½ km south-west of Much Wenlock, Shropshire (SO 5972 9861).

PLATE 1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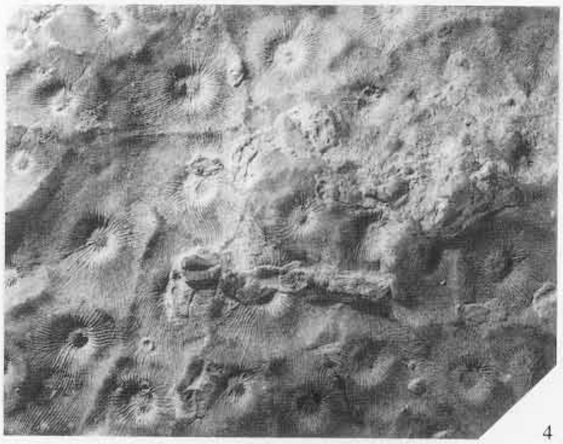
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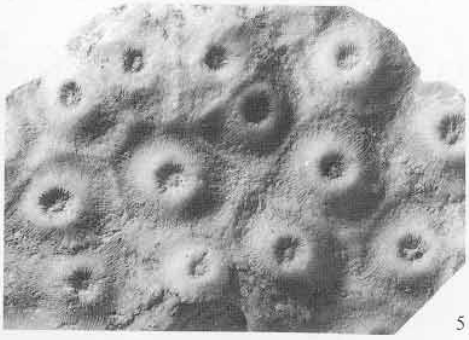
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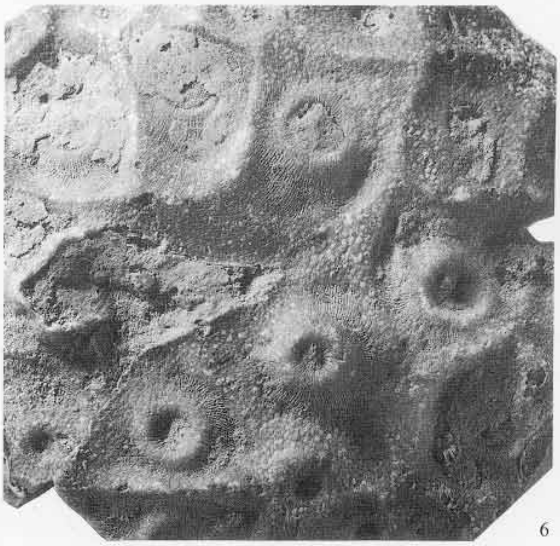
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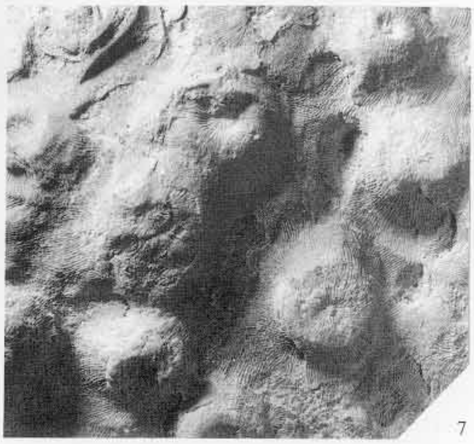
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SCRUTTON, *Arachnophyllum*

Material. English material: BM R53616–53617 (?same colony), Silurian, Llandovery, Upper Haugh Wood beds (*Petalocrinus* Limestone); temporary trench in Haugh Wood, 2·3 km west of Woolhope, Hereford and Worcester (SO 58853558) [SM A5700, Woolhope Limestone; Wenlock ridge (label almost certainly a transpositional error for Wenlock Limestone, Woolhope, there being no Woolhope Limestone on the ridge of Wenlock Edge)]. SM A46667, Silurian, Wenlock, Wenlock Shale; Blaisdon Hall, May Hill, Glos. BGS 37964, Silurian, Wenlock, (Much) Wenlock Limestone (Formation); May Hill Longhope, Glos. MNHN IP S11669, Silurian; Dudley (figured Edwards and Haime 1855, pl. 70, fig. 1*c*). IP S11667, no details recorded but almost certainly Much Wenlock Limestone Formation; England. BMNH R52622, Much Wenlock Limestone Formation; old quarry on Lincoln Hill, Ironbridge, Shropshire (SJ 67050390). R52623–52627, Much Wenlock Limestone Formation; roadside exposure on B4378 (Farley Dingle), 2·5 km north of Much Wenlock, Shropshire (SJ 633023). R52628–52630, Much Wenlock Limestone Formation; Farley Quarry, Gleedon Hill, 1·7 km north of Much Wenlock, Shropshire (SJ 629017). R52631, Much Wenlock Limestone Formation; Coates Quarry, north side of B4371, 2 km south-west of Much Wenlock, Shropshire (SO 60419935). R53513, Much Wenlock Limestone Formation; Lea Quarry, north side of B4371, 2·75 km south-west of Much Wenlock, Shropshire (SO 59809875).

Gotland material: RM Cn20146, 66040–66045, 67213–67215, 67075, Silurian, Wenlock, Mulde Marl; Eksta, Djupvik. Cn20155, 55254, Silurian; Gotland. SGU 6110, Silurian, Wenlock, Klinteberg Beds; 4·75 m south-south-west of point 35,2 on railway line, Frojel Parish, Hemse. RM Cn12366, Silurian, Wenlock, Halle Beds; Hörsna Canal.

North American material: GSC 91554, Silurian, Telychian, La Vieille Formation; Little Port Daniel River, Gaspé, Quebec. GSC 90726, Silurian, ?upper Wenlock, Sayabec Formation; 1 m east-north-east of La Redemption, Quebec. MCZ 8071, Niagara 'red clay' (Silurian, late Wenlock (?early Ludlow), Louisville Limestone); first quarry on Beargrass Creek, East Louisville, Kentucky. UMMP 5307, 34212, USNM 422818–422819, Louisville Limestone; Louisville, Kentucky. USNM 422820–422821, Lobelville Limestone (Silurian, Ludlow, Brownsport Formation); Sewell's Spring, Tennessee.

Range. Silurian, late Llandovery, La Vieille Formation, Quebec; latest Llandovery, *Petalocrinus* Limestone; Wenlock (?Woolhope Limestone), Wenlock Shale, Much Wenlock Limestone Formation, England; Wenlock, Halle Beds, Mulde Marl, Klinteberg Beds, Gotland; late Wenlock (?early Ludlow), Louisville Limestone, Kentucky; mid Ludlow, Brownsport Formation, Tennessee; Wenlock—early Ludlow (probably later Wenlock part), Sayabec Formation, Quebec.

Description. Astraeoid to thamnasterioid colonies $< 300 \times 200 \times 150$ mm. Colony form thin tabular sheets to thick tabular or domal masses with or without ragged margins, irregular to subcircular in plan. A majority have moderate to well-developed intercorallite walls $< 2{\cdot}5$–3 mm, exceptionally 8 mm high, formed by uparching of the dissepimental surface between adjacent corallites (Pl. 1). In these, corallites are polygonal with straight to slightly curved walls, equidimensional to elongate, with the longer axis $< 1{\cdot}6\times$ the shorter. Corallite size highly variable, 0·70–6·33 cm^2 in area. All gradations exist to colonies in which an intercorallite ridge is completely absent and adjacent tabularia are separated by a flat or gently depressed common dissepimentarium. The peritabularial area may be a broadly inflated mamelon, or flat or gently depressed, curving down to the edge of the more steeply declined wall of the tabularial pit, normally 1–2 mm deep with a small but often prominent axial boss.

In transverse section, tabularia prominent but rather imprecisely defined, 1·8–4·7 mm diameter and 5–33 mm apart centre to centre (Pl. 2, figs. 1, 2, 4, 6, 8, 10; Pl. 3, figs. 1, 3, 5, 7). Corallite margins either undefined (Pl. 2, figs. 2 and 6) or weakly to strongly defined by a more or less distinct row of subcircular dis-

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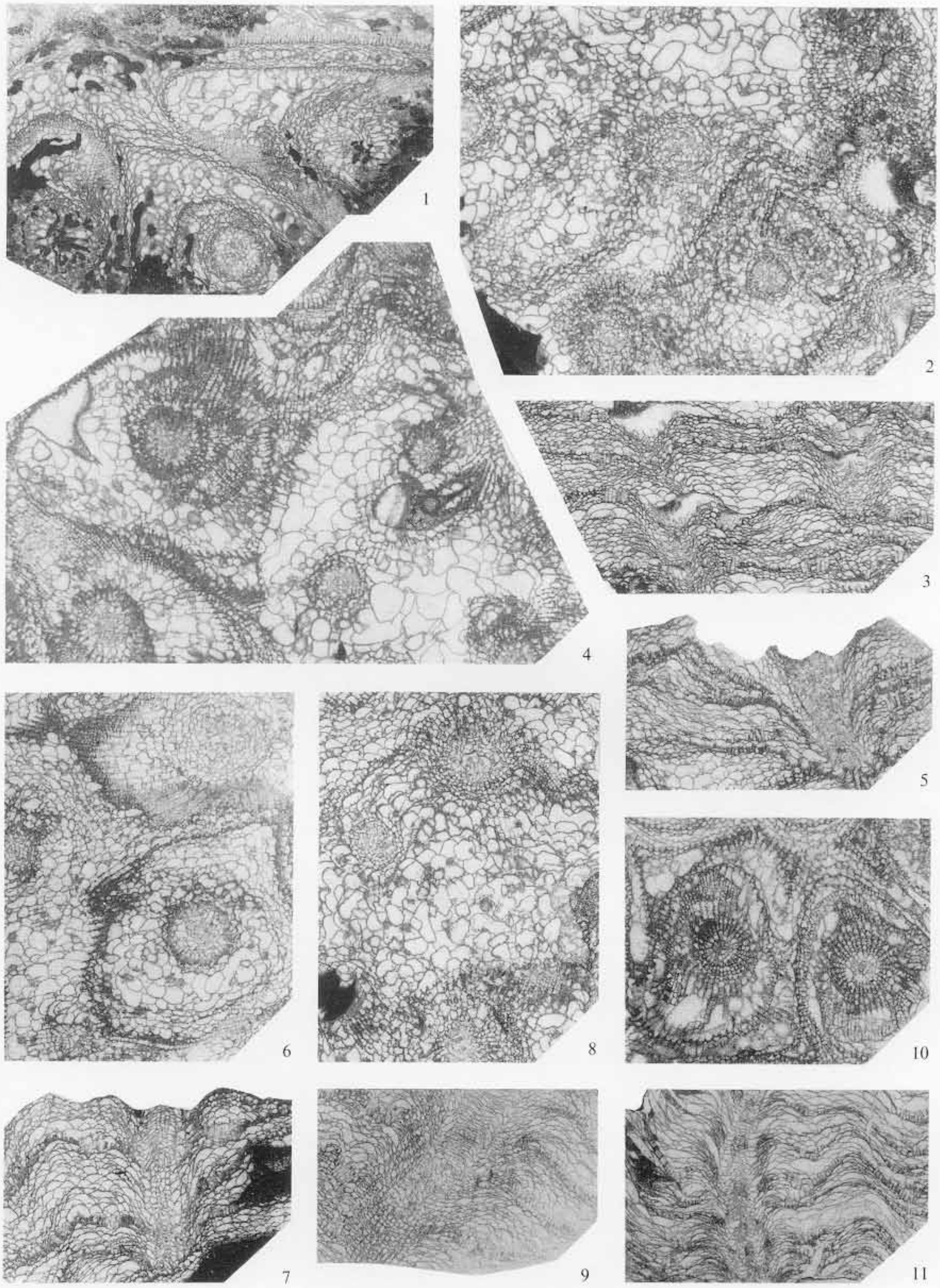
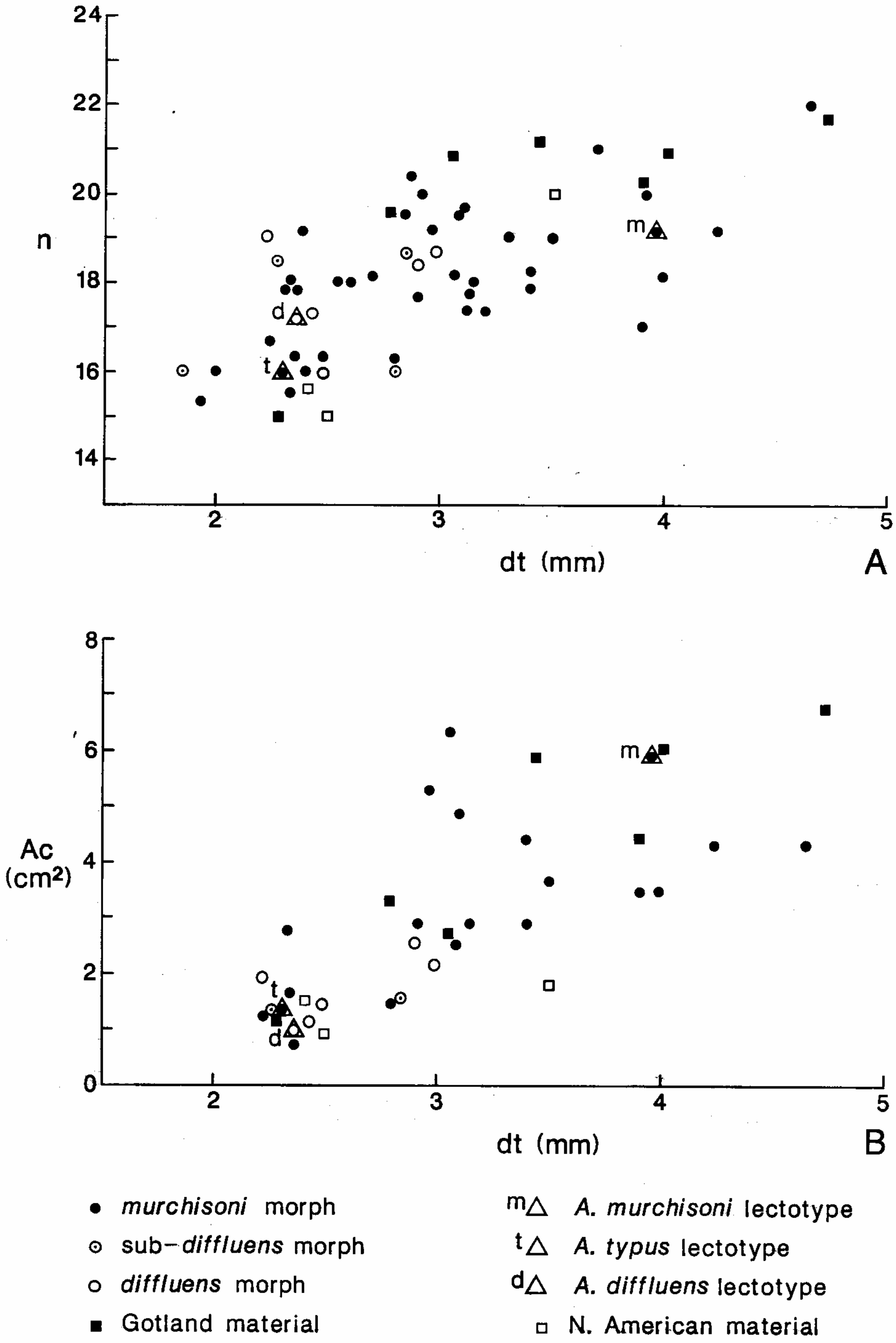
EXPLANATION OF PLATE 2

Figs. 1–11. *Arachnophyllum murchisoni*, internal structure of type and Gotland material, all × 2·5. 1, cross-section of lectotype of *A. murchisoni* (BGS PF4533); Wenlock Limestone; Shropshire. 2, cross-section and 3, longitudinal section of lectotype of *Strombodes diffluens* (MNHN IP S11664); Wenlock Limestone; Wenlock. 4, cross-section and 5, longitudinal section of lectotype of *A. typus* (SM A4828*c*, *d*); Wenlock Limestone; Aymestry. 6, cross-section and 7, longitudinal section of lectotype of *Strombodes labecheii* (MNHN IP S11666); Wenlock Limestone; Wenlock. 8, cross-section and 9, longitudinal section (RM Cn67214); Mulde Marl; Eksta, Djupvik, Gotland. 10, cross-section and 11, longitudinal section (SGU 6110); Klinteberg Beds; Frojel Parish, Hemse, Gotland.

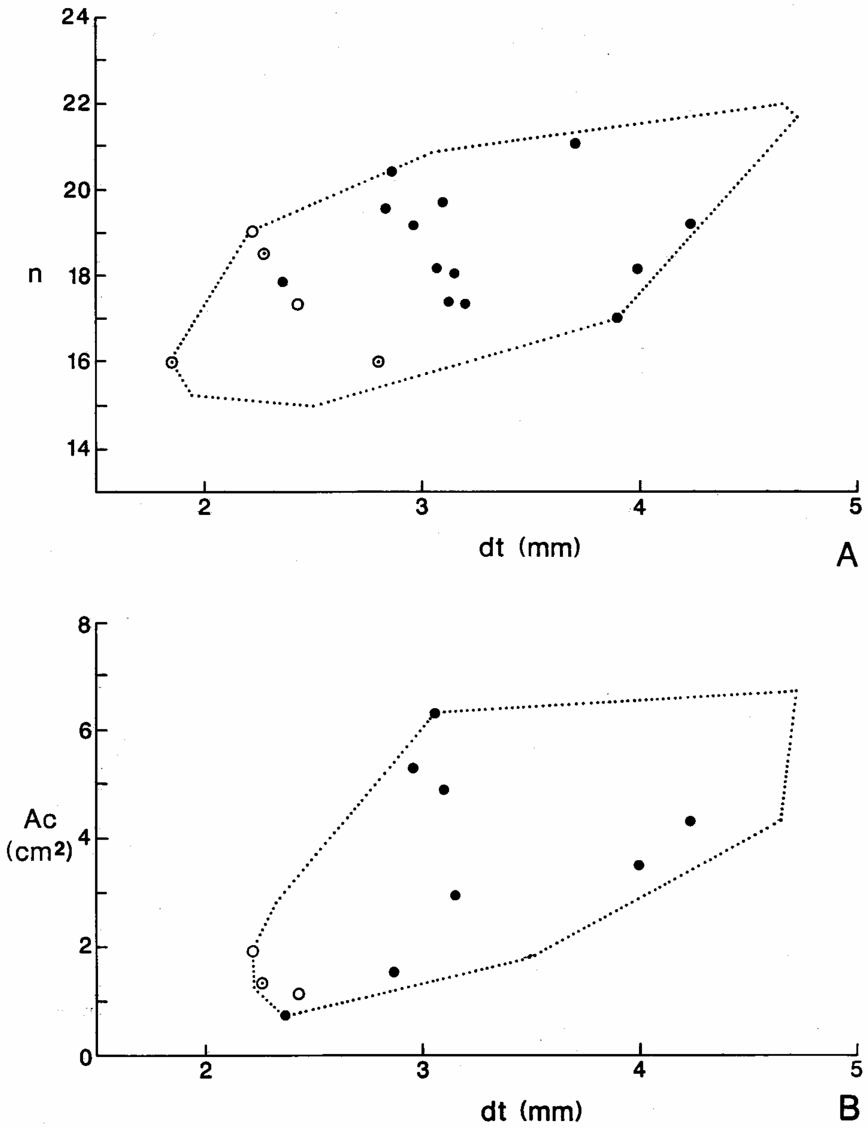
PLATE 2



SCRUTTON, *Arachnophyllum*



TEXT-FIG. 5. Variation in A, mean number of major septa (n) and B, mean corallite area (Ac in cm^2), both plotted against mean tabularium diameter (dt in mm) for *Arachnophyllum murchisoni*. For discussion see text.



