

# Systematics, shell structure and affinities of the Palaeozoic Problematicum *Cornulites*

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Received January 2006; accepted for publication December 2006

The genus *Cornulites*, with the type species *C. serpularius* Schlotheim, 1820, from the Silurian of Gotland, comprises annulated, conical or tubular calcite shells, often found attached to the hard parts of other organisms. No consensus has ever been reached over the zoological affinities of the taxon, and no examples of soft-part preservation are known: detailed examination of shell structures and growth patterns provide the only means of assessing its systematic position. Using transverse and longitudinal thin sections of *C. serpularius* Vine, 1882, and *C. cellulosus* sp. nov., from the Much Wenlock Limestone Formation of England, the shell structure of *Cornulites* is shown to be lamellar, but with conspicuous internal chambers (camerae) at the apical end of the shell and, particularly in *C. cellulosus*, numerous smaller vacuities (cellulae) between the lamellae in the apertural shell region. Growth of the shell was by the secretion of low-magnesian calcite increments within one another, giving a cone-in-cone structure, with the prominent development of cellulae in *C. cellulosus* probably a constructional feature relating to an upright life position. By comparison of morphology and shell structure with other taxa, the zoological affinities of *Cornulites* are re-examined; previously suggested affinities with annelids, foraminifers, molluscs and poriferans can be ruled out. Specific shell structures, most notably pseudopuncta similar to those of bryozoans and brachiopods, have led some recent workers to interpret cornulitids as lophophorates. However, it is shown that they can be interpreted alternatively as solitary, aseptate members of the stem-Zoantharia (Cnidaria: Anthozoa). Four cornulitid species are recognized in the Much Wenlock Limestone Formation: *C. cellulosus* sp. nov., *C. gremialis* sp. nov., *C. scalariformis* and *C. serpularius*. In the absence of the type material, *C. serpularius* is here restricted to cornulitids closely resembling the specimens originally figured by Schlotheim. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 150, 681–699.

ADDITIONAL KEYWORDS: Anthozoa – Bryozoa – Cnidaria – lophophorates – ontogeny – Phoronida – rugose corals – Silurian – Wenlock.

## INTRODUCTION

Techniques for analysing molecular and genetic data in a phylogenetic context have improved dramatically in recent years, enabling investigations of metazoan phylogeny to utilize more than just morphological and developmental characters. Thus, previous hypotheses of relationships between metazoan clades, such as the uniting of arthropods and annelids by virtue of their body segmentation, have been contradicted by new

studies indicating, for example, that arthropods belong to one major clade, the Ecdysozoa, and annelids to another, the Lophotrochozoa (see, for example, Peterson & Eernisse, 2001; Glenner *et al.*, 2004; Halanych, 2004). However, even as a more stable classification of extant taxa is approached, the systematic position of many extinct metazoan groups remains poorly understood. As these problematical groups can shed much light on the diversification of metazoan body plans and the early evolution of the clade, detailed examination of the fossil record, particularly in the Palaeozoic, has a key role to play.

Exceptional preservation of soft parts or the histological analysis of skeletal structures is required to enable accurate assessment of these extinct taxa with

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living groups. Thus, the high-quality preservation of shell structures seen in fossils from the Much Wenlock Limestone Formation (Silurian) of England has the potential to yield much information on the zoological affinities of problematical taxa. An excellent example of this is the genus *Cornulites*, many specimens of which occur in the Much Wenlock Limestone Formation, but whose systematic placement has never been satisfactorily resolved. Of particular significance is the type species *C. serpularius* Schlotheim, 1820, which, despite having been erected using material from the Silurian of Gotland, has been diagnosed generally on the basis of specimens from the English Midlands (see, for example, Murchison, 1859; Salter, 1873; Bather, 1923; Fisher, 1962).

Since its initial description, many species have been referred to *Cornulites*, or described as closely related taxa, but there have been very few detailed studies of shell structure, and without this the affinities of *Cornulites* cannot be determined reliably. In this study, the diversity of cornulitids in the Much Wenlock Limestone Formation has been reassessed, with four species of *Cornulites* recognized: a redefined *C. serpularius*, *C. scalariformis* Vine, 1882, *C. cellulosus* sp. nov., and *C. gremialis* sp. nov. The microstructure of the shell wall of *Cornulites* is described, based on sections of *C. cellulosus* and *C. scalariformis*, and the likely zoological affinities of *Cornulites* are then discussed.