TEXT-FIG. 6. Variation in A, mean number of major septa (n) and B, mean corallite area (Ac in cm^2), both plotted against mean tabularium diameter (dt in mm) for the Farley Dingle sample of *Arachnophyllum murchisoni.* Dotted line outlines field of variation for the total sample of *A. murchisoni*; legend otherwise as for text-fig. 5. For discussion see text.

sepimental sections reflecting a strong wall on the calicular surface (Pl. 2, fig. 1; Pl. 3, Figs. 1, 3, 7). Septa generally well developed in the tabularium as usually continuous, slightly and uniformly thickened vertical plates; occasionally they are weakly developed, or even rarely locally absent (Pl. 3, fig. 3). Division into major and minor septa may be rather irregular but usually more or less clearly distinguished. Minor septa may or may not just penetrate the tabularium. Major septa extend into the axial area, sometimes with free axial ends which may be slightly rhopaloid, or more commonly fused with corresponding septa of the adjacent quadrant to form a more or less strongly bilaterally symmetrical pattern. Septa best developed, thickest, and sometimes coated with sclerenchyme on tabularial surfaces. Axial intersections of arched tabulae may thus suggest substellate or aulate axial structures. In the dissepimentarium, septa reduced to crests on discrete dissepimental surfaces. Intracolonial development of crests slightly variable, but intercolonial variation from scarcely developed to very dense. At the tabularium boundary, corresponding with the peritabularial zone of steeply dipping dissepiments, septa usually carinate, with yard-arm or zigzag carinae, and may be discontinuous or naotic in structure. As the dissepimental surface curves over to a sub-horizontal attitude towards the corallite periphery, the septa are either present or absent depending on their degree of development and the level of section. Where present, further septa intercalate between those radiating from the tabularium to maintain a constant lateral spacing of 0·2–0·3 mm. Carinae become regularly and well developed, four to seven per mm, crossbar to zigzag in form, and fused with those of adjacent septa to form a distinctive reticulate pattern in cross-section (text-fig. 7A, E). Septa may be multi-trabecular and contiguous immediately above the dissepimental surface on which they are based, bounding the reticulate pattern by a more or less narrow band of dense tissue where this surface is intersected, creating the impression of one or more partial false walls around the corallite (Pl. 2, figs. 6 and 10; Pl. 3, figs. 1 and 7). In some specimens, carinae clearly extend higher than the septal crest so that isolated crossbars may occur in otherwise aseptate parts of the dissepimentarium. Dissepimental sections vary considerably in size and shape, from irregularly arcuate to subcircular, twelve to eighteen in 5 mm.

In longitudinal section, tabularia well defined, more or less vertical, and generally of uniform width. Axial tabellae arched and dense, occasionally flat-topped domes and less dense, about three-quarters of the tabularium wide, fifteen to forty in 5 mm. They may be disrupted by septal sections. A peripheral series of flat to dished tabellae of variable development, ten to thirty in 5 mm, interlock with axial tabellae and dissepiments. Dissepiments dominantly weakly inflated, rather elongate, regular to irregular vesicles. Highly inflated dissepiments rare but may occasionally occur in zones. Dissepimental size highly variable overall, $<3 \times 3{\cdot}5$ mm. Layers of coarser dissepiments grade distally into finer dissepiments capped by septal crests, these units strongly and pervasively developed, 0·1–3·5 mm thick (Pl. 2, figs. 6 and 11; Pl. 3, figs. 2 and 8). Septal crests appear as successive surfaces bearing thin, parallel and regularly spaced, more or less vertical sections through carinae, varying from barely discernible thorns to continuous structures penetrating <6 layers of dissepiments and 3 mm high (Pl. 2, figs. 5 and 11; Pl. 3, figs. 2 and 8; text-fig. 7B). Usually, they are about 0·5 mm high and penetrate only one or possibly two layers. Their orientation is approximately normal to dissepimental surfaces of low to moderate relief but intermediate between normal and the vertical when surfaces are of high relief. Carinae may be associated with one or more thickened dissepimental surfaces and may merge into solid plates when the septal plane is sectioned. When well developed, successive septal crests may become locally vertically continuous but normally, intervening zones of uninterrupted dissepiments are wider than septate zones, although the former may sometimes show scattered, isolated, and low carinal sections. Dissepimental surface steeply inclined downwards to the tabularium boundary, gently arched or flat peritabularially and flat to sharply arched between tabularia. A distinctive vertical column of particularly globose dissepiments, usually discontinuous vertically, or of limited vertical extent may correspond to well-developed intercorallite ridges on the calicular surface (Pl. 3, figs. 6 and 8). Uparching of the dissepimentarium profile maximized at calicular surfaces based on zones of small dissepiments.

Increase marginarial non-parricidal, more common in peripheral areas of colonies. Rare offsets in central areas occur more or less equidistant from surrounding established tabularia.

Septa and carinae constructed of equidimensional, smooth to tufted monocanths generally 0·06–0·10 mm diameter (text-fig. 7A, B). All or nearly all of any thickening of these elements appears to be trabecular; lamellar sclerenchyme is rarely developed. Dissepiments and tabulae constructed of fibronormal tissue.

EXPLANATION OF PLATE 3

Figs. 1–8. *Arachnophyllum murchisoni*, variation in internal structure in Farley Dingle sample and North American material, all ×2·5. 1, cross-section and 2, longitudinal section (BMNH R52626). 3, cross-section and 4, longitudinal section (BMNH R52627). 5, cross-section and 6, longitudinal section (BMNH R52623). All Much Wenlock Limestone Formation; roadside exposure on B4378 ('Farley Dingle'), 2·5 km north of Much Wenlock, Shropshire (SJ 633023). 7, cross-section and 8, longitudinal section (UMMP 34212); Louisville Limestone; Louisville, Kentucky.

PLATE 3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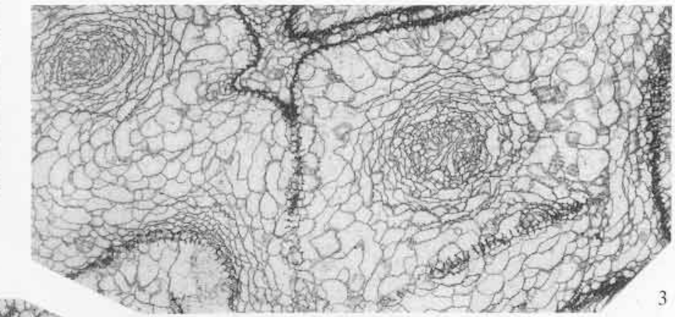
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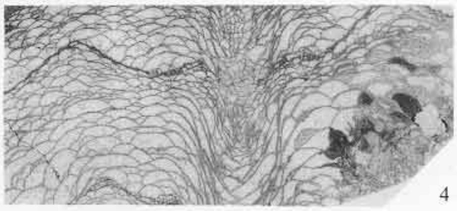
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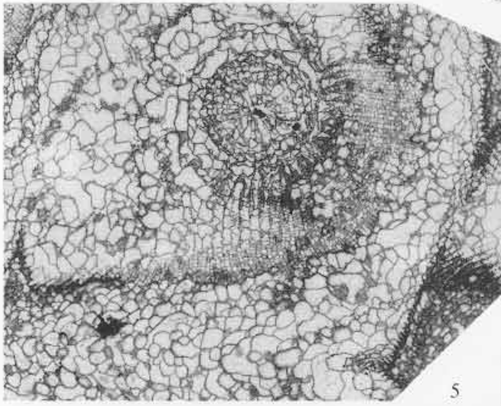
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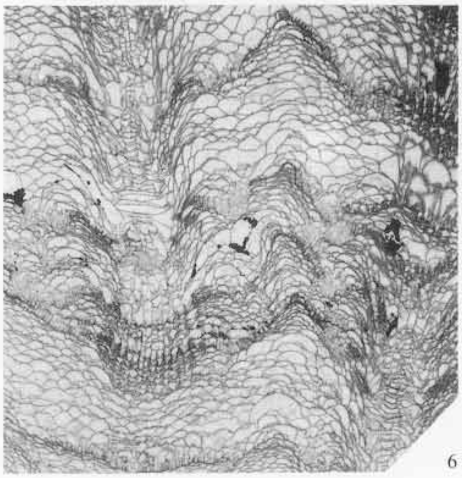
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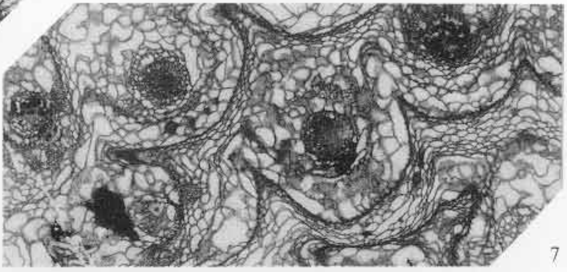
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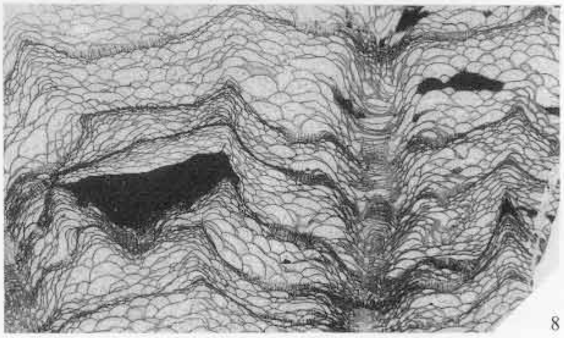
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SCRUTTON, *Arachnophyllum*

Discussion. Five species of *Arachnophyllum* have been described from the Much Wenlock Limestone; *Actinocyathus phillipsii* d'Orbigny, *Arachnophyllum typus* M'Coy, *Strombodes labecheii* Edwards and Haime, *S. murchisoni* Edwards and Haime, and *S. diffluens* Edwards and Haime. D'Orbigny's species name has been unused as a senior synonym since Edwards and Haime (1855, p. 294), who even then remarked on the close similarity of *phillipsii*, *murchisoni*, and *typus*. In the same work, they placed their own species *S. labecheii*, without illustration, in synonymy with M'Coy's species.

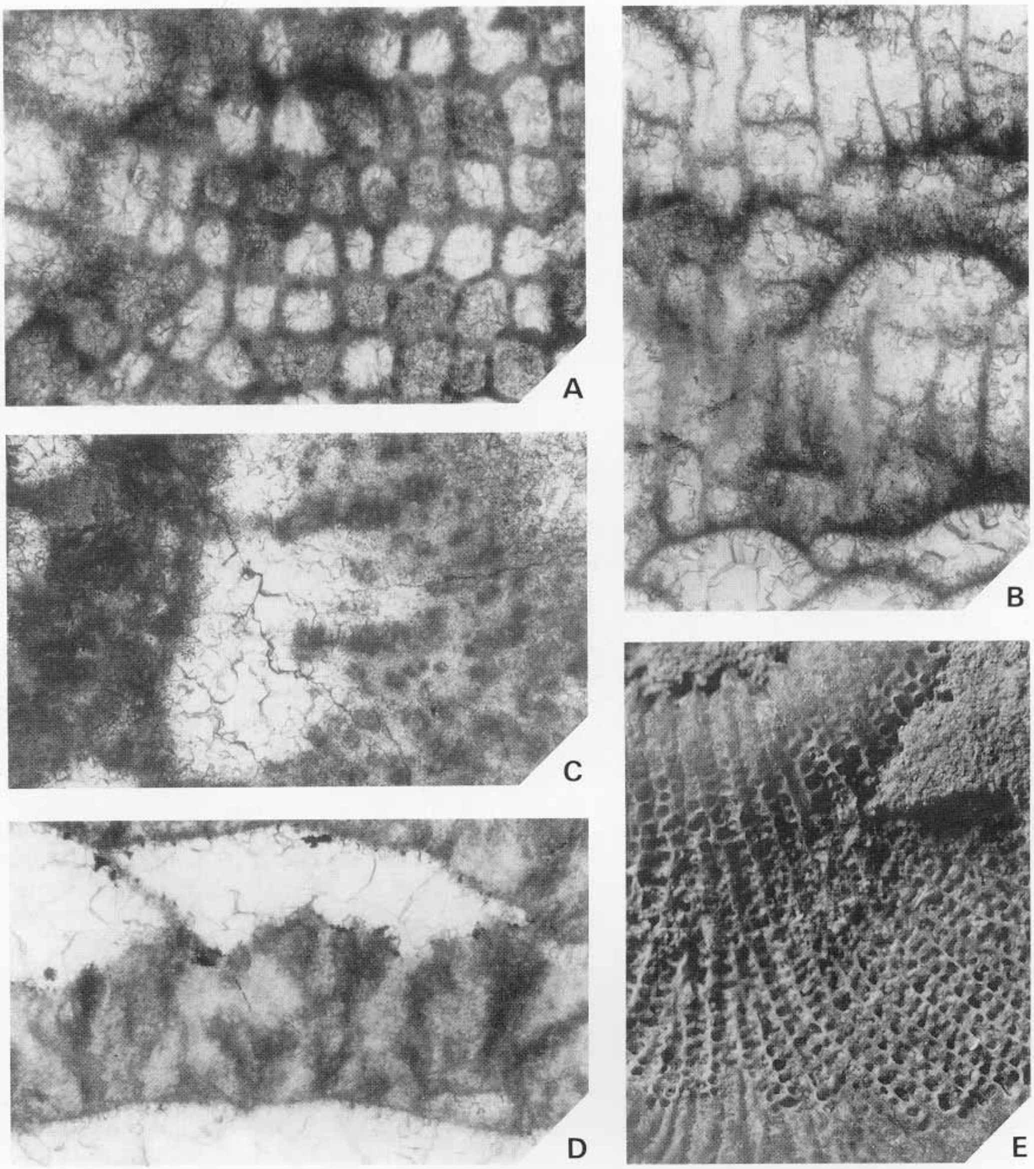
Lang and Smith (1927, p. 467 et seq.) placed *phillipsii* and *murchisoni* in synonymy but, in apparent ignorance of d'Orbigny's priority, described the species as *Arachnophyllum murchisoni*. The paliform lobes attributed to *Strombodes phillipsii* by Edwards and Haime (1855, p. 294) they dismissed as unmodified intrathecal portions of the septa. However, the appearance, rather exaggerated in Edwards and Haime's illustration, is real and a consequence of a prominent and well-preserved axial boss in the calice. Lang and Smith (1927, p. 469) maintained *A. typus* distinct from *A. murchisoni*, which it very closely resembles in surface features, by virtue of its smaller corallite size. The type material of *A. diffluens*, the third species they recognized, lacks the intercorallite ridges of the previous two species. Whilst maintaining these three separate species, Lang and Smith (1927, p. 465) clearly recognized that they represented morphological varieties of what 'would probably more correctly be considered as . . . a single species'.

Iwanowskii (1965, p. 115) placed *A. diffluens* in synonymy with *A. murchisoni*, although the specimen he figures (p. 28, fig. 3) is certainly not conspecific with this species. McLean (1975, p. 54 *et seq.*), on the other hand, considered that there might be value in distinguishing two species groups, one with and the other without intercorallite ridges. However, although other species, such as *A. pentagonum* and *Prodarwinia mamillare*, consistently possess or lack ridges, there is no doubt in the British material of *A. murchisoni* that this feature is variable to some extent within individual colonies, and completely so in the sample as a whole.

In the large sample of English Wenlock material described here, considerable variation is recorded not only in the development of intercorallite ridges but also in other exterior features such as the presence of an annular swelling surrounding the tabularium, corallite area, and the form of the colony as a whole. On the other hand, in sections, although septa may vary in the strength of their development, their structure otherwise, together with dissepimental and tabularial characteristics, is broadly consistent throughout the sample. Thus only one species of *Arachnophyllum* is recognized in the English Wenlock. In the relatively limited recent discussion of the English material, only the species names *murchisoni* and *diffluens* have been considered, both of which have extant lectotypes, and of which *murchisoni* is clearly the senior synonym. In addition, *A. murchisoni* is type species for the genus. Thus, although the names *phillipsi*, *typus*, and *labecheii* have priority, I make a case for the use of the name *murchisoni* for this species in the interests of stability.

McLean (1975, p. 55) disputed Lang and Smith's (1927, p. 466) description of the septal structure in this species. However, whilst in certain details the description of septal structure given here also differs from that of Lang and Smith, the reticulate structure produced in cross-section by septal crests and their carinae is a constant and distinctive feature of this species. Lang and Smith's description of 'vertical and horizontal rows of spines' appears to arise from the appearance of the carinae in cross and longitudinal section. They describe these spines as forming a solid boxwork with secondary tissue, whereas in fact the septal crests, which are usually solid blades, and the carinae appear to be more or less wholly trabecular. The floors and ceilings of the boxwork are provided by intersected dissepiments. In fact, Lang and Smith's (1927, pp. 452–453, figs. 5–7) line drawings are very accurate despite their description.

A. murchisoni also occurs in North America (Pl. 3, figs. 7 and 8), where it has usually been recorded as *A. pentagonum* or more rarely *A. striatum*, and in Gotland (Pl. 2, figs. 8–11). *A. pentagonum*, *A. pygmaeum*, and *A. striatum* all differ in possessing dissepimentaria in which the vesicles, although variable in size as in this species, are consistently and significantly on average larger. The only other species possessing similar reticulate septal structure in cross-section are *A. sinemurum* and *A. separatum*, whose relationships are discussed below.



TEXT-FIG. 7. A, B, *Arachnophyllum murchisoni*; Silurian, Wenlock, Much Wenlock Limestone Formation; roadside exposure on B4378 (Farley Dingle), 2·5 km north of Much Wenlock, Shropshire (SJ 633023) (BMNH R 52625), ×40. A, cross-section, edge of tabularium at upper left; B, Longitudinal section in dissepimentarium. C, D, *Prodarwinia speciosa*; Silurian, upper Aeronian, Rumba Formation; Päri, 1 km north-west of Tallinn–Virtsu road, Estonia (BMNH R53511), ×40. C, cross-section, edge of tabularium at left; D, longitudinal section in dissepimentarium. E, *Arachnophyllum murchisoni;* Silurian, Wenlock, Mulde Marl; Eksta, Djupvik, Gotland (RM Cn67214), ×8; detail of septal carination on weathered surface, edge of tabularium at top left.

A. murchisoni is recorded here for the first time from the English latest Llandovery as the result of recent trenching across the outcrop of the *Petalocrinus* Limestone in the Woolhope Inlier.

Arachnophyllum sinemurum (Davis, 1887)

Plate 4, figs. 1–6; text-fig. 8

e.p. 1887 *Strombodes sinemurus* Davis, pl. 121, fig. 4, pl. 122, figs. 4 and 6; *non* pl. 123, fig. 3.
1887 *Strombodes quadrangularis* Davis, pl. 122, fig. 3.
1965 *Arachnophyllum sinemurum* (Davis) Stumm, p. 31, pl. 21, fig. 2.
1965 *Arachnophyllum quadrangulare* (Davis) Stumm, p. 31, pl. 21, figs. 7–10.

Diagnosis. Broadly based, low colonies of variable form, from a single large corallite with one or a few small peripheral offsets to a small number of more equidimensional large corallites. Corallite walls broad to sharp ridges, fading at periphery of colony. Internal structure of *murchisoni* type. Mean tabularium diameter ranging from 3·4–4·75 mm with sixteen to twenty-two major septa and corallite areas typically 8–16 cm^2.

Type material. Lectotype of *A. sinemurum* (chosen by Stumm 1965, p. 31): MCZ 8072 (original of Davis 1887, pl. 121, fig. 4), Silurian, Upper Niagara 'white clay' (late Wenlock (?early Ludlow), Louisville Limestone); fourth quarry on Beargrass Creek, East Louisville, Jefferson Co., Kentucky. Lectoparatypes: MCZ 8070 (original of Davis 1887, pl. 122, fig. 4), Silurian, Upper Niagara 'white clay'; quarry on Poplar Level Road, 4·8 km east of Louisville, Jefferson Co., Kentucky. MCZ 8073 (original of Davis 1887, pl. 122, fig. 6), Silurian, Upper Niagara 'red clay' (late Wenlock (?early Ludlow), Louisville Limestone); Workhouse Quarry, East Louisville, Jefferson Co., Kentucky.

Holotype of *S. quadrangularis:* MCZ 8059, Silurian, Upper Niagara 'red clay'; Daly Farm, 3·2 km south-east of Charlestown, Clark Co., Indiana.

Other material. UMMP 21400, USNM 422822, Silurian, late Wenlock (?early Ludlow), Louisville Limestone; Louisville, Kentucky. ?USNM 37376, Niagara Group (?late Telychian or early Wenlock, La Porte City Formation); Masonville, Iowa. BMAG Cc1259–1260, Much Wenlock Limestone Formation; Dudley, West Midlands.

Range. Silurian, ?late Telychian–early Wenlock, La Porte City Formation; Iowa. Late Wenlock, Much Wenlock Limestone Formation; West Midlands. Late Wenlock (?early Ludlow), Louisville Limestone; Indiana and Kentucky.

Description. Colonies either small, $< 60 \times 65 \times 23$ mm, with a flat to broadly conical base (Pl. 4, figs. 1, 3, 5), or tabular $< 950 \times 850 \times 30$ mm with a flat base and a gently to strongly arched upper surface (Pl. 4, fig. 6). Small colonies, circular in plan, consisting of one or two large mature corallites with one to four immature peripheral offsets, delimited by sharply ridged walls towards the colony centre which fade and disappear towards the edge of the colony. Larger colonies with several large, more equidimensional corallites separated by well-defined to more diffuse ridges, and occasionally with peripheral offsets. Maximum corallite area may

EXPLANATION OF PLATE 4

Figs. 1–6. *Arachnophyllum sinemurum.* 1–4, lectotype (MCZ 8072). 1, calicular surface, × 1. 2, cross-section, × 2·5. 3 and 4, longitudinal section; 3, × 1, 4, × 2·5. Silurian, upper Niagara 'white clay' (Louisville Limestone); fourth quarry on Beargrass Creek, East Louisville, Kentucky. 5, calicular surface (BMAG Cc1259); Wenlock Limestone; Dudley, West Midlands, × 1. 6, calicular surface of holotype of *Strombodes quadrangularis* (MCZ 8059); Silurian, upper Niagara 'red clay' (Louisville Limestone); Daly Farm, 2 m south-east of Charlestown, Indiana, × 1.

Figs 7–9. *Arachnophyllum separatum*, all × 1. 7, 8, lectotype of *A. separatum* (AMNH Fl 36584); 7, calicular view; 8, side view; Silurian, Niagara Group (Louisville Limestone); Louisville, Kentucky. 9, holotype of *Strombodes unicus* (MCZ 8076); Silurian, upper Niagara 'red clay' (Louisville Limestone); Workhouse Quarry, East Louisville, Kentucky.

PLATE 4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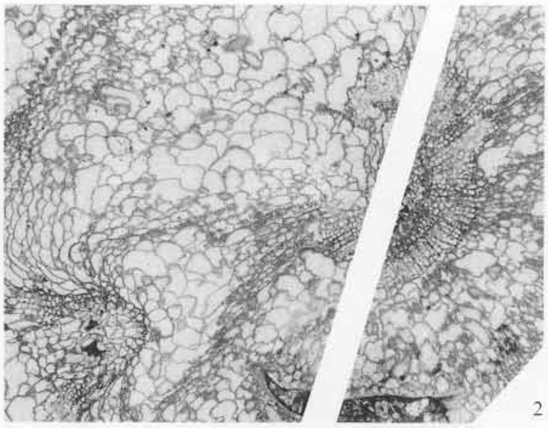
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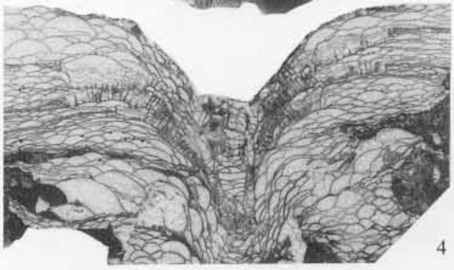
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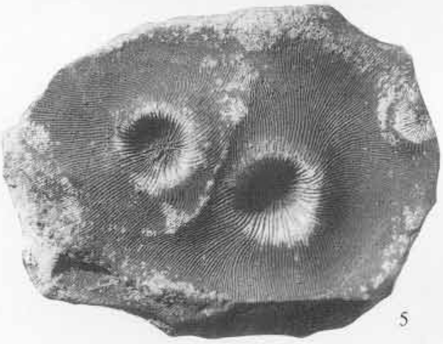
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SCRUTTON, *Arachnophyllum*

reach 22·5 cm^2 (text-fig. 8B). All corallites flat-floored to saucer-shaped with deep tabularial pits <3 mm deep containing a prominent axial boss.

In cross-section, tabularia circular, well defined, 3·4–4·75 mm mean diameter with sixteen to twenty-two major septa (text-fig. 8A). Major septa thin to slightly thickened in tabularia, some reaching and fusing in axis. Minor septa irregularly developed, just penetrating tabularium. Septa may be weakly naotic at the dissepimentarium–tabularium boundary. In dissepimentarium, septal traces sporadic as thin crests on discrete dissepimental surfaces. Small, suboval dissepiment sections bearing septal crests more or less distinctly radially orientated. Characteristic *murchisoni* carination well developed, usually three to four carinae per mm but sometimes rather irregularly spaced. New septa are intercalated in the dissepimentarium to maintain a lateral spacing of 0·25–0·33 mm. Septa may be thickened almost to contiguity immediately above dissepimental surface, apparently composed of thickened multiple trabeculae. Dissepiment sections arcuate to subcircular, crowded, about twelve to fourteen in 10 mm. In larger colonies, positions of walls on colony surface marked by rows of elliptical dissepimental sections flanked by arcuate sections sometimes bearing septal crests.

In longitudinal section, tabularia defined by very steep, small dissepiments. Tabellae flat to dished peripherally with a very wide axial zone of gently arched tabellae. Spacing of tabellae fifteen to twenty in 5 mm. Dissepiments very low to moderately inflated, averaging about 1·5 × 0·3 mm with a maximum of 4 × 1·5 mm. Dissepimentarium prominently zoned with septal crests, averaging 2·5 mm apart, developed on successive surfaces of small, crowded dissepiments. Sections of carinae <2 mm high, constructed of monacanthine trabeculae.

Offsets peripheral, non-parricidal.

Discussion. Although typical *sinemurum* and *quadrangulare* colonial morphologies appear distinct, they share corallites with identical structure and similar dimensions. I conclude that *sinemurum*-morphs represent colonies aborted at an early stage of development, probably by unfavourable environmental conditions, and that the *quadrangulare*-morph represents colonies that survived to form several generations of offsets.

A. sinemurum is closely related to *A. murchisoni*, with which it shares almost identical internal structure. The former is distinguished by the very large size of the corallites (text-fig. 8B).

Arachnophyllum separatum (Ulrich, 1886)

Plate 4, figs. 7–9; text-fig. 8

1886 *Strombodes separatus* Ulrich, p. 32, figs. 1 and 2.
1887 *Strombodes unicus* Davis, pl. 122, fig. 5.
1965 *Arachnophyllum separatum* (Ulrich) Stumm, p. 31, pl. 21, figs. 3–6.

Diagnosis. Colonies or pseudocolonies of up to three trochoid to turbinate corallites. Internal structure apparently of *murchisoni* type. Tabularial diameters approximately 4·0–4·3 mm with about eighteen major septa and corallite areas in the range 4–8 cm^2.

Type material. Lectotype (here designated): AMNH F1 36584 (Ulrich 1886, p. 32, fig. 1). Paralectotype: F1 36585 (Ulrich 1886, p. 32, fig. 2). Both Niagara Group (Silurian, late Wenlock (?early Ludlow), Louisville Limestone); Louisville, Kentucky.

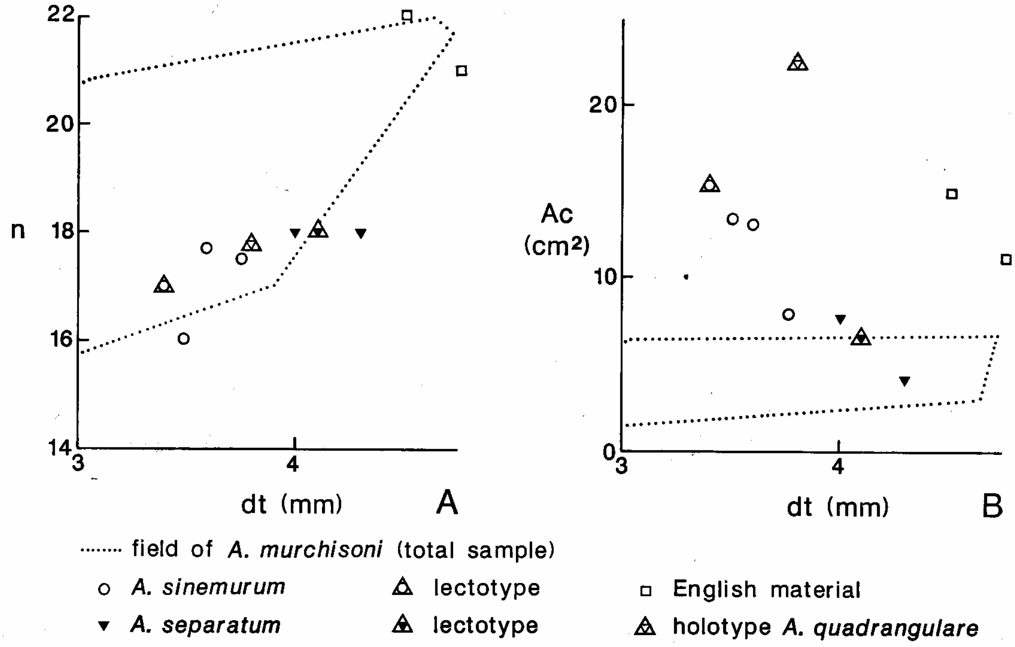
Holotype of *S. unicus*: MCZ 8076, Upper Niagara 'red clay' (Louisville Limestone); Workhouse Quarry, East Louisville, Jefferson Co., Kentucky.

Other material. BMNH R5186, R52632–52635, Niagara Group (Louisville Limestone); Louisville, Kentucky.

Range. Silurian, late Wenlock (?early Ludlow), Louisville Limestone; Kentucky.

Description. Unfortunately all of this material is variably but badly beekitized and is unsuitable for sectioning (Pl. 4, figs. 7–9). From external appearance, although some groups of corallites are clearly associated through offsetting, others may be the result of fusion of solitary coralla. Ulrich (1886, p. 32) describes the corallum as '. . . consisting of one or more individuals, . . .' implying that it may be solitary. All are trochoid to narrowly turbinate, 40 mm high and 20 mm (35 mm according to Ulrich) diameter.

Corallites have flat to slightly dished surfaces with shallow to deep tabularial pits in which a low, axial boss is sometimes preserved. Mean tabularium diameters approximately 4·0–4·3 mm with eighteen major



TEXT-FIG. 8. Variation in A, mean number of major septa (n) and B, maximum corallite area (Ac in cm²), both plotted against mean tabularium diameter (dt in mm) for *Arachnophyllum sinemurum* and *A. separatum*. For discussion see text.

septa and corallite areas up to 8 cm² (text-fig. 8A, B). In some cases, septal structure is clearly visible on the corallite surface, showing the typical *murchisoni*-type carinate meshwork with carinae spaced four per mm. Tabulae cannot be seen but dissepiments appear to be small and weakly inflated.

Discussion. I agree with Stumm (1965, p. 31) that *S. unicus* (Pl. 4, fig. 9) is a junior synonym of *A. separatum*. From what can be seen, *A. separatum* is closely related to *A. murchisoni*, having the same internal structure. The former is distinguished through its growth form, pseudocolonial or weakly colonial structure and rather large corallite area. Colonial structure and growth form also distinguish *A. separatum* from *A. sinemurum*, both species occurring together specifically at the type locality of *S. unicus* and generally in the Louisville Limestone.

Arachnophyllum pentagonum group

Arachnophyllum pentagonum (Goldfuss, 1826)

Plate 5, figs. 1-4; text-figs. 3C, D and 9A, 10

1826 *Strombodes pentagonus* Goldfuss, p. 62, pl. 21, fig 3*a*, *b*.
1851 *Strombodes pentagonus* Goldfuss; Edwards and Haime, p. 430.
e.p. 1876 *Strombodes pentagonus* Goldfuss; Rominger, p. 131, pl. 48, fig. 2 only.
1901 *Arachnophyllum pentagonum* (Goldfuss) Lambe, p. 181, pl. 15, figs. 3 and 3*a*.
1966 *Arachnophyllum pentagonum* (Goldfuss); Bolton, pl. 9, fig. 4.
1981 *Arachnophyllum mamillare* (Owen); Bolton, pl. 4, fig. 7.
non 1887 *Strombodes pentagonus* Goldfuss; Davis, pl. 121, figs. 2 and 3.
non 1949 *Arachnophyllum pentagonum* (Goldfuss); Amsden, p. 104, pl. 26, figs. 1-6.
non 1965 *Arachnophyllum pentagonum* (Goldfuss); Stumm, p. 30, pl. 20, figs. 1-3; pl. 21, fig. 1.

Diagnosis. Tabular colonies of pentagonal corallites, mean area 1·2–4·1 cm^2, separated by more or less sharply defined straight or more rarely curved ridges. Well-defined tabularial pit with axial boss. Major septa, fourteen to nineteen, well developed in tabularia, mean diameter 2·4–3·4 mm. Minor septa, variably developed, may penetrate tabularium or are limited to dissepimentarium where both orders are reduced to low crests on dissepimental surfaces and develop typical *murchisoni*-type carination. Tabularium with flat to slightly dished tabellae surrounding a narrow axial zone of arched tabellae or merging directly with axial septal traces. Dissepiments typically coarse. Increase peripheral, non-parricidal.

Type material. Neotype (here selected): GSC 90730, Silurian, Llandovery, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario.

Other material. GSC 20550, Fossil Hill Formation; Ridge in Long Bay area, south-west bay of Lake Manitou, Manitoulin Island (Bolton 1966, pl. 9, fig. 4). GSC 30534, Silurian, upper Llandovery (?lower Wenlock), Thornloe Formation; roadside exposure, lot 12, concessions V–VI, Dymond Township, Ontario (Bolton and Copeland 1972, pl. 12, fig. 11). BMNH R36122, R36124, Silurian, Niagara Group; Drummond Island, Lake Huron, Michigan, USA. R32154, Silurian, Lockport Formation (Fossil Hill Formation); Fossil Hill, Manitoulin Island. SM A6298, Silurian, Niagaran Formation (Fossil Hill Formation); Manitouwakning, Manitoulin Island. BMNH R20864 Silurian, Niagaran (Fossil Hill Formation); Manitoulin Island. GSC 66806, Silurian, Upper Llandovery, Telychian, La Vieille Formation (lower member); west end of railroad cut, east of highway 132(6) crossing east of Gascons, Gaspé, Quebec (Bolton 1981, pl. 4, fig. 7). GSC 90725, 91555, La Vieille Formation (lower member); railroad cut above Anse-à-la-Vieille, east of Port Daniel, Quebec. GSC 91556, La Vieille Formation; Point La Roche, Charlo area, east New Brunswick.

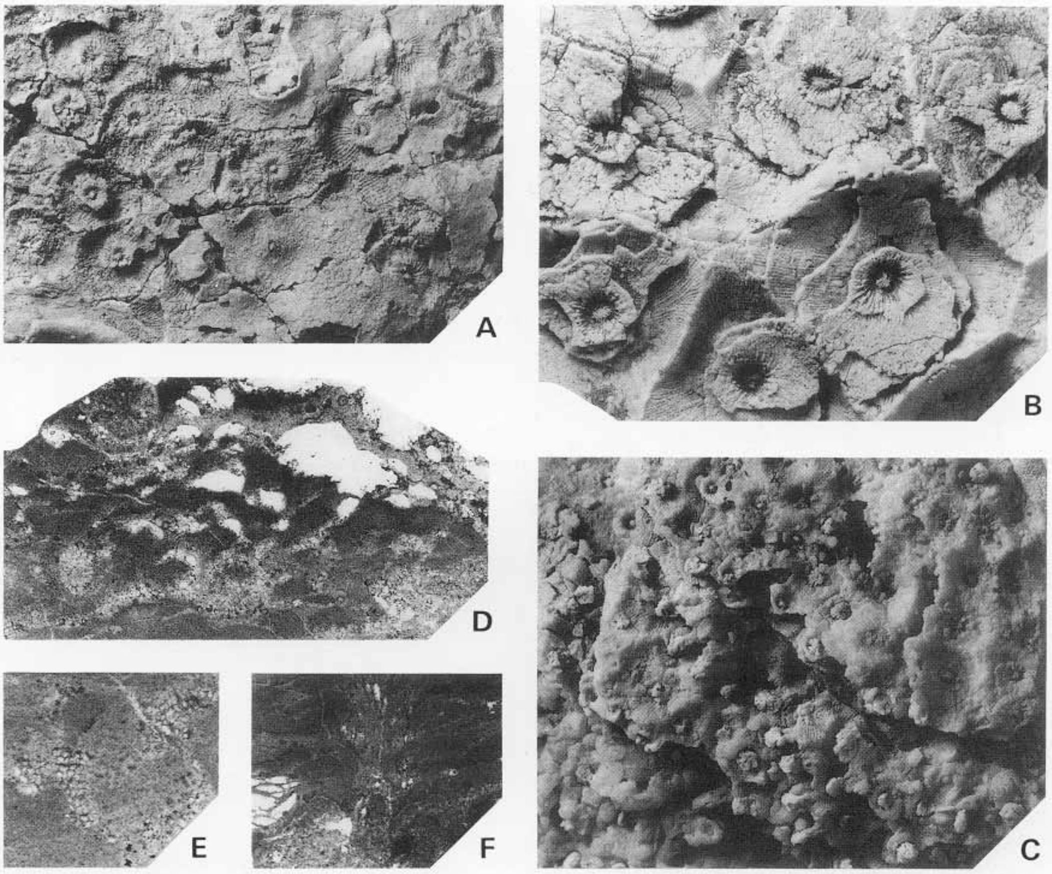
Range. Silurian, Llandovery, Telychian (?Lower Wenlock); Michigan and Ontario and Quebec.