## MATERIAL AND METHODS

The specimens studied are in the Lapworth Museum of Geology, University of Birmingham (prefix BU), and the Natural History Museum, London (BMNH). The shell structure of *Cornulites* described below was obtained using existing and new thin sections of *C. cellulosus* and *C. scalariformis*. Additionally, two specimens of *C. cellulosus* (BU 4371 and 4378) were sectioned, and the apertural end of the holotype of *C. cellulosus* was polished, etched and stained, and studied as an acetate peel. Thin sections were examined petrographically using a Zeiss Axioskop transmitted light microscope. A longitudinal and one transverse section of BU 4371 were etched for 3 h using a saturated solution of EDTA in deionized water prior to examination under a Philips XL30 FEG environmental scanning electron microscope (ESEM).

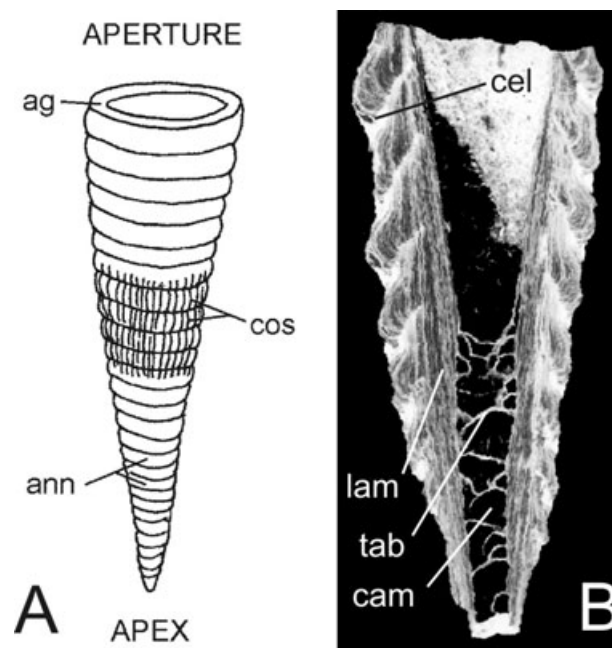
## TERMINOLOGY

The only published cornulitid terminology is that of Vinn & Mutvei (2005), but their annotated diagram does not have accompanying explanatory notes and their terminology requires clarification and minor modification. The terms 'tabulae', 'cellulae' and 'costae'

are here preferred to the 'septa', 'vesicles' and 'striae' of Vinn & Mutvei: in standard biological terminology, vesicles are liquid-filled sacs of soft, non-skeletal tissue, and striae are narrow grooves or channels, not positive ribs, whilst in many organisms (e.g. cnidarians) septa are vertical rather than horizontal structures. As the skeleton of *Cornulites* is compared in detail with cnidarian skeletons below, using the same term for non-analogous structures causes confusion and should be avoided. Hence the morphological terms used here are as follows:

**External morphology** (Fig. 1A): 'apex', narrow, pointed end of shell; 'aperture', wide, round, open end of shell; 'annulations', transverse rings around body, parallel or subparallel to aperture; 'costae', rib-like longitudinal ornamentation, perpendicular to annulations.

**Internal morphology** (Fig. 1B): 'lamellae', continuous layers of calcite forming shell wall and running round shell interior, parallel or subparallel with shell surface; 'tabulae', layers of calcite running approximately at right angles to lamellae across shell interior near apex, and connecting lamellae; 'camera', vacuity occurring between tabulae at apex of shell; 'cellulae', small vacuities occurring between lamellae towards apertural end of shell; 'apertural groove', narrow, flat-



**Figure 1.** Morphology of *Cornulites*. A, external morphology, showing apertural groove (ag), annulations (ann) and costae (cos). B, internal morphology in longitudinal section. BU 4390, *C. cellulosus*, apical and mid-region, showing lamellar shell wall (lam), with internal tabulae (tab) and camerae (cam) in apical region,  $\times 6$ . Cellulae (cel) occur towards the apertural end of the specimen.

based groove around aperture, formed by undulation of lamellae, normally lenticular in plan view.