Description. Thin to thick discoidal to tabular colonies < 150 × 140 × 30 mm (present sample). Calicular surface flat to gently arched. Corallites regularly to irregularly pentagonal, separated by well defined, generally sharply crested, straight or less commonly curved walls (text-fig. 9A). Tabularial pit, with or without a weak peritabularial arch, about 1 mm deep with a more or less strong axial boss.

In cross-section, tabularia clearly but sometimes crudely defined by arcuate sections of steeply inclined dissepiments. Major septa, uniformly thin, generally well but sometimes irregularly developed, usually reach or almost reach the axis where they may fuse, are sometimes slightly thickened and rarely coated with minor amounts of stereome. Rarely a weak vortex is developed, or bilateral symmetry may be evident. Minor septa may penetrate tabularia up to half the radius, but are usually poorly developed and limited to the dissepimentarium. Septal development may be so irregular that major and minor septa are not clearly distinguished. In the dissepimentarium, further septa are intercalated to maintain a regular spacing of about 0·25 mm. Here, all septa are restricted to low crests on discrete dissepimental surfaces and appear in arcuate zones and patches where these surfaces are intersected by the plane of section. Septal traces may be sparse (text-fig. 3C). Septa are thickened almost to contiguity at dissepimental surfaces, becoming successively strongly carinate with typical *murchisoni*-type reticulate structure, more weakly carinate and non-reticulate, and non-carinate at higher levels in the septal crest (Pl. 5, figs. 1 and 3). There are four to five carinae per mm. Dissepimentarium with sparse, irregular dissepimental traces, usually about five to seven sections in 10 mm. Chains of smaller, elliptical dissepimental sections mark the position of the intercorallite ridge.

In longitudinal section, tabularia well defined by steeply inclined, usually smaller dissepiments. Tabellae flat to dished peripherally, rising to a slight peak in the axis where they are disrupted by septal traces, or merging with a narrow axial zone of arched to flat-topped tabellae about a third the tabularium in width. There are fifteen to twenty-five tabellae in 5 mm. Dissepiments coarse, generally rather irregular, usually flat and elongated, poorly to moderately inflated, < 11 × 2 mm, rarely more highly inflated < 5 × 3·5 mm. They are organized into crude zones by size 4–8 mm thick, with septal crests developed on surfaces of smaller dissepiments (Pl. 5, figs. 2 and 4). Sections of carinae < 1·5 mm high, normal to the dissepimental surface or between normal and vertical when the surface is highly inclined. Dissepimental surface generally flat, funnelling into tabularium and strongly arched to a vertical zone of slightly smaller dissepiments to define the intercorallite ridge.

Mean tabularium diameters 2·42–3·44 mm with 14·6–19 major septa. Mean corallite areas 1·24–4·14 cm^2. Increase peripheral, non-parricidal.



TEXT-FIG. 9. A, *Arachnophyllum pentagonum* (neotype); Silurian, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario (GSC 90730). B, *A. striatum* (neotype); same horizon and locality (GSC 90731). C, *A. pygmaeum* (syntype); Silurian, 'Niagaran' (?Telychian); Point Detour, Michigan (UMMP (Rominger Collection) 5310). A–C, all × 1. D–F, *A. pygmaeum* (?syntype of *Astraeophyllum gracile*); Silurian, 'Niagaran' (?Telychian); Owen Sound, Ontario (UAGC 518). D, cross-section, × 2·5; E, detail of cross-section showing *murchisoni*-type carination, × 5; F, longitudinal section, × 2·5.

Discussion. The original of Goldfuss (1826, pl. 21, fig. 3*a*, *b*), from Drummond Island in Lake Huron, appears to be lost (Professor Dr Winifred Haas, pers. comm.). There can be little doubt as to the identity of the species both from Goldfuss' illustrations and the relatively consistent contemporary and subsequent interpretation of the species from the type area of Michigan and Ontario. I select a neotype from Manitoulin Island, adjacent to Drummond Island, from where *in situ* material is available. *A. pentagonum* is abundant at the neotype locality, colonies reaching 500 mm across and 100–200 mm thick (Dr Paul Copper, pers. comm.).

In most respects, *A. pentagonum* is structurally similar to *A. murchisoni*, both sharing in particular the distinctive reticulate septal structure in the dissepimentarium. *A. pentagonum* is distinguished through its consistently and considerably coarser dissepiments, a feature noted by Rominger (1876, p. 132) in contrast to Louisville Limestone material, but apparently subsequently overlooked. North American material of *A. murchisoni* has usually been referred to *A. pentagonum*. In addition in this species, axial arched to flat-topped tabellae tend to be narrower or absent in comparison to the generally broadly arched tabellae of *A. murchisoni*. Neither does *A. pentagonum* appear to show the wide variety of surface morphology found in *A. murchisoni*.

A. striatum and *A. pygmaeum* both have similar internal structure to *A. pentagonum*, including the characteristically coarse dissepiments. These two species are distinguished principally on size, *A. striatum* having much larger corallites and *A. pygmaeum* having smaller coralites than *A. pentagonum* (text-fig. 10).

Arachnophyllum striatum (d'Orbigny, 1850)

Plate 5, figs. 7–8; text-figs. 9B and 10

1850 *Favastraea striata* d'Orbigny, p. 48.
1851 *Strombodes striatus* (d'Orbigny) Edwards and Haime, p. 430.
e.p. 1876 *Strombodes pentagonus* Goldfuss; Rominger, p. 131, pl. 48, fig. 1 only.
1966 *Arachnophyllum striatum* (d'Orbigny); Bolton, pl. 9, fig. 1.
non 1887 *Strombodes striatus* (d'Orbigny); Davis, pl. 121, fig. 1; pl. 122, figs. 1 and 2.
non 1965 *Arachnophyllum striatum* (d'Orbigny) Stumm, p. 30, pl. 20, figs. 4–6.

Diagnosis. Tabular colonies with large, regularly pentagonal corallites, about 8 cm^2 mean area, separated by sharply defined ridges. Major septa, twenty-two in tabularium diameter 5·0 mm, reach axis in well-defined tabularia. Minor septa just penetrate tabularium. In dissepimentarium, septa developed only on discrete dissepimental surfaces as low crests with typical *murchisoni*-type carination. Tabellae gently arched in axial third of the tabularium. Dissepiments coarse.

Type material. Neotype (here selected): GSC 90731, Silurian, Llandovery, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario.

Other material. GSC 20547, Fossil Hill Formation; 0·48 km south of Manitowaning–South Baymouth Road, lot 9, concession I, Assiginack township, Manitoulin Island (Bolton 1966, pl. 9, fig. 1). BM R32153, Silurian, Lockport Formation (Fossil Hill Formation); Fossil Hill, Manitoulin Island.

Range. Silurian, Landovery, Telychian; Michigan and Ontario.

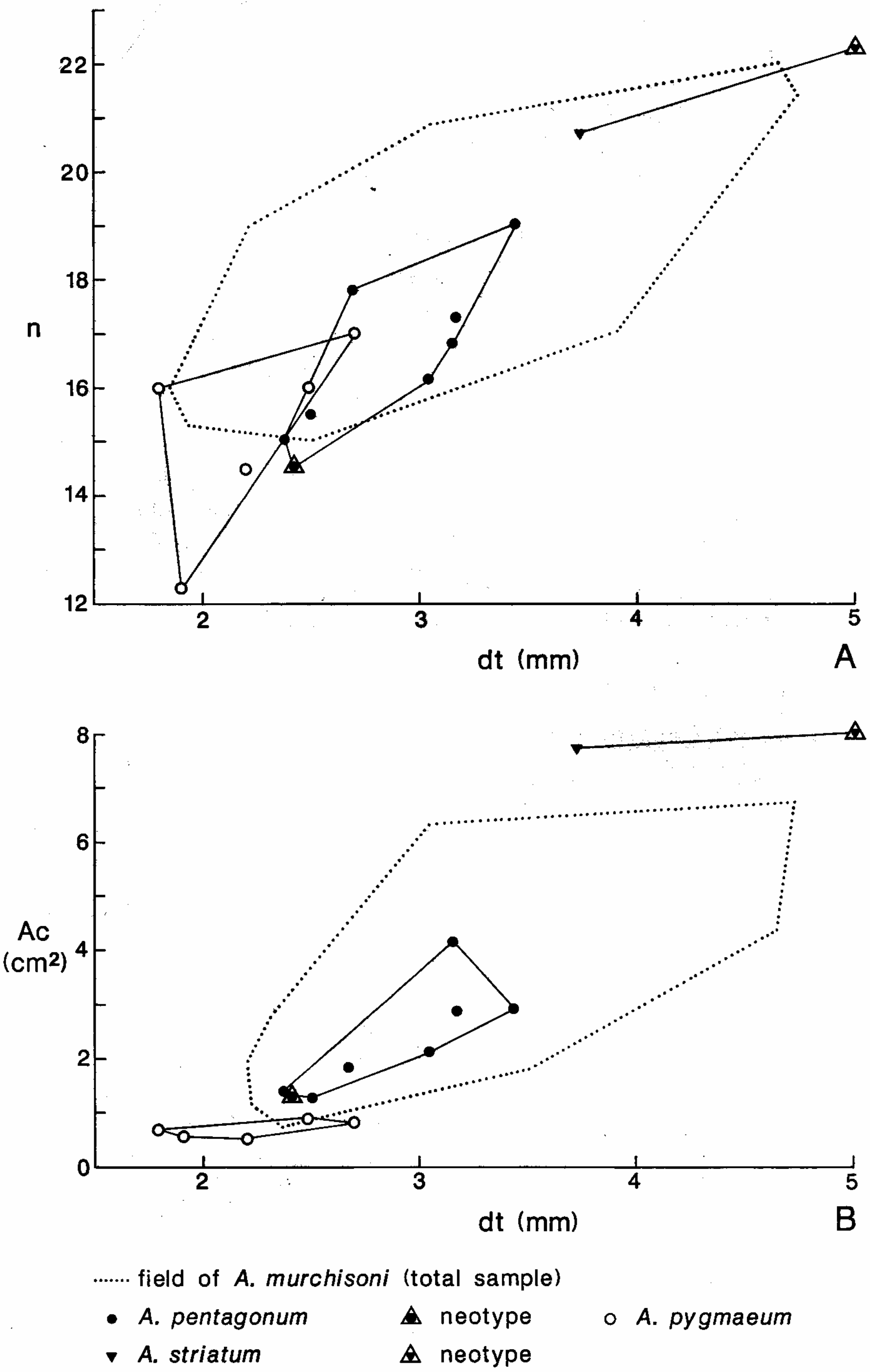
Description. Colonies tabular, $<100 \times 80 \times 40$ mm. Corallites separated by straight, sharply crested walls <4 mm high, curving down into saucer-shaped dissepimental surface, with a central tabularial pit <3 mm deep containing a prominent axial boss (text-fig. 9B).

Tabularia well defined by smaller, steeply inclined dissepiments, usually with a thickened surface. Major septa well developed, tapering to uniformly attenuate, most just reaching and a few fusing in the axis (Pl. 5, fig. 7). Minor septa just penetrate tabularium. In the dissepimentarium, septa present only as low crests on dissepimental surfaces and develop typical *murchisoni*-type reticulate structure, with carinae four to five per mm and septa about 0·25 mm apart. Sections of dissepiments wide spaced and irregular, about six in 10 mm. Arcuate traces of septal crests symmetrically distributed about the positions of intercorallite walls in peripheral parts of corallites.

In longitudinal section, tabularia fairly well defined (Pl. 5, fig. 8). Peripheral flat to dished tabellae interlock with gently arched plates in the axial third of the tabularium, where they are disrupted by septal traces. Tabellae spaced fifteen in 5 mm. Peritabularial dissepiments relatively small and steeply inclined adaxially, becoming coarse, moderately inflated and shallowly inclined adaxially away from tabularium. Intercorallite wall intermittently strongly defined by short columns of very small dissepiments. Dissepiments $<10 \times 3$ mm. Septal crests 3–4 mm apart on surfaces of slightly smaller dissepiments with characteristic sections of carinae up to 1 mm high.

Tabularium diameter < 5 mm with twenty-two major septa and mean corallite area of 8 cm^2.

Discussion. D'Orbigny's specimen cannot be found (Dr Pierre Semenoff-Tian-Chansky, pers. comm.). According to Edwards and Haime (1851, p. 430), d'Orbigny gave the location of his specimen as the Falls of the Ohio in error; it should have been Drummond Island, Lake Huron. Although neither d'Orbigny nor Edwards and Haime figured this species, there seems to be little



TEXT-FIG. 10. Variation in A, mean number of major septa (n) and B, mean corallite area (Ac in cm^2), both plotted against mean tabularium diameter (dt in mm) for *Arachnophyllum pentagonum*, *A. striatum*, and *A. pygmaeum*. For discussion see text.

doubt from their descriptions of its identity as a large corallite equivalent of *A. pentagonum* (text-fig. 10). Rominger (1876, p. 131) considered the two species to grade into one another, but Dr Paul Copper (pers. comm.), who kindly provided the neotype specimen, states that in the Fossil Hill Formation the range of size variation is discontinuous between *A. pentagonum* and *A. striatum*. I therefore retain the species here on that basis.

This species name has occasionally been applied to North American material of *A. murchisoni*.

Arachnophyllum pygmaeum (Rominger, 1876)

Plate 5, figs. 6 and 7; text-figs. 9C–F and 10

1874 *Astraeophyllum gracile* Nicholson and Hinde, p. 138, fig. 4*a*, *b*.
1876 *Strombodes pygmaeus* Rominger, p. 132, pl. 48, fig. 3.
non 1887 *Strombodes pygmaeus* Rominger; Davis, pl. 123, fig. 1

Diagnosis. Laminar to tabular colonies of small, equidimensional polygonal corallites, mean area 0·5–0·9 cm^2, separated by straight, low rounded walls. Major septa extend to axis in tabularia, twelve to seventeen in mean diameter 1·8–2·7 mm, forming a boss in the tabularial pit. Septa in dissepimentarium very sparsely developed as crests on dissepiments, showing typical *murchisoni*-type reticulate structure. Tabularium with or without narrow axial series of flat-topped tabellae. Dissepiments coarse, very variably inflated.

Type material. Syntypes UMMP 8604 and 5410, Silurian, Niagaran; Drummond Island and Point Detour, Michigan respectively.

Syntypes? of *A. gracile*: UAGC 518, 12101–12103 (Of these four specimens, one, UAGC 12103, is probably a specimen of *Prodarwinia speciosa*), Niagaran; Owen Sound, Ontario.

Other material. GSC 2639, Middle Silurian, Lockport; Derby, lot 13, concession 2, near Owen Sound, Ontario. BMNH R36121, R36123, Silurian, Niagaran; Drummond Island, Lake Huron.

Range. Silurian, upper Llandovery, Telychian (?Wenlock); Michigan and Ontario.

Description. Thin laminar to thick tabular colonies $<100 \times 80 \times 60$ mm composed of small, equidimensional polygonal corallites (text-fig. 9C). Calices saucer-shaped with or without slight peritabularial ridge and tabularial pit <2 mm deep containing prominent axial boss. Calices separated by low ridges, highest at wall junctions.

In cross-section, tabularia subcircular, outlined by arcuate sections of small steeply inclined dissepiments. Major septa, slender, extend to axis and fuse to form a boss of variable size and definition. Minor septa just penetrate tabularium. Dissepimentarium consisting of dissepiment sections of very variable size and shape, but typically four to five sections in 10 mm. Traces of septa rare as very low unthickened crests on discrete dissepimental surfaces. Typical *murchisoni*-type reticulate structure developed but seldom observed in cross-section (Pl. 5, fig. 5; text-fig. 9E). No distinct arrangement of dissepiments in area of corallite wall.

In longitudinal section, tabularia well defined (Pl. 5, fig. 6). Peripheral flat to slightly dished tabellae curve upwards to meet axial septal traces, or to narrow axial series, about 0·25 tabularium wide, of flat-topped tabellae where septal traces are poorly developed. There are twelve to twenty tabellae in 5 mm. Dissepiments

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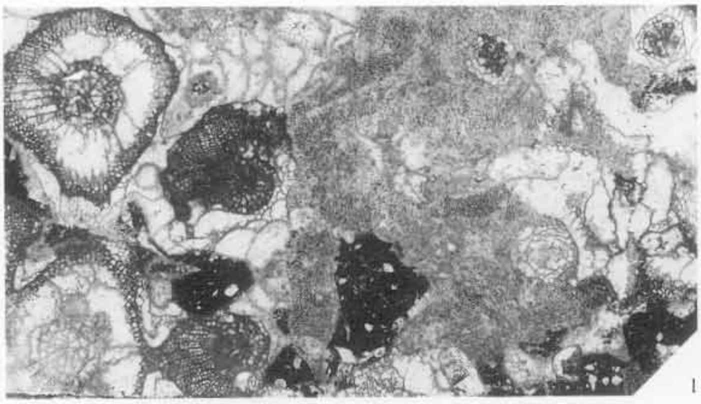
EXPLANATION OF PLATE 5

Figs. 1–4. *Arachnophyllum pentagonum*. 1, cross-section and 2, longitudinal section of neotype (GSC 90730); Silurian, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario. 3, cross-section and 4, longitudinal section (BMNH R20864); Silurian, Niagaran; Manitoulin Island, Ontario.

Figs. 5 and 6. *A. pygmaeum* (BMNH R36121). 5, cross-section and 6, longitudinal section; Silurian, Niagaran; Drummond Island, Lake Huron, Michigan. Figs. 7 and 8. Neotype of *Arachnophyllum striatum* (GSC 90731). 7, cross-section and 8, longitudinal section; Silurian, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario.

All figs. ×2·5.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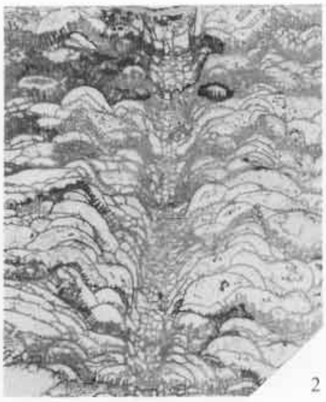
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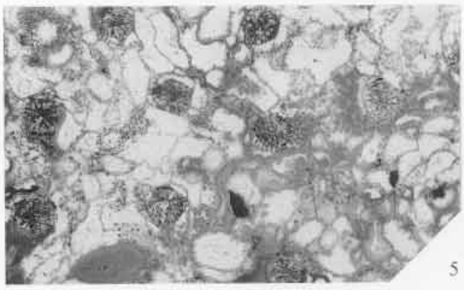
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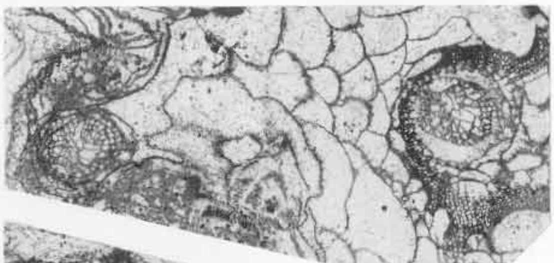
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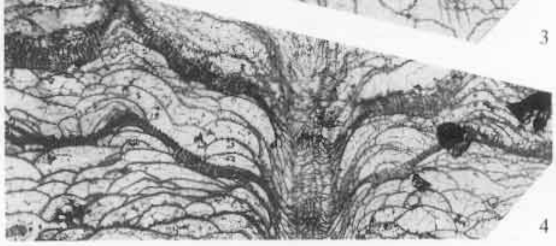
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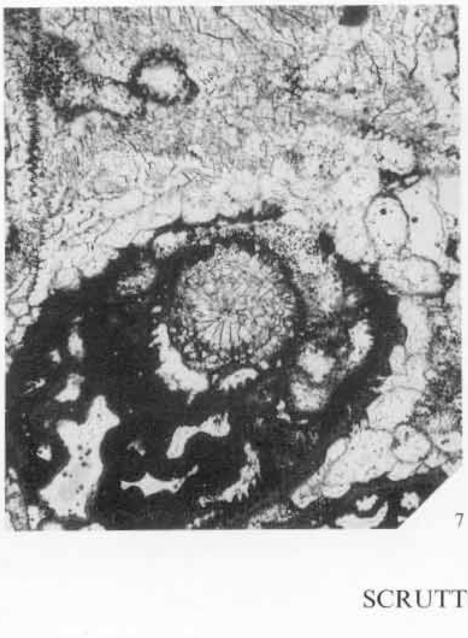
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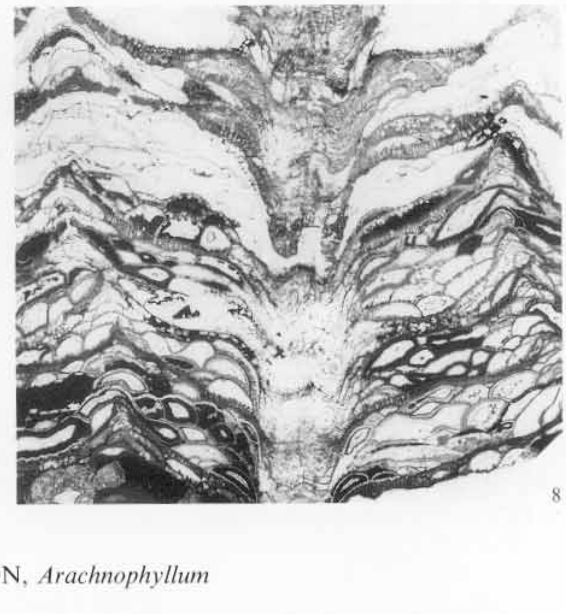
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SCRUTTON, *Arachnophyllum*

very variable, poorly to strongly inflated, coarse, $<6 \times 2$ mm. Smaller dissepiments occur in ill-defined zones. Septal crests thin and sparse with sections of carinae $<0{\cdot}75$ mm high.

Tabularium diameters 1·8–2·7 mm with 12·3–17 septa and mean corallite areas 0·49–0·89 cm^2.

Discussion. Benton (1979, p. 31) has recognized UAGC 518, 12101–12103 as Nicholson material, and possibly therefore the syntype set of *Astraeophyllum gracile*, among other Nicholson type specimens in the University of Aberdeen. Unfortunately, the four badly preserved fragments cannot be recognized from Nicholson and Hinde's (1874, p. 138, fig. 4*a*, *b*) very stylized figures although they could have been the basis for them. The material is so poor that sections of the only specimen suitable for preparation, UAGC 518, reveal little more than a trace of typical *murchisoni*-type septal reticulation, proving beyond doubt that the specimen belongs to *Arachnophyllum*, and the general dimensions and sparse septal development of *A. pygmaeum* (text-fig. 9D–F). UAGC 12103, of doubtful identity, is unsuitable as a basis for firmly establishing *A. gracile* as a junior synonym of *Prodarwinia speciosa*. Thus, it would simply be better to set *gracile* aside in favour of the better established species.

Unfortunately, the original of Rominger's (1876, pl. 48, fig. 3) figured specimen, UMMP 8604, the most suitable lectotype for *A. pygmaeum*, is mislaid but probably not lost (Dr J. A. Kitchell, pers. comm.). I therefore refrain from making a type selection for this species at the moment. The identity of the species appears to be quite clear from Rominger's illustration and account.

A. pygmaeum is most closely related to *A. pentagonum*, from which it differs principally is its small size (text-fig. 10), particularly its small corallite area, its relatively weak intercorallite walls, and the very weak development of septa in the dissepimentarium.

Unrecognizable species of ?*Arachnophyllum*

Lamellopora infundibularia Owen, 1844

1844 *Lamellopora infundibularia* Owen, p. 70, pl. 14, fig. 1.
1851 *Strombodes infundibularius* (Owen) Edwards and Haime, p. 432.

Type material. Owen's figured specimen is lost. It was recorded from the 'coralline beds of the Upper Magnesian Cliff Limestone of Iowa and Wisconsin', likely to represent either the Hopkinton or Kankakee Dolomite according to Laub (1979, p. 194).

Discussion. Edwards and Haime (1851) thought Owen's species to be either a small *S. pentagonum* or perhaps *S. mamillaris*. From Owen's figure, which is a side view of the colony, little can be deduced except that it could be an amural arachnophyllid or even a stromatoporoid (Lang *et al.* 1940, p. 74; Hill 1981, p. 669). The species is unrecognizable.

Genus PRODARWINIA Cotton, 1973

1873 *Darwinia* Dybowski, pp. 336, 404.
1940 *Darwinia;* Lang, Smith and Thomas, p. 49.
1973 *Prodarwinia* Cotton, p. 161.

Diagnosis. Astraeoid to thamnasterioid coralla lacking intercorallite ridges. Tabularia usually set on more or less prominent mamelons. Septa monacanthine thin continuous plates in tabularium, but multitrabecular, becoming pseudorhabdacanthine in the dissepimentarium, weakly and irregularly carinate or non-carinate. Solid septal laminae of variable thickness may develop on successive discrete dissepimental surfaces by trabecular thickening and/or embedding in lamellar sclerenchyme. Tabellae flat to dished peripherally, merging axially into septal sections or with axial series of flat topped tabellae. Dissepiments variable in size and weakly inflated.

Type species. Darwinia speciosa Dybowski, 1873.

Discussion. The generic name *Darwinia* Dybowski, 1873 is preoccupied by *Darwinia* Bate, 1857 for a crustacean (Lang *et al.* 1940, p. 49). The genus was therefore renamed *Prodarwinia* by Cotton (1973, p. 161).

Prodarwinia is almost identical in structure to the Devonian genus *Iowaphyllum* (see Oliver and Galle 1971; Oliver 1978). The only distinctions are of uncertain significance, such as the lack of corallite walls on the external calicular surface and the pseudorhabdacanthine trabeculae of *Prodarwinia*. Species of *Iowaphyllum* usually have external corallite walls which are sometimes reflected in the internal structure by other than the form of the dissepimentarium surface alone. The septa in *Iowaphyllum* may be unitrabecular coarse simple monacanths or multitrabecular. Septal structure in *Prodarwinia* is distinctive (text-fig. 7C, D). Septa are multitrabecular and in the dissepimentarium when solid septal crests are developed, trabeculae appear to be thin, <c. 0·1 mm diameter, and loosely branching (pseudorhabdacanthine), embedded in lamellar sclerenchyme. The possibility that this appearance is a preservational artefact has been considered, but the standard of preservation, its appearance in material from several different localities, and its relationship with the surface topography of the septal crests suggest that it is an original structure. Although species of *Iowaphyllum* appear to have little additional sclerenchyme in their septa, traces of a similar microstructure to that in *Prodarwinia* are illustrated in *I. nisbeti* from the Upper Devonian (Frasnian) of Arizona by Oliver (1978, fig. 3*b*, *d*, *f*).

The principal reason for maintaining two distinct genera is the long stratigraphical gap between the Silurian and Devonian species groups. No species referable to either genus are known from the Ludlow (or at least later Ludlow), Přídolí, or Lochkov. Coral faunas are sufficiently well known from these levels to suggest that this gap is real and not a preservational or descriptive artefact. I conclude that the two genera represent an extreme case of homoeomorphy.

Range. Llandovery (Aeronian)-late Wenlock (?early Ludlow); Estonia, Gotland, USA, southern Canada.

Prodarwinia speciosa (Dybowski, 1873)

Plate 6, fig. 1; Plate 7, figs. 1-7; text-figs. 7C, D, 11, 12

1858 *Strombodes diffluens* Edwards and Haime; Schmidt, p. 232.
1873 *Darwinia speciosa* Dybowski, p. 404, pl. 2, fig. 8 and 8*a*.
? 1901 *Arachnophyllum diffluens* (Edwards and Haime); Lambe, p. 183, pl. 14, fig. 12.
e.p. 1927 *Arachnophyllum diffluens* (Edwards and Haime); Lang and Smith, p. 468 (syn. only).
1973 *Prodarwinia speciosa* (Dybowski) Cotton, p. 161.

Diagnosis. Flat, tabular astraeoid to thamnasterioid colonies. Tabularial pits set in broad, low, rounded mamelons; no intercorallite walls. Tabularia fairly well defined. Mean tabularium diameter 1·82–3·23 mm with fifteen to twenty-one major septa and mean corallite area 0·63–2·41 cm^2. Major septa usually extend to axis and fuse to form columella. In dissepimentarium, septa may extend a short distance from tabularium as discontinuous or continuous attenuate blades. More frequently, septa are multitrabecular and contiguous, forming arcuate belts and patches of solid tissue with unthickened, coarse, irregular dissepimental sections in between. Tabularia clearly defined by steeply inclined dissepimental sections in longitudinal section. Tabellae periaxial, dished, merging with septal sections in axis. Dissepiments very variable, poorly to strongly inflated, crudely zoned. Solid septal crests usually developed on specific dissepimental surfaces, but may be reduced to discrete trabeculae in some specimens.

Type material. Lectotype (chosen by Lang *et al.* 1940, p. 49): the original of Dybowski's (1873) pl. 2, fig. 8 of *Darwinia speciosa* var. *major*, which is IGT Co1334; Silurian, Adavere Stage, Rumba Formation (late Aeronian), Päri (ex Kattentack), Estonia.

Other material. IGT Co1348, BMNH R53510-53512, horizon and locality as for lectotype. Co1349, Silurian, Adavere Stage, Rumba Formation; Tammikaäre, Estonia. Co1350, Rumba Formation; Väike Röhda, Estonia. GSC 2639*a*, Lockport; Owen Sound, Ontario (?figured Lambe 1901. pl. 14, fig, 12). GSC 90732, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario. ?UAGC 12103, Niagaran; Owen Sound, Ontario. UCBL EM 15171 (de Verneuil Collection), (?Silurian, Hopkinton Formation); Wisconsin.

Range. Silurian, Llandovery, late Aeronian-Telychian; Estonia, USA, Canada.

Description. Thin, tabular astraeoid–thamnasterioid colonies $< c.$ 240 mm diameter and 35 mm thick. Calicular surface undulose to flat. Tabularial pits with strong axial boss set in broad, low, rounded mamelons (Pl. 6, fig. 1; text-fig. 11A,D). Septa more or less sharp granular ridges, more often continuous than abutting between corallites.

In cross-section, tabularia fairly well defined by thickened sections of one to three concentric series of steeply inclined dissepiments, or set in solid septal material (Pl. 7, figs. 1, 2, 4, 6; text-fig. 11B). Major and minor septa clearly distinguished. Majors usually extend to axis, attenuate to slightly thickened $< 0{\cdot}1$ mm, where they fuse together, or in groups, sometimes forming a stellate axial structure with periaxial tabellae and occasional minor sclerenchyme. Minor septa just penetrate tabularium, but individual septa rarely may be longer. Outside tabularium, septa may extend a short distance as unitrabecular attenuate blades, either continuous or as alligned series of septal crests, or are absent. In specimens with well-developed solid septal crests tabularia more usually set in annular, arcuate, or irregular patches of solid material in which individual multitrabecular septa are difficult to distinguish. Margins of solid areas dentate where septa rapidly taper and disappear. Elsewhere, unthickened dissepiment sections are coarse and irregular, four to eight in 10 mm.

In longitudinal section, tabularia well defined by steeply inclined inner dissepiment faces. Tabellae peripherally dished, close-spaced twelve to twenty-two in 5 mm, rising to axial septal sections. Where major septa do not reach the axis, there may be a narrow axial series of flat tabellae. Dissepiments very variable in form, poorly to strongly inflated, $< 8 \times 1{\cdot}5$ mm, crudely zoned. Solid septal crests of varying thickness < 4 mm thick, rarely 7 mm where several coalesce laterally, usually developed on discrete dissepimental surfaces (Pl. 7, figs. 5 and 7), but may be reduced to discrete trabeculae in some specimens (Pl. 7, fig. 3). There may be four to seven crests in 5 mm vertical growth. In some specimens, layers of thin septal crests may be capped or sandwiched between zones of more or less solid septal material < 15 mm thick (text-fig. 11C). In dissepimentarium, crests with dentate upper surfaces formed of thin, $< c.$ 0·1 mm diameter, crudely branching trabeculae (pseudorhabdacanths) set in lamellar sclerenchyme (text-fig. 7D), but becoming solidly trabecular at tabularium.

Mean tabularium diameters vary 1·82–3·23 mm with 15–20·5 major septa and mean corallite area 0·63–2·41 cm^2 (text-fig. 12).

Discussion. Dybowski (1873, pp. 404–406) distinguished *major* and *minor* varieties of *D. speciosa*, of which the original of var. *minor* is now missing. He recorded both varieties from Päri and the small collection of topotypic material described here suggests continuous variation in the sample, although it may not include the extreme limit represented by var. *minor*.

P. speciosa is very close to *P. striata*. The latter has smaller tabularium diameters and septal number but more overlap in corallite area (text-fig. 12). In addition, the weak mamelons on the calicular surface of *P. striata* are confined to the immediate peritabularial area in contrast to the equally weak but broader swellings bearing the tabularia in *P. speciosa* (compare Pl. 6, fig. 1 and text-fig. 11A, D with Pl. 6, fig. 2).

EXPLANATION OF PLATE 6

Fig. 1. *Prodarwinia speciosa*, calicular surface (BMNH R53512); Silurian, Aeronian, Rumba Formation; Päri, Estonia.

Fig. 2. *P. striata*, calicular surface (RM Cn20154); Silurian, Telychian, Rode Mergel; Norderstrand, Visby, Gotland.

Figs. 3 and 4. *P. distans*, calicular surfaces. 3, lectotype (USNM 113639); Silurian, Llandovery, Noland Formation. Waco Member; Irvine, Kentucky; 4, BMNH R50215; Silurian, Telychian, Hopkinton Formation; Manchester, Iowa.

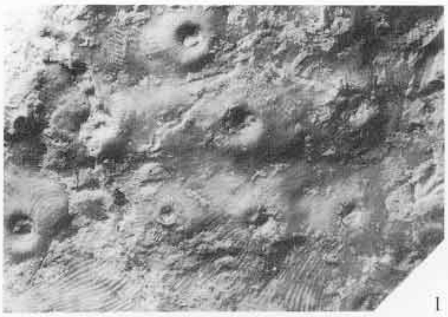
Figs. 5 and 6. *P. mamillaris*, calicular surfaces. 5, GSC 20534; Silurian, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario; 6, USNM 422823; Silurian, Louisville Limestone; Louisville, Kentucky.

Figs. 7 and 8. *P. striata* (USNM 422827). 7, cross-section and 8, longitudinal section; Silurian, Telychian, Dayton Formation; Todd's Fork, 3·2 km north of Wilmington, Ohio.

Figs. 9 and 10. *P. distans* (USNM 422825). 9, cross-section and 10, longitudinal section; Silurian, Llandovery, Noland Formation, Waco Member; Indian Fields, Kentucky.

Figs. 1–6, ×1. Figs. 7–10, ×2·5.

PLATE 6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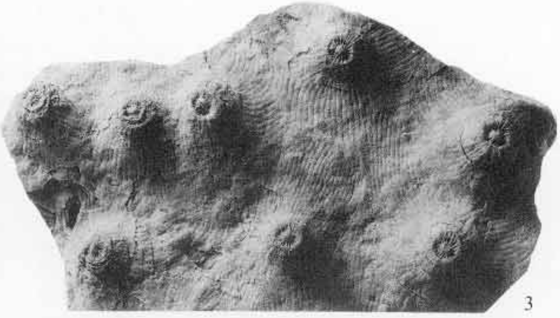
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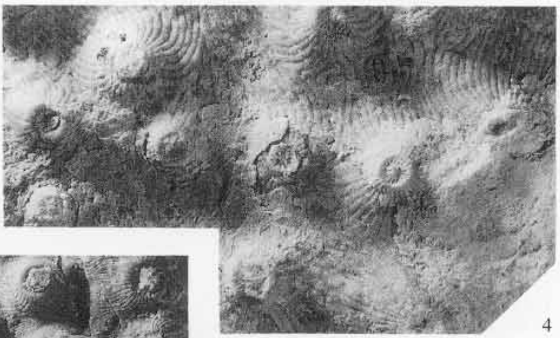
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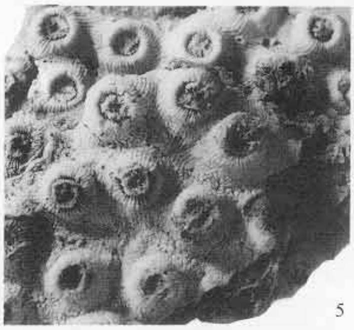
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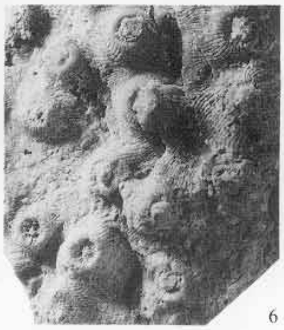
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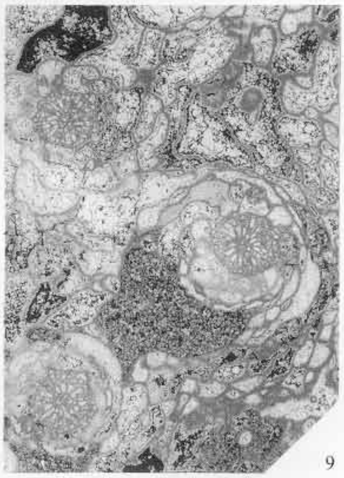
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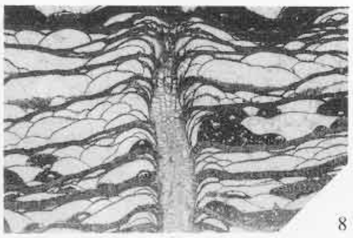
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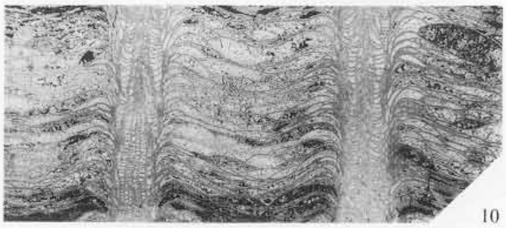
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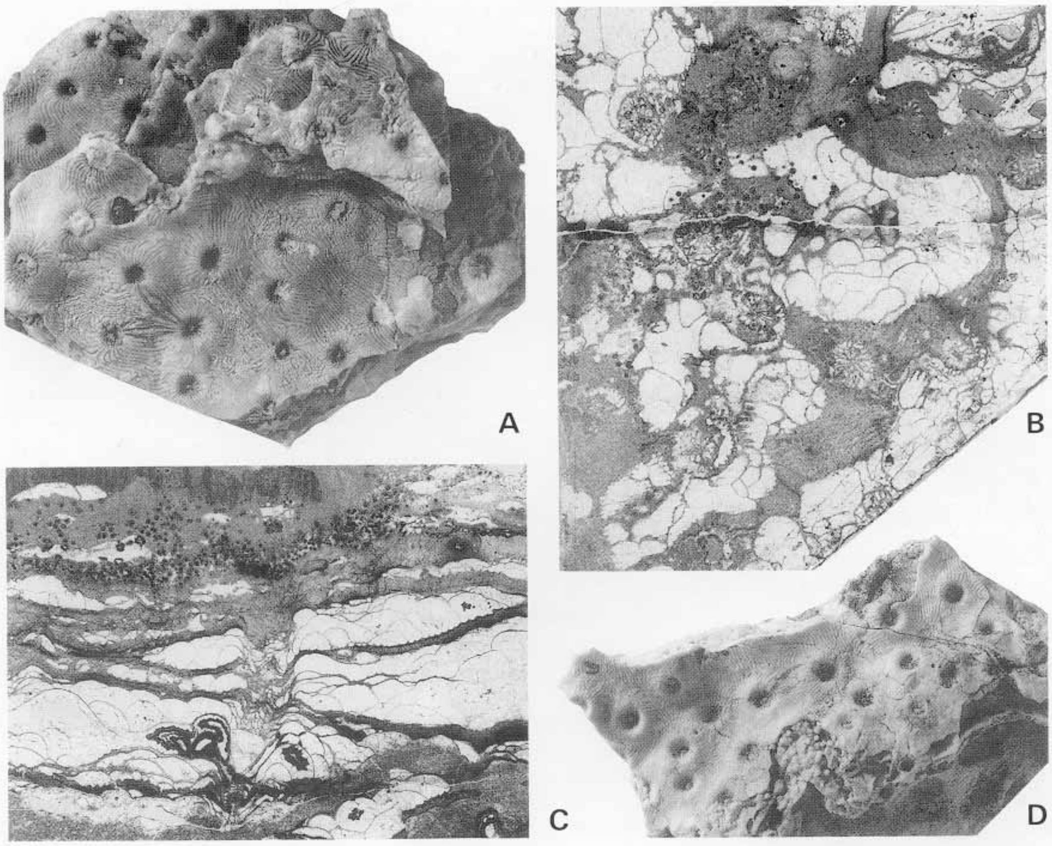
SCRUTTON, *Prodarwinia*