Additionally, in the discussions below, the shell of *Cornulites cellulosus* is divided into three regions – apical, mid-region and apertural – based on features seen in longitudinally sectioned specimens (e.g. Fig. 1B). The apical region is defined as the part of the shell from the apex to the most distal tabula, the mid-region as that from the most distal tabula to the first undulation of the internal shell surface, and the apertural region from the first undulation of the internal shell surface to the aperture. These subdivisions are used for convenience of description and are not intended to indicate significant ontogenetic stages.

The symbols and conventions used in the synonymy lists below follow Matthews (1973).

## CORNULITID SYSTEMATICS

### CORNULITIDAE FISHER, 1962

*Remarks:* Fisher (1962) erected the Cornulitidae as a family containing four genera – *Cornulites* Schlotheim, 1820, *Conchicolites* Nicholson, 1872a, *Cornulitella* Howell, 1952 and *Kolihaia* Prantl, 1946. Only Silurian species of *Cornulites* are described here, and a revision of the whole group is not attempted, but previously published descriptions and illustrations suggest that cornulitids have been excessively subdivided at generic level. For example, *Cornulitella* [a name proposed by Howell (1952) to replace *Ortonia* Nicholson, 1872b, which Howell showed to be preoccupied] was originally described by Nicholson (1872b) as separable from *Cornulites* on the grounds that its shell was smaller, entirely attached to other organisms, devoid of costae, and had a cellular structure restricted to just one side of the shell. However, this comparison was based on *Cornulites* being defined as a large, unattached shell with distinct costae, rather than the small form originally figured by Schlotheim (1820). If the type species of *Cornulitella* – *C. conica* (Nicholson, 1872b) – is compared with Schlotheim's illustration of *Cornulites serpularius*, the only clear morphological difference is the presence of a cellular structure on one side of the shell of *C. conica*. The degree of attachment of a cornulitid is at least partly dependent on the availability of suitable substrate (Hall, 1888; also see below) and is an unreliable character upon which to found a genus.

The criteria originally used to define *Conchicolites* are also dubious, since Nicholson (1872a) erected the taxon to include cornulitids that were smaller than *Cornulites* and occurred in large clusters attached to a foreign body. Unlike *Cornulitella*, no cellular shell structure was observed and the tube wall was thin, but Nicholson (1872b) separated *Conchicolites* from

*Cornulitella* essentially on ecological grounds, the latter being more completely attached to its substrate and never occurring in such large clusters. Nevertheless, subsequent authors (e.g. Prantl, 1950; Vinn & Mutvei, 2005) have argued that *Conchicolites* is generically distinct, emphasizing that its thinner, non-cellular shell wall structure distinguishes it clearly from *Cornulites*. Indeed, Vinn & Mutvei (2005: 726) suggested that 'the two taxa were probably unrelated and that cornulitids may be a polyphyletic taxon.'

The fourth taxon included in the Cornulitidae by Fisher (1962) – *Kolihaia eremita* Prantl, 1946 – was diagnosed as a tubular shell with 'radical [proximal] expansions that may bifurcate' (Fisher, 1962: W138), indicating a taxon quite unlike *Cornulites*; *Kolihaia* is now regarded as an epiplanktic anthozoan (Kříž, Fřýda & Galle, 2001).

In his brief account of Cornulitidae from the Silurian of Gotland, Larsson (1979a) identified four new genera, but did not describe, illustrate or propose names for them. Vinn & Mutvei (2005) reviewed the material, but did not erect formal taxonomic names, although Vinn (2004) named *Cornulites gotlandicus* from the Ludlow age Hemse Beds and later recognized the putative cornulitid genus *Septalites*, also of Ludlow age (Vinn, 2005). Although *Cornulites* is the only cornulitid genus recognized in the Much Wenlock Limestone Formation, other genera certainly exist, and the diversity of the group through the Palaeozoic requires further assessment.

### CORNULITES SCHLOTHEIM, 1820

*Type species.* *Cornulites serpularius* Schlotheim, 1820, from the Silurian of Gotland. By monotypy.