TEXT-FIG. 11. *Prodarwinia speciosa*, North American material. A, calicular surface; Silurian (?Hopkinton Formation); Wisconsin (UCBL (de Verneuil Collection) EM 15171), × 1. B, cross-section and C, longitudinal section; Silurian, Telychian, Fossil Hill Formation; Fossil Hill, Manitoulin Island, Ontario (GSC 90732), both × 2·5. D, calicular surface; Silurian, Lockport; Owen Sound, Ontario (GSC 2639*a*), × 1.

Specimens of *P. striata* consistently develop solid septal crests, but some specimens of *P. speciosa* do not. These approach *P. distans* and *P. mamillaris* in internal structure but lack the strong calical surface features of these species.

P. speciosa has most frequently been referred to as *Arachnophyllum diffluens* in the literature. There is some similarity between the calicular surfaces of the *diffluens*-morph of *A. murchisoni* and *P. speciosa* but considerable contrasts in their internal structures, particularly with the lack of *murchisoni*-type carination in the latter (contrast Pl. 2, figs. 2 and 3 of the lectotype of *Strombodes diffluens* with Pl. 7, figs. 1–7).

Prodarwinia striata (James, 1878)

Plate 6, figs. 2, 7, 8; Plate 7, figs. 8–12; text-fig. 12

1878 *Lyellia striata* James, p. 10.
? 1888 *Strombodes pygmaeus* Rominger; Foerste, p. 120, pl. 13, fig. 18.
1906 *Arachnophyllum mamillare-wilmingtonensis* Foerste, p. 320.
e.p. 1979 *Arachnophyllum mamillare* (Owen); Laub, p. 194, pl. 7, fig. 3 only.

Diagnosis. Tabular astreoid to thamnasterioid colonies with tabularial pits surrounded by low peritabularial swellings; no intercorallite walls. Tabularia strongly defined with major septa extending to axis and fusing to form prominent columella. Mean tabularium diameter 1·52–1·93 mm with 11–16·5 major septa; mean corallite area 0·78–1·52 cm². In dissepimentarium, major and minor septa present as contiguous, multitrabecular laminae on dissepimental crests. Tabularium with peripheral series of dished tabellae merging with septal traces in axis. Dissepiments variable in size, weakly inflated.

Type material. Neotype (here selected): USNM 422826, Silurian, late Telychian, Dayton Limestone; Todds Fork, 3·2 km north of Wilmington, Ohio.

USNM 422826 is labelled '*Lyellia striata*, James' and was collected by James and donated to the National Museum of Natural History in 1883. It agrees closely with James' description of his species, based on one of two specimens, but cannot certainly be identified as that syntype; it does not agree in size with the other syntype. In this case, stability seems best served by designating the available specimen as neotype for the species.

The original of Foerste's *Strombodes pygmaeus* (Foerste 1888, pl. 13, fig. 18) from the Dayton Limestone of Ohio, for which he later erected the subspecies *wilmingtonensis*, has not been located. However, Foerste (1906, p. 320) also stated that *A. mamillare-wilmingtonensis* '. . . was described as *Lyellia striata*, by U. P. James . . .' and could therefore be considered technically as an objective synonym of James' species. USNM 422826 has a second label bearing Foerste's subspecies name and the specimen could have been seen by Foerste at that time.

Material. USNM 422827, Dayton Limestone; Todd's Fork, 3·2 km north of Wilmington, Ohio. RM Cn20114, Cn 20135-6, Cn20154, Cn67085, Silurian, Upper Llandovery, Rode Mergel (*Arachnophyllum* Bed); Norderstrand, Visby, Gotland.

Range. Silurian, Llandovery (Telychian); Ohio and Gotland.

Description. Tabular colonies $<150 \times 80 \times 40$ mm. Calicular surface flat but for peritabularial ridge about 1 mm high surrounding tabularial pit 1–2 mm deep crossed by thin radiating septal plates to prominent axial boss (Pl. 6, fig. 2). Outside tabularium, septa low granular ribs tending to parallel perferred orientations, predominantly confluent with those of adjacent corallites.

In cross-section, tabularia clearly defined with thin to thickened, 0·025–0·15 mm thick, major septa, sometimes slightly tapering, extending to the axis where they fuse, sometimes coated with a little sclerenchyme, to form a prominent columella. Minor septa may or may not just penetrate tabularium. Tabularium surrounded by thick to thin wall of steeply inclined dissepiments bearing septal crests, or set in an area of solid trabecular material in which individual septa are not usually clearly distinguished (Pl. 6, fig. 7; Pl. 7, figs. 8, 9, 11). In places, small trabeculae 0·05–0·1 mm diameter are set in sclerenchyme; elsewhere thickened trabeculae may be contiguous. Laterally in the dissepimentarium, individual septa consists of three to four trabeculae abreast and taper more or less abruptly to a point or short, unitrabecular blade. Between septal material, dissepiment sections coarse and irregular, five to ten in 10 mm.

In longitudinal section, tabularia sharply defined with periaxial, close-spaced, trough-shaped tabellae merging into an irregular axial septal columella (Pl. 6, fig. 8; Pl. 7, figs. 10 and 12). Tabellae eighteen to thirty in 5 mm. Dissepimentarium, arched adjacent to tabularium but flat elsewhere, consists of thick solid septal crests based on successive series of wide, poorly inflated dissepiments, <8 mm $\times$ 2 mm. Septal crests up to 5 mm thick but usually 0·5–1 mm thick. Three to eight discrete crests separated by dissepiments may be superposed in 5 mm and crests may coalesce laterally to form thicker solid laminae. Trabeculae about 0·13 mm wide in plane of septa, either contiguous or set in lamellar sclerenchyme when they may appear pseudorhabdacanthine in form.

Mean tabularium diameter range from 1·52–1·93 mm with 11·46–16·5 major septa. Mean corallite areas 0·78–1·52 cm².

Increase intercalicinal.

Discussion. The neotype from Ohio is almost indistinguishable from material from the *Arachnophyllum* Bed at the very base of the succession on Gotland.

P. striata is closest to *P. speciosa* with which it is likely to have a direct evolutionary relationship as discussed earlier. The two species are compared under the discussion of the latter.

Prodarwinia mamillaris (Owen, 1844)

Plate 6, figs. 5 and 6; Plate 8, figs. 1–5; text-fig. 12

	1844	*Astrea mamillaris* Owen, p. 70, pl. 14, fig. 3.
	1876	*Strombodes mamillatus* (Owen) Rominger, p. 133, pl. 48, fig. 4.
	1887	*Strombodes mamillaris* (Owen); Davis, pl. 123, fig. 4.
	1965	*Arachnophyllum mammillare* (Owen); Stumm, p. 31, pl. 20, figs. 7–9.
	1966	*Arachnophyllum mammillare* (Owen); Bolton, pl. 6, fig. 15.
e.p.	1979	*Arachnophyllum mamillare* (Owen); Laub, p. 194, *non* pl. 7, figs. 2 and 3; pl. 25, figs. 1 and 3.
?*non*	1901	*Arachnophyllum mamillare* (Owen) Lambe, p. 182, pl. 15, fig. 4.
non	1981*c*	*Arachnophyllum mammillare* (Owen); Bolton, pl. 4, fig. 7.

Diagnosis. Tabular colonies of close-spaced corallites, mean area 1·3–2·4 cm^2. Deep tabularial pit with axial boss in centre of prominent, broadly rounded mamelons. No intercorallite walls. Major and minor septa usually not distinguished, twenty-four to thirty-six total in mean tabularium diameter 2·6–3·4 mm. All septa thin, extending more or less to axis of tabularium. Dissepiments very variable, coarse, with weakly developed septal crests. Crests may be solid, multitrabecular on dissepimental surface, irregularly carinate or non-carinate slender blades above. Tabellae variable, with or without broad axial series of flat-topped domes.

Type material. Owen's material appears to be lost. It was stated as coming from the 'coralline beds of the Upper Magnesian Cliff Limestone of Iowa and Wisconsin'. Laub (1979, p. 194) considered this to represent either the Hopkinton or Kankakee Dolomite. As no material of this species is available from these horizons, I refrain from selecting a neotype (but see discussion).

Other material. GSC 20534, Silurian, Landovery, Telychian, Fossil Hill Formation; Manitoulin Island, Ontario. BMNH 90001, Silurian, Niagaran; Lake Huron. USNM 422823, UMMP 34296, Silurian, upper Wenlock (?lower Ludlow), Louisville Limestone; Louisville, Kentucky.

Range. Silurian, Llandovery (Telychian) to late Wenlock (?early Ludlow); northern USA and southern Canada.

Description. Tabular colonies $<110 \times 80 \times 40$ mm with close-spaced, prominent, broadly rounded mamelons on flat to gently undulating calicular surface (Pl. 6, figs. 5 and 6). Mamelons <5 mm high, with central tabularial pit <2 mm deep containing an axial boss. Septa thin blades in tabularium, expressed as broad, low arched to ridged, radiating granular bands separated by furrows on dissepimental surface. Septa of adjacent corallites astraeoid to thamnasterioid; no corallite walls.

In cross-section, tabularia clearly but often crudely outlined by arcuate sections of steeply inclined dissepiments with slightly thickened surfaces (Pl. 8, figs. 1, 3, 4). Septa usually not clearly divisible into major and minor series, all extending as thin, rarely thickened blades to or almost to axis, where some may fuse. Septa may fail between tabularial surfaces which may be cut in cross-section to form an aulos. In dissepimentarium, dissepiment sections very variable but generally coarse, four to thirteen sections in 10 mm, irregularly circular to elliptical except adjacent to tabularium. Septa developed as very thin crests on discrete dissepiment surfaces. Septal traces rare in cross-section, either contiguous and solid (Pl. 8, fig. 1), with granular

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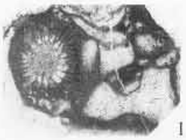
EXPLANATION OF PLATE 7

Figs. 1–7. *Prodarwinia speciosa*. 1 and 2, cross-sections and 3, longitudinal section of lectotype (IGT Co1334). 4, cross-section and 5, longitudinal section (BMNH R53511). 6, cross-section (BMNH R53510). 7, longitudinal section (IGT Co1348). All Silurian, Aeronian, Rumba Formation; Päri, Estonia.

Figs. 8–12. *P. striata*. 8 and 9, cross-sections and 10, longitudinal section of neotype (USNM 422826); Silurian, Telychian, Dayton Formation; Todd's Fork, 3·2 km north of Wilmington, Ohio. 11, cross-section and 12, longitudinal section (RM Cn20154); Silurian, Telychian, Rode Mergel; Norderstrand, Visby, Gotland.

All figs. ×2·5.

PLATE 7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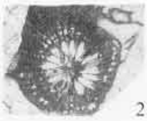
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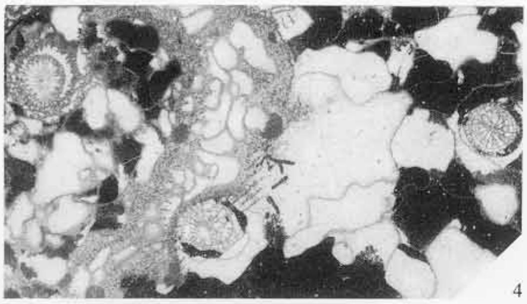
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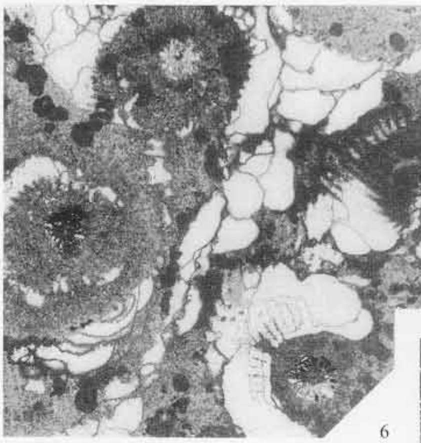
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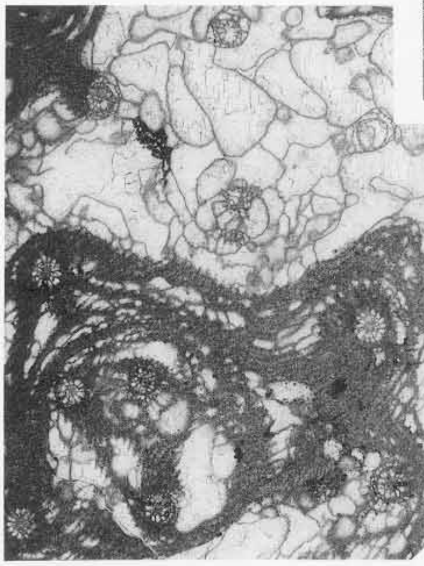
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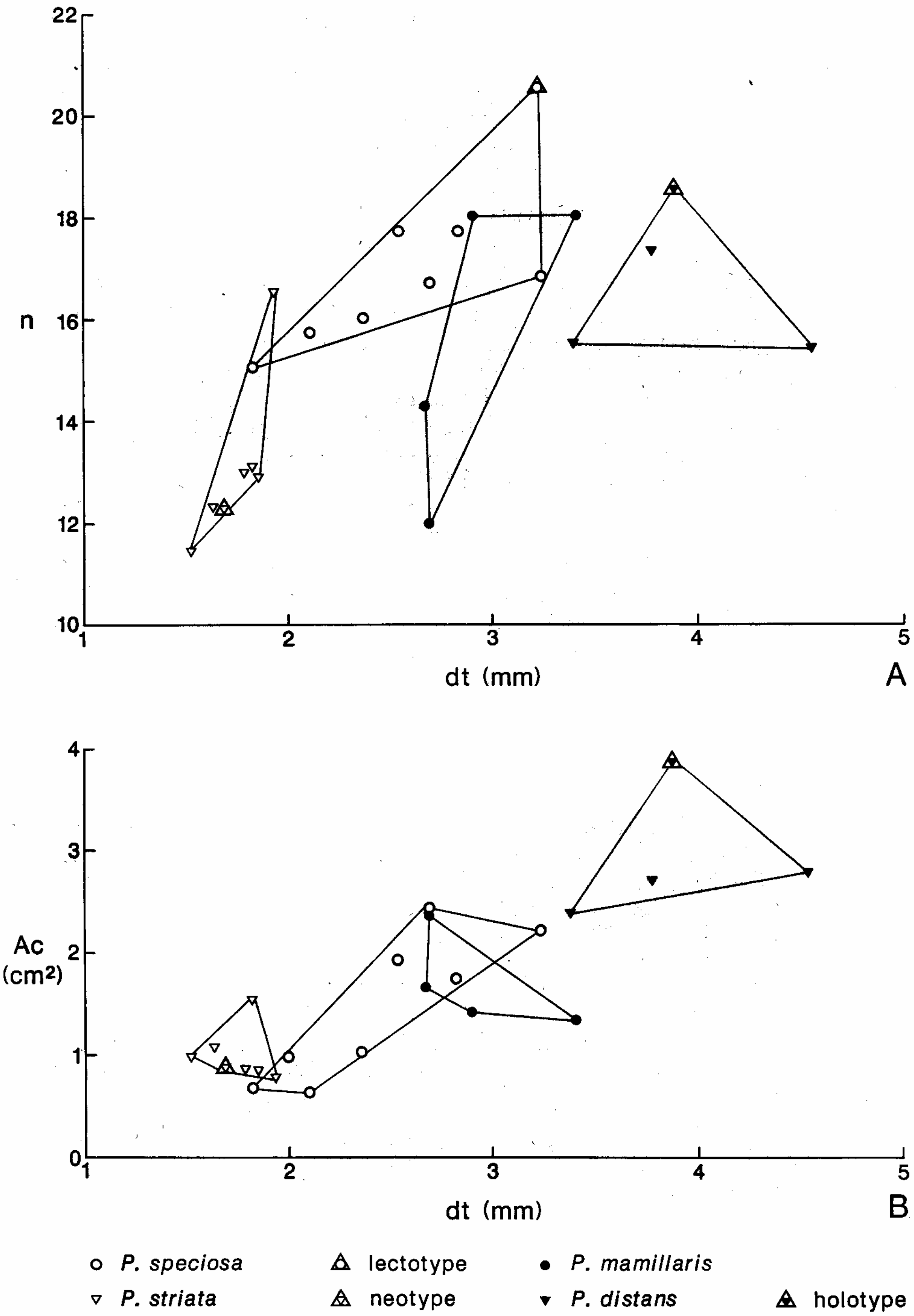
12

SCRUTTON, *Prodarwinia*



TEXT-FIG. 12. Variation in A, mean number of major septa (n) and B, mean corallite area (Ac in cm^2), both plotted against mean tabularium diameter (dt in mm) for *Prodarwinia speciosa*, *P. striata*, *P. mamillaris*, and *P. distans*. For discussion see text.

multitrabecular structure, or irregularly carinate or non-carinate and present in narrow arcuate zones where crested dissepiment surfaces are cut (Pl. 8, fig. 3). Reticulate structure of *murchisoni* type not developed.