*Emended diagnosis:* Conical calcite shells with varying angle of taper, ranging from narrow, almost tubular forms, to widely inflated cones; transversely annulated, commonly with longitudinal costae. Shells straight or slightly sinuous, rounded or ovoid at origin; sinuous forms often straightening in later growth stages. Shell microstructure of stacked lamellae, apically straight, but becoming undulating towards aperture, finally forming apertural groove. Lamellae connected internally at apex by horizontal tabulae; separated distally by cellulae that become prominent towards aperture, particularly in large forms.

*Remarks:* Four species from the Much Wenlock Limestone Formation are here placed in *Cornulites*: *C. serpularius*, *C. scalariformis*, *C. cellulosus* and *C. gremialis*. The cellular shell structure is known from both *C. scalariformis* and *C. cellulosus*, but material of *C. serpularius* suitable for sectioning has not been found. Dzik (1991: 129) regarded cellulae as 'typical only for adult Silurian *Cornulites*': if they are

absent from the type species, other taxa may be better placed in a separate genus.

*CORNULITES SERPULARIUS* SCHLOTHEIM, 1820  
(FIG. 2A, B)

- \* 1820 *Cornulites serpularius* Schlotheim, p. 378, pl. 29, fig. 7.
- ? 1859 *Cornulites serpularius* Schloth.; Murchison, p. 221, pl. 16, fig. 3 [only these specimens resemble Schlotheim's syntypes of *C. serpularius*, all others figured by Murchison being examples of *C. cellulossus*].
- ? 1873 *Cornulites serpularius* Schloth.; Salter, pp. 85, 93, 128, 177.
- ? 1875 *Cornulites serpularius* Schlotheim; Baily, p. xlii.
- ? 1882 *Cornulites serpularius* Schlot.; Vine, p. 377.
- 1888 *Cornulites serpularius* Schlotheim; Hall, p. 8.
- ? 1923 *Cornulites serpularius* Schlotheim; Reed, p. 269.
- 1962 *Cornulites serpularius* Schlotheim; Fisher, p. W137, fig. 80 [reproduction of Schlotheim's original illustration].
- ? 1972 *Cornulites serpularius* Schlotheim; Blind, p. 5.
- 1979a *Cornulites serpularius* Schlotheim; Larsson, p. 208 [noted dissimilarity between Schlotheim's illustration of syntypes and material assigned to species by subsequent authors].
- ? 1991 *Cornulites serpularius* Schlotheim; Dzik, p. 126, pl. 2, figs 5, 6 [specimens probably examples of *C. cellulossus*].
- 2005 *Cornulites serpularius* Schlotheim; Vinn & Mutvei, p. 726.

**Material:** The type specimens figured by Schlotheim (1820) from the Silurian of Gotland cannot be located (Larsson, 1979a; D. Korn pers. comm., 2003; O. Vinn pers. comm., 2005). This account is based on two specimens attached to the brachiopod BU 4376 from the Much Wenlock Limestone Formation of Dudley, England. Other specimens attached to brachiopods