In longitudinal section, tabularium with peripheral series of flat to dished, horizontal to abaxially declined tabellae and usually an axial series, <0·6 tabularium wide, of flat to mesa-shaped tabellae (Pl. 8, figs. 2 and 5). There are fifteen to thirty tabellae in 5 mm. Dissepiments very variable in size and inflation, 0·3–7·5 mm across, height-width ratio varying from 1 : 11·5 to 1 : 1 but mostly 1 : 2–3. Surface of dissepimentarium strongly arched 1–2 mm outside tabularium. Dissepimentarium zoned with coarse dissepiments grading distally to finer dissepiments; zones about 2·5 mm thick. Very low septal crests, <0·5 mm high, on surface of smaller vesicles.

Mean tabularium diameter 2·67–3·4 with 23·8–36 total septa and mean corallite area 1·34–2·37 cm^2.

Discussion. Despite the fact that Owen's material is missing, the species seems to be readily identified from his figure (Owen 1844, pl. 14, fig. 3), and subsequently has been generally consistently interpreted. There is a possibility that Owen's specimen could be an example of *P. speciosa*, which is known from the type area (text-fig. 11A). This cannot be resolved until the type is located and/or substantial new collections are available from Iowa and Wisconsin but in any case, stability is best served by retaining the traditional interpretation of the species.

P. mamillaris is a very distinctive species, the main point of dispute being its relationship to *P. distans* and *P. striata*, both of which have been considered subspecies of *P. mamillaris* but which are treated as distinct species here. *P. mamillaris* can be readily distinguished from *P. striata* through the prominent mamelons on the calicular surface, the larger tabularium diameter (text-fig. 12), lack of septal differentiation, and lack of well-developed solid septal crests in the former. It is compared with *P. distans* in the discussion under that species.

Prodarwinia distans (Foerste, 1906)

Plate 6, figs. 3, 4, 9, 10; plate 8, figs. 6 and 7; text-fig. 12

1906 *Arachnophyllum mamillare-distans* Foerste, p. 319, pl. 3.
e.p. 1979 *Arachnophyllum mamillare* (Owen); Laub, p. 194, pl. 7, fig. 2; pl. 25, figs. 1 and 3 only.

Diagnosis. Large, flat, thin tabular colonies with wide-spaced conical mamelons bearing shallow tabularial pits. Mean corallite area 2·7–3·9 cm^2, with fifteen to nineteen major septa in mean tabularium diameter 3·4–4·5 mm. Major septa cross tabularium to axis. Minor septa may reach <0·5 tabularium diameter but both orders reduced to sparse low crests on dissepiments in dissepimentarium. Tabularia with peripheral series of close-spaced dished tabellae rising to meet septal traces in axis. Dissepiments characteristically low, elongate vesicles.

Type material. Holotype: USNM 113639, Silurian, Niagaran, Clinton–Waco (?late Aeronian–early Telychian, Waco Member); Irvine, Kentucky.

Other material. USNM 422825, Clinton–Waco; Indian Fields, Kentucky. USNM 422124, Silurian, Telychian, Hopkinton Formation; Quarry SW ¼ sec. 30′, T.88N., R.3E., Dubuque South Quadrangle, Iowa. BMNH R50215, Silurian, Telychian, Hopkinton Formation; Manchester, Iowa.

Range. Silurian, Llandovery, ?Aeronian, Telychian; Kentucky and Iowa.

Description. Large, flat, thin tabular colonies <210 × 140 × 50 mm. Calicular surface flat to gently undulating, bearing wide-spaced conical mamelons <6 mm high with central, shallow tabularial moat crossed by septal blades to a prominent axial boss (Pl. 6, figs. 3 and 4). Septa continue outside tabularium as very low, broad ribs with 0·1 mm scale granular ornament, separated by narrow grooves. Septa of adjacent corallites mainly abutting.

In cross-section, tabularia well defined, with thin, tapering major septa extending more or less to axis, where some may fuse. Septa may show weak bilateral distribution. Minor septa variably developed, sometimes reaching <0·5 distance to axis but in other cases only just penetrating tabularium boundary. Outside tabularium, traces of septa mainly seen as thin discontinuous blades cresting dissepiments in immediate peritabularial area (Pl. 6, fig. 9; Pl. 8, fig. 6). Rare crossbar carinae may occur. Septa almost absent elsewhere but rarely solid multi-trabecular septal deposits are seen cresting dissepiments. Dissepimentarium with variable but generally large and irregular to subcircular dissepiment sections, five to eight in 10 mm.

In longitudinal section, tabularia well defined with close-spaced peripheral series of flat to dished tabellae rising to the axis where they are cut by septal traces (Pl. 6, fig. 10; Pl. 8, fig. 7). There may be some steeply inclined tabellae in the axial area. Peripheral tabellae spaced eleven to twenty-five in 5 mm. Septal trabeculae inclined axially and upwards at about 20° at edge of tabularium, increasing in inclination to about 70° near axis. Trabeculae about 0·1 mm diameter, either tufted monacanths or possibly pseudorhabdacanths. Dissepiments characteristically low and elongate, $<8{\cdot}3$ mm wide and 1:3·5–12 height:width ratio. Crest of dissepimentarium 0·7–2·5 mm outside tabularium, funnelling steeply into tabularium but sloping gently abaxially to generally flat or undulating peripheral calicular surface. Dissepiments may be weakly zoned by size. Septal crests not evident.

Discussion. Although *P. distans* was originally described as a subspecies of *P. mamillaris*, I consider there to be sufficient difference between them to justify full separation at the species level. Externally, *P. distans* is characterized by wide but variably spaced conical mamelons and very flat septal ribs in contrast to the close-spaced, broadly rounded mamelons and more arched to ridged septal ribs of *P. mamillaris*. *P. distans* consequently has a higher mean corallite area, as well as a larger mean tabularium diameter, than *P. mamillaris* (text-fig. 12). Internally, *P. distans* has clearly distinguished minor septa, rather more uniform, less inflated dissepiments and lacks an axial series of arched or mesa-shaped tabellae in contrast to typical *P. mamillaris*. Furthermore, although both have only weakly developed septa in the dissepimentarium, they are notably more weakly developed in *P. distans*.

P. distans is readily distinguished from both *P. speciosa* and *P. striata* by its distinctive calicular surface morphology and lack of solid septal crests. However, occasional specimens of *P. speciosa* also lack well-developed septal crests (see discussion under that species). In addition, *P. striata* has much smaller tabularium diameters and mean corallite areas (text-fig. 12). These parameters are larger in *P. speciosa* but still slightly smaller than in *P. distans*.

Prodarwinia sp. nov.

Text-fig. 13A–C

Material. USNM 79840, Silurian, Clinton, Dayton Limestone (late Telychian); Todds Fork, 3·2 km north of Wilmington, Ohio.

Description. Small ovoid hand specimen, 80 × 60 × 35 mm with domed upper surface bearing two or three very large tabularial pits 30–40 mm apart on low conical to rounded elevations (text-fig. 13A). Septa gently arched ribs, astreoid to thamnasterioid.

In cross-section, tabularia well defined by slightly thickened dissepiment sections, 5–6·67 mm diameter with seventeen to twenty major septa (text-fig. 13B). Major septa thin, tapering in tabularium to axis, or as short septal crests on tabulae. Minor septa weakly developed, just penetrating tabularium, and both orders discontinuous or rarely continuous in dissepimentarium within 3–4 mm of tabularium, where they may appear faintly beaded or develop very weak crossbar carinae. Here also septa may be multitrabecular, three or more trabeculae across, and thickened to contiguity in a very thin zone on discrete dissepimental surfaces. Dissepimental sections somewhat irregular and moderately coarse.

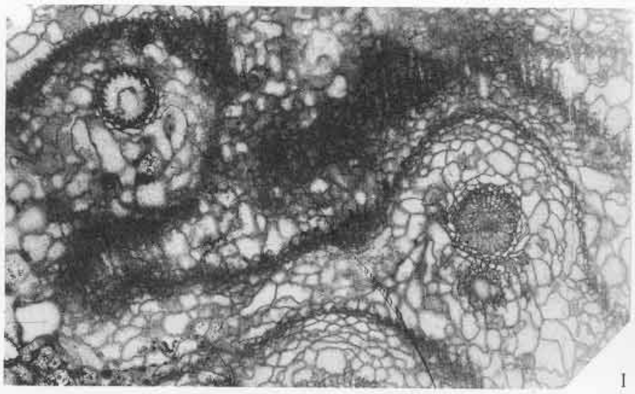
EXPLANATION OF PLATE 8

Figs. 1–5. *Prodarwinia mamillaris*. 1, cross-section and 2, longitudinal section (UMMP 34296); 3, cross-section (USNM 422823); all Silurian, Louisville Limestone; Louisville, Kentucky. 4, cross-section and 5, longitudinal section (BMNH 90001); Silurian, Niagaran; Lake Huron, Michigan.

Figs. 6 and 7. *P. distans* lectotype (USNM 113639). 6, cross-section and 7, longitudinal section; Silurian, Llandovery, Noland Formation, Waco Member; Irvine, Kentucky.

All figs. × 2·5.

PLATE 8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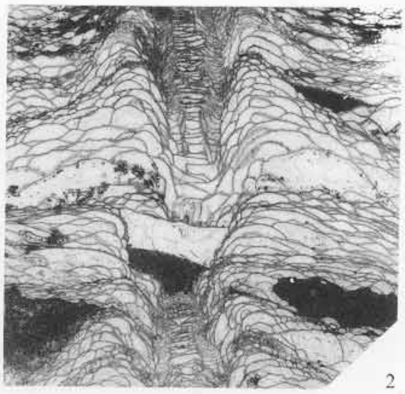
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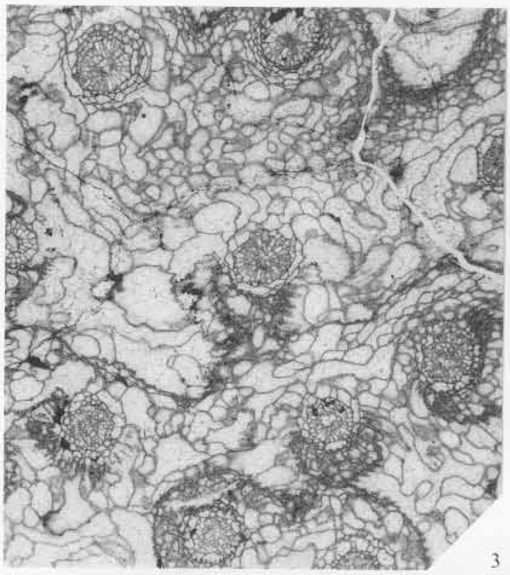
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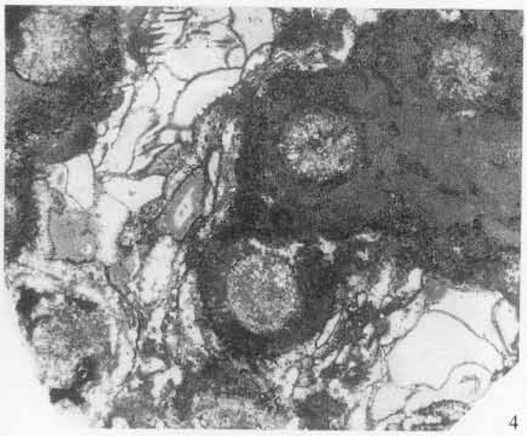
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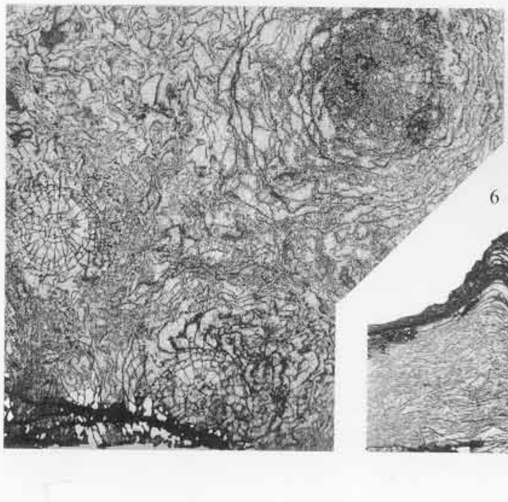
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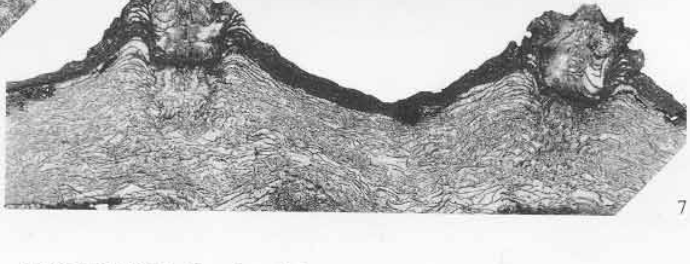
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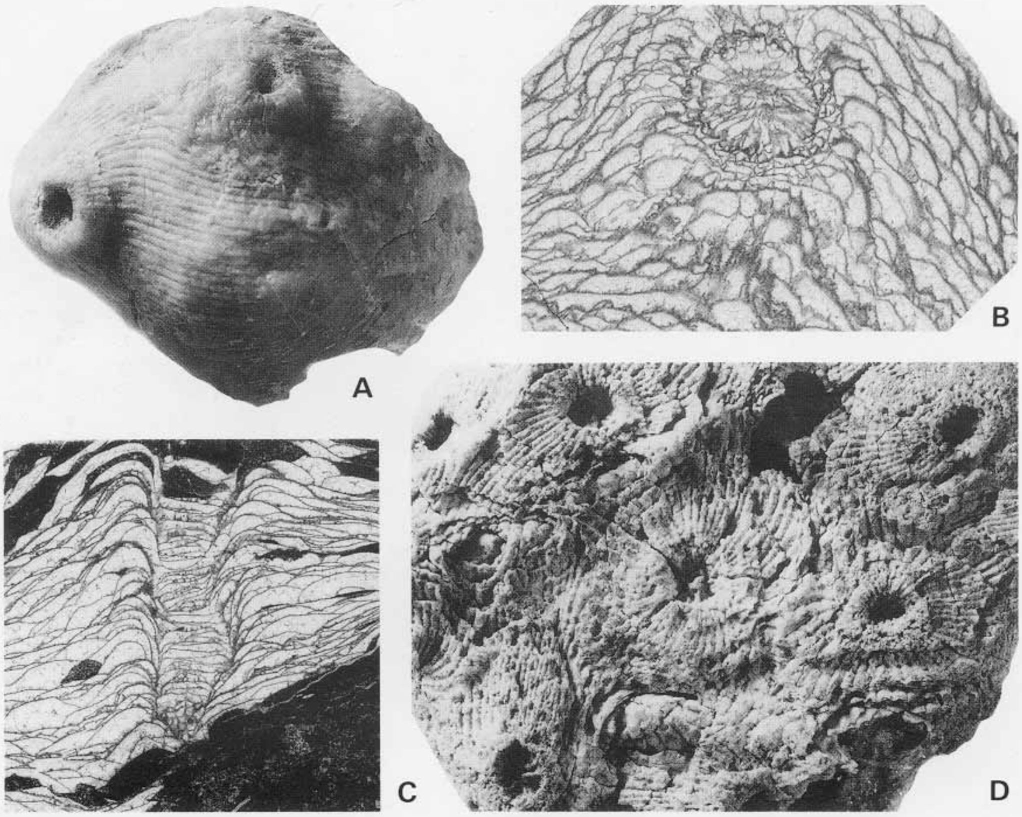
SCRUTTON, *Prodarwinia*



TEXT-FIG. 13. A–C, *Prodarwinia* sp. nov.; Silurian, Telychian, Dayton Formation; Todd's Fork, 3·2 km north of Wilmington, Ohio (USNM 79840). A, calicular surface, × 1; B, cross-section, × 2·5; C longitudinal section, × 2·5. D, ?*Prodarwinia gigas* (holotype of *Strombodes eximius*); Silurian, 'Lockport' (?Telychian); Manitoulin Island, Ontario (GSC 2633), × 1.

In longitudinal section, tabularium somewhat irregularly defined by steep, vertical, inner faces of peritabularial series of dissepiments, some of which may extend into and across the tabularium as flat to dished plates (text-fig. 13C). Tabulae complete or incomplete, flat or low, wide flat-topped domes, fifteen to sixteen in 5 mm. Dissepiments generally scarcely to poorly inflated, except the peritabularial series when the dissepimentarium surface is arched there. Dissepiments $<7 \times 1{\cdot}5$ mm, not clearly zoned and bearing scattered septal spines which tend to be more common on discrete surfaces, with thin dense septal crests developed adjacent to the tabularium. Crests are $<0{\cdot}25$ mm thick and individual spines $<0{\cdot}75$ mm long.

Discussion. This specimen is unique. It is like no well-established species of *Prodarwinia* and only resembles ?*P. gigas* (see below) in the size of its corallites. Septal structure is similar to that in *P. mamillaris* but tabularium and corallite size, as well as the character of the dissepiments set this specimen apart. It is inappropriate to name a new species on a single specimen. Further material is necessary to establish its range of variation and to confirm its status.

Unrecognizable species of ?*Prodarwinia*

?*Prodarwinia verneuili* (Edwards and Haime, 1851)

1851 *Phillipsastrea verneuili* Edwards and Haime, p. 447, pl. 10, fig. 5.
non 1859 *Phillipsastraea verneuili* Edwards and Haime; Billings, p. 127, fig. 24.
non 1876 *Phillipsastraea verneuilli* Edwards and Haime; Rominger, p. 128, pl. 38, fig. 2.
non 1917 *Phillipsastraea* (*Billingsastraea*) *verneuili* (Edwards and Haime) Grabau, p. 957.
non *Billingsastraea verneuili* of authors (= *Asterobillingsa magdisa* Oliver, 1974).

Type material. Edwards and Haime's figured specimen is unlocated and possibly missing. It was recorded as from Wisconsin.

Discussion. Phillipsastraea verneuili Edwards and Haime was designated as type species of *Billingsastraea* by Grabau (1917, p. 957) who quoted the species name as *Phillipsastraea* (*Billingsastraea*) *verneuili* (M.E. & H.) in a species list. The species was thought to be of Devonian age and *Billingsastraea* became widely used for a North American group of astraeoid, thamnasterioid, and aphroid Devonian corals lacking horseshoe dissepiments and characterized by undilated septa. Billings's material, which probably seeded the misconception to judge from Grabau's choice of name, together with Rominger's illustrated specimen from the drift of Michigan, belong to this group. Oliver (1974, p. 167; 1976, p. 88) finally unravelled the confusion, renaming this group of Devonian corals as *Asterobillingsa*. On the basis of another specimen in the de Verneuil Collection very close in character to Edwards and Haime's illustration, he suggested that *P. verneuili* was probably an *Arachnophyllum* and likely to have come from the Hopkinton Dolomite of north-east Iowa and south-west Wisconsin. That specimen, UCBL EM 15171, has been re-examined and is illustrated here (text-fig. 11A); it is assigned to *Prodarwinia speciosa*.

This species is probably therefore a *Prodarwinia*, and possibly a senior synonym of *P. speciosa*, although this cannot be confirmed until the illustrated specimen is found.

?*Prodarwinia gigas* (Owen, 1844)

Text-fig. 13D

1844 *Astrea*? *gigas* Owen, p. 70, pl. 14, fig. 7.
? 1866 *Strombodes eximius* Billings, p. 93.
1893 *Strombodes gigas* (Owen) Calvin, p. 111, pl. 5, fig. 5.
? 1901 *Arachnophyllum eximium* (Billings) Lambe, p. 184, pl. 16, figs. 3, 3*a*, 4.

non 1859 *Phillipsastrea gigas* (Owen) Billings, p. 128.
non 1876 *Phillipsastraea gigas*(?) (Owen); Rominger, p. 129, pl. 37, fig. 3.
non 1887 *Phillipsastrea gigas* (Owen); Davis, pl. 118, figs. 1 and 2.

Type material. Owen's original material, said to be from the 'coralline beds of the Upper Magnesian Cliff Limestone of Iowa and Wisconsin' interpreted by Laub (1979, p. 194) as either the Hopkinton or Kankakee Dolomite, is lost.

Holotype of *Strombodes eximius:* GSC 2633, Silurian, Lockport (Telychian); Manitoulin Island, Ontario.

Discussion. Owen's species was widely interpreted subsequently as a Devonian coral. Calvin (1893, p. 109) considered that 'The specimen collected and studied by Owen is a *Strombodes*' and renamed Billings's (1859) misidentified *Phillipsastrea gigas* (Owen) as *Phillipsastrea billingsi*. Oliver (1976, pp. 91, 129, 132) subsequently showed that *Phillipsastrea billingsi* and Rominger's material are species of *Heliophyllum*, and Davis's specimen probably also belongs to the same Devonian genus.

Calvin's (1893, pl. 5, fig. 5) illustration of *Strombodes gigas* does look to be conspecific with Owen's illustration. Furthermore, both appear likely to be conspecific with *S. eximius* Billings, of which the holotype, GSC 2633, is in existence. Unfortunately it is a poorly preserved, silicified specimen unsuitable for sectioning. Its external features suggest that it is a unique species of

Prodarwinia with *mamillaris*-type septal structure and tabularia about 5 mm diameter with eighteen major septa. No other material referable to this species is known although *Prodarwinia* sp. nov. shows some similarity and when more material is available to show variation in these corals, could possibly prove to be conspecific.

?*Prodarwinia granulosa* (Foerste, 1906)

1906 *Arachnophyllum* (*Strombodes*) *granulosum* Foerste, p. 318, pl. 3, fig. 1.
1979 *Arachnophyllum granulosum* Foerste; Laub, p. 199.

Type material. Foerste's material appears to be lost. It was described as from the Silurian, Waço Limestone (?late Aeronian–early Telychian) from near Waco, Kentucky.

Discussion. Foerste compared his species with *Strombodes alpenensis* Rominger, which was shown more recently to be an *Iowaphyllum* from the Devonian, Hamilton Group of Michigan (Stumm 1953; see Oliver 1978). Laub (1979, p. 199) compared Foerste's species with *A. pentagonum*.

Foerste's illustration certainly looks more like an iowaphyllid than an *Arachnophyllum*. Therefore, his species is most probably a *Prodarwinia*, close to if not conspecific with *P. striata*, but fundamentally unrecognizable from Foerste's description and illustration alone.

Species excluded from *Arachnophyllum* and *Prodarwinia*

Genus IOWAPHYLLUM Stumm, 1949

1949 *Iowaphyllum* Stumm, p. 50.
1978 *Iowaphyllum*; Oliver, p. 797.

Discussion. Oliver (1978) lists species he considers properly assigned to *Iowaphyllum* and briefly discusses the relationships of the genus. I regard *Iowaphyllum* as a member of the Arachnophyllidae (see discussion above).

Iowaphyllum alpenensis (Rominger, 1876)

1876 *Strombodes alpenensis* Rominger, p. 133, pl. 38, fig. 1.

Discussion. Stumm (1953) has shown that Rominger's species, which is from the Devonian Hamilton Group of Michigan, is an *Iowaphyllum* (see Oliver 1978, p. 798).

Genus ZENOPHILA Hill, 1940

1940 *Zenophila* Hill, p. 414.
1981 *Zenophila*; Hill, p. 217.

Discussion. I regard *Zenophila* as likely to belong to the Arachnophyllidae, as tentatively indicated by Hill (1981).

?*Zenophila kayi* (Merriam, 1974)

1974 *Arachnophyllum kayi* Merriam, p. 43, pl. 5, figs. 7 and 8.

Remarks. Merriam's species, from the Llandovery of Nevada, does not appear to agree with the concept of *Arachnophyllum* as revised here, appearing to have much more continuous septa in the dissepimentarium. A full revision of this species is outside the scope of this paper, but I suggest that it is more closely allied to *Zenophila*. Pickett (1975, p. 153) had reached the same conclusion. If correct, this would significantly extend the range of this genus, previously recorded from the Upper Silurian of Australia.

Suborder COLUMNARIINA Soshkina, 1941
Family DISPHYLLIDAE Hill, 1939
Subfamily PARADISPHYLLINAE Jell, 1969
Genus RADIASTRAEA Stumm, 1937

1937 *Radiastraea* Stumm, p. 439.
1976 *Radiastraea*; Pedder and McLean, p. 135.
1982 *Radiastraea*; Pedder, p. 77.

Diagnosis. Astraeoid or thamnasterioid, more rarely aphroid or pseudocerioid colonies. Septa uniformly attenuate or slightly fusiform, smooth but more commonly carinate. Major septa may more or less reach axis usually with a counter-clockwise vortex. Dissepiments small, moderately inflated, uniformly developed; dissepimentarium surface may be broadly arched periaxially with a broad fan of monacanthine trabeculae. Tabulae complete or incomplete, usually with broad flat-topped tabellae in axial area.

Type species. R. arachne Stumm, 1937. Devonian, Zlichovian; Lone Mountain, Nevada.

Discussion. Pedder (1982, p. 77) has revised *Radiastraea* and removed the genus from the Arachnophyllinae where it was placed by Pedder and McLean (1976). In both papers, the possibility that *Radiastraea* evolved from *Arachnophyllum* (and in turn gave rise to some species at least of *Phillipsastrea*) was advanced. It seems more likely to me that *Radiastraea* evolved from an ancestor with thin, solid septal blades, and more uniform small dissepiments, such as an entelophyllid, with the acquisition of an astraeoid growth form.

Radiastraea richardsoni (Salter, 1852)

Text-fig. 14A–C

1852 *Arachnophyllum richardsoni* Salter, p. 232, pl. 6, figs. 10 and 10*a*.
1878 *Arachnophyllum richardsoni* Salter; Etheridge, p. 585.

Diagnosis. Thin tabular astraeoid to thamnasterioid colonies. Well-defined circular tabularia 2·3–3·0 mm diameter with twelve to fifteen major septa extending just short of or to the axis with a pronounced counter-clockwise vortex. Septa uniformly attenuate or weakly fusiform, minors just penetrating tabularium. Tabellae flat to dished periaxially, rising to septal sections in axis. Dissepiments small, globose; dissepimental surface gently arched peritabularially with broad trabecular fan.

Type material. The original of Salter (1852, pl. 6, figs. 10 and 10*a*) appears to be lost. The type locality was given as Niagaran, Pt. Eden, South side of Baring Bay, Arctic America. Neotype: BMNH R4959, Upper Silurian; Cape Riley, North Devon, Arctic America.

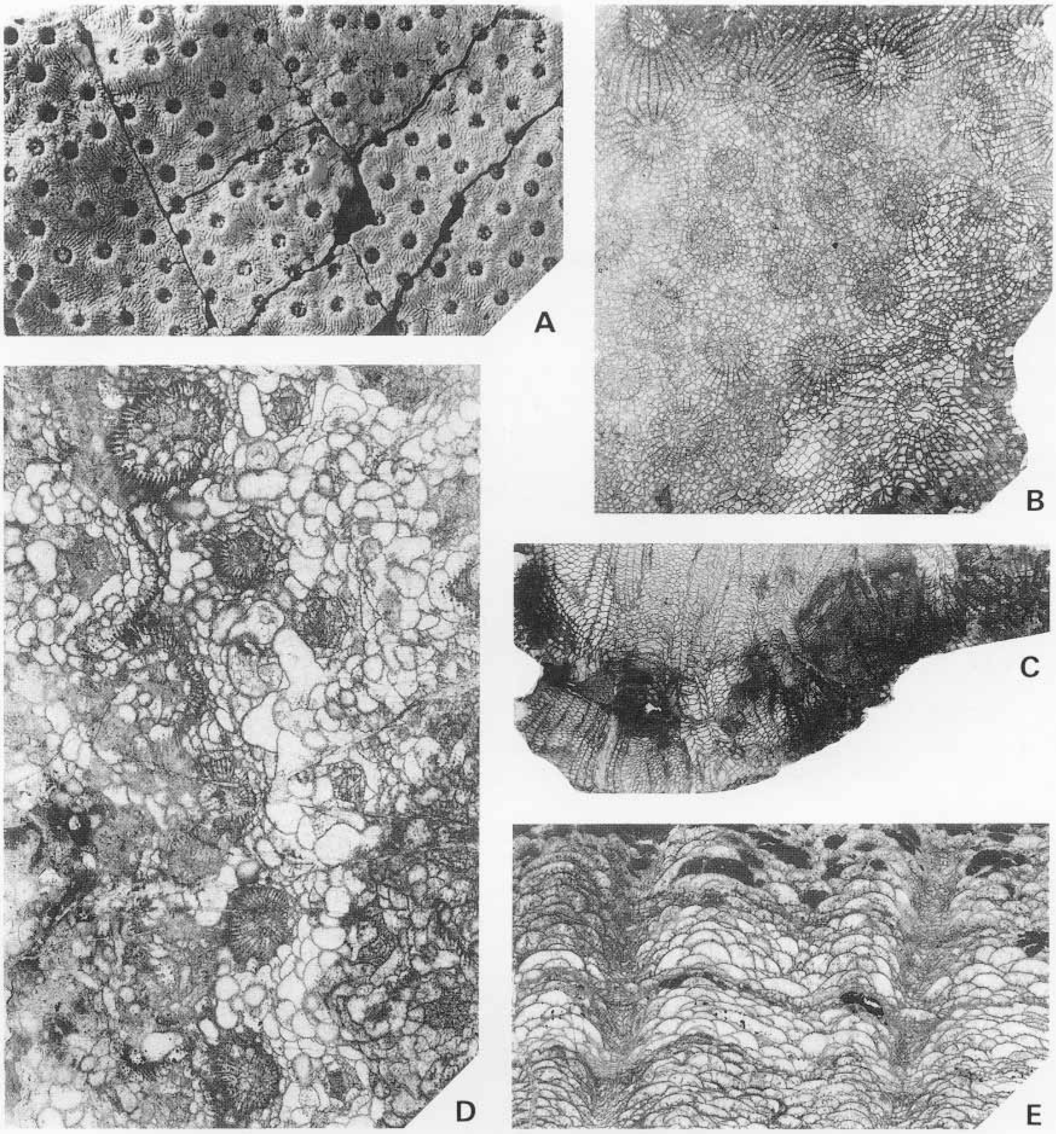
Other material. ?BMNH R4934, Silurian, Wenlock; Cape Hilgard, Dobbin Bay, west of Kane Sea, Arctic America (described as *Arachnophyllum richardsoni* by Etheridge 1878, p. 585).

Range. Silurian, ?Ludlovian; Arctic Canada.

Description. Tabular colonies $<120 \times 100 \times 10$–$22$ mm with very broadly conical lower-surface and flat to undulose calicular surface (text-fig. 13A). Tabularial pits, with or without slight peritabularial swelling, near vertically sided, $<1{\cdot}5$ mm deep, with low, weak axial boss.

In cross-section, tabularia circular, well defined by innermost two to three series of close-spaced, adaxially concave sections of steeply inclined dissepiments (text-fig. 13B). Major septa extend two-thirds to full radius to axis, strongly curved in pronounced counter-clockwise vortex, with some septa fused at their axial ends. All septa thin, uniformly attenuate to weakly fusiform peritabularially. Minor septa just penetrate tabularium. In the dissepimentarium, septa straight to weakly zigzag with scattered weak, thorn-like carinae, continuous with or less frequently abutting septa from adjacent corallites. Dissepimental sections regular, uniserial between septa.

In longitudinal section, tabellae flat to dished periaxially, rising towards axis where, with scattered subsidiary steeply abaxially inclined tabellae, they mingle with septal sections (text-fig. 13C). There is a narrow axial



TEXT-FIG. 14. A–C, *Radiastraea richardsoni* (neotype); Silurian, ?Ludlow; Cape Riley, North Devon, Arctic Canada (BMNH R4959). A, calicular surface, × 1; B, cross-section, × 2·5; C, longitudinal section, × 2·5. D, E, ?*Mazaphyllum approximatum* (holotype); Silurian, late Telychian, La Vieille Formation; Anse-à-la-Vieille, Gascons, Quebec (GSC 9149). A, cross section; B, longitudinal section; both × 2·5.

zone 0·3 diameter wide of flat tabellae. There are twenty-three tabellae in 5 mm. Dissepiments small, globose, < 1·5 × 1 mm but generally 1 × 0·5 mm. Dissepimentarium surface gently arched peritabularially with broad trabecular fan and steep dissepiment flanks facing and defining tabularium.

Trabeculae 0·04–0·08 mm thick, monacanths or tufted monacanths. Mean tabularium diameter 2·48–2·75 mm, with 13·7–15 major septa and corallite areas 0·31–0·59 cm^2 (neotype first in each case).

Discussion. Salter's original would be expected to be housed in the British Museum (Natural History) with the rest of the material collected during the series of Arctic voyages searching for traces of the Franklin expedition. Although it cannot be traced, two other specimens collected from the same general area as the figured specimen during these expeditions and identified as Salter's species are available. Of these, R4959 is closest to the original description and is selected as neotype. The species is clearly a *Radiastraea.*

Although *Radiastraea* is predominantly a Lower and Middle Devonian genus, Pedder and McLean (1976) have described new unnamed species from the Upper Silurian, mainly of Přídolí age but with two specimens, from the Douro Formation of the Grinnell Peninsula, Devon Island, Arctic Canada, possibly of Upper Ludlow age. These latter specimens (Pedder and McLean, 1976, figs. 24.15–24.18) are almost certainly conspecific with *R. richardsoni*, the neotype cross-section matching fig. 24.15, and the longitudinal section that of the other specimen, fig. 24.18.

Order CYSTIPHYLLIDA Nicholson, 1889
Family CYSTIPHYLLIDAE Edwards and Haime, 1850
Subfamily CYSTIPHYLLINAE M'Coy, 1951

1976*b* Cystiphyllinae; McLean, p. 52.
1981 Holmophyllidae; Hill, p. 105.

Discussion. McLean (1976*b*, p. 52) took a broad view of the composition of the Cystiphyllidae given the great variability in internal structure of this group of corals. Within this large group, the species described below agrees most closely with members of Hill's Holmophyllidae, although lacking the relatively well-defined tabularium usually found in that group in contrast to most cystiphyllids.

Genus MAZAPHYLLUM Crook, 1955

1955 *Mazaphyllum* Crook, p. 1052.
1976 *Mazaphyllum;* Pedder, p. 287.
1981 *Mazaphyllum;* Hill, p. 107.

Diagnosis. Thamnasterioid or aphroid colonies. Septa present as discrete spines piercing several dissepimental layers, randomly distributed but usually showing radial alignment in cross-section. Tabularium more or less well defined, surface profile flat to shallowly sagging and composed of vesicular tabulae. Dissepiments small, weakly inflated. Trabeculae rhabdacanthine and holacanthine.

Type species. Mazaphyllum cortisjonesi Crook, 1955. Silurian, Wenlock; Palmer's Oaky District, New South Wales, Australia.

Discussion. The genus is known mainly from the Wenlock and Ludlow of eastern Australia, although the new, unnamed, species described by Pedder (1976, p. 287) comes from the Přídolí of Arctic Canada.

?*Mazaphyllum approximatum* (Parks, 1933)

Text-fig. 14D, E

1933 *Strombodes approximatus* Parks, p. 38, pl. 8, fig. 5.
1939 *Arachnophyllum approximatum* (Parks) Northrop, p. 145.

Diagnosis. Tabular, aphroid colony. Tabularia vaguely defined in cross-section. Acanthine septa densely developed in peritabularial area and less densely in tabularium; sparse elsewhere. Tabulae vesicular in funnel-shaped tabularium, merging with surrounding dissepiments. Dissepimentarium zoned, with septal spines short and sparse on crests of smaller dissepiments, becoming dense, thicker and longer around tabularia. Tabularium diameter about 1·7 mm with twenty-six septa. Mean corallite area 0·44 cm^2.

Type material. Holotype: GSC 9149, Silurian, Telychian, La Vieille Formation; Anse-à-la-Vieille, Gascons, Quebec.

Description. Tabular colony 120 × 100 × 40 mm with no clear surface features.

In cross-section, tabularia vaguely defined by annular zones of arcuate dissepiment sections steeply inclined (text-fig. 14D). Septa acanthine, not separated into two orders, well developed in area of tabularia, sparse elsewhere. Colony aphroid, with no trace of intercorallite walls. Septal spines developed in zones on dissepimental and tabularial crests, densest immediately peritabularially where spine bases are thickened almost to contiguity and spines taper adaxially penetrating one or two vesicular layers. Spines may extend to the axis. Spines only rarely seen elsewhere in the dissepimentarium. Dissepiment sections irregularly elliptical, fifteen in 10 mm.

In longitudinal section, tabularia rather better defined, about 1·7 mm diameter (text-fig. 14E). Dissepiments moderately inflated, $< 3{\cdot}5 \times 1$ mm. Surface broadly arched in dissepimentarium, with slightly smaller, less inflated and steeply inclined dissepiments adjacent to tabularium, merging with small, slightly inflated vesicular to flat tabellae in tabularium. Tabellae twenty to twenty-two in 5 mm. Dissepimentarium zoned with layers of slightly smaller dissepiments, 3–4 mm apart, bearing sporadic very short septal spines. Spines well developed in area of tabularia, 0·75 mm long. Microstructure obscure, either tufted monacanths or possibly rhabdacanths.

There are about twenty-six septa at a diameter of 1·7 mm in cross-section. Mean corallite area 0·44 cm^2.

Discussion The holotype of *Strombodes approximatus* had not previously been sectioned. The species is clearly not an *Arachnophyllum*. The vesicular tabellae and acanthine septa suggest affinities with the Cystiphyllida, possibly as a colonial holmophyllid. The only existing genus with which it can be compared is *Mazaphyllum*, although the latter has a relatively well-defined tabularium and very long septal spines, pervasively developed in the dissepimentarium but more or less excluded from the tabularium. This species probably represents a new genus but as at the moment it is known only from this single specimen, the establishment of a new generic name is not felt to be justified.

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