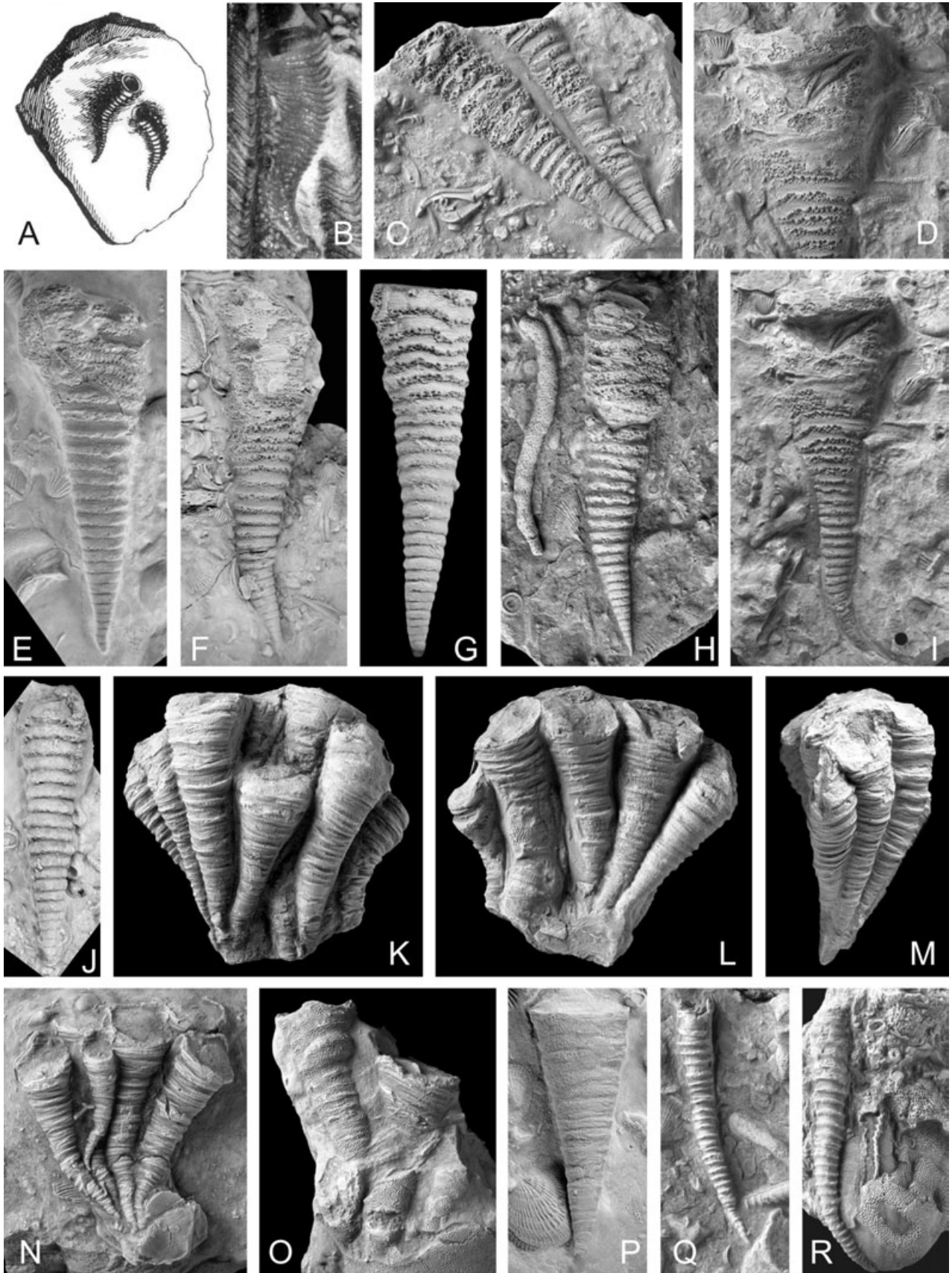
BMNH 58209, B8926 and B34691 (all from Dudley), B23134 (Aldridge, West Midlands), B34653 (Tickwood, Shropshire), and B3921 and B10115 (localities unknown), all of Wenlock age, are also referred to *C. serpularius*.

**Emended diagnosis:** Very closely annulated, slightly sinuous species of *Cornulites* without costae. Aperture shows uniform increase in size, giving shell a regular conical shape.

**Description:** Specimens of type series 6–7 mm long, with 20–25 annulations per shell. Annulations regular in shape, running parallel to circular aperture. Specimens on BU 4376 slightly smaller, ~5 mm long; aperture more elliptical, slightly irregular; annulations slightly undulating, not always parallel to aperture margin.

**Remarks:** Larsson (1979a) first noted the discrepancy between *Cornulites serpularius* as figured by Schlotheim (1820) and most of the specimens assigned to the type species by later authors. There are in fact very few cornulitids from the Much Wenlock Limestone Formation that closely resemble Schlotheim's illustration of two small, closely annulated specimens without costae. As the material upon which Schlotheim based his figure cannot be found, comparisons with other specimens are necessarily somewhat speculative, but the difference between the syntypes of *C. serpularius* and most other Wenlock cornulitids may be due in part to the drawing not being an exact representation of the specimens. Schlotheim's figure of *C. serpularius* shows the two syntypes to be unattached and resting free on an apparently homogeneous substrate, whereas all small cornulitids from the Much Wenlock Limestone Formation are found partly or wholly attached to the hard parts of another organism and, where it is preserved, in a matrix of bioclastic limestone. *C. serpularius* is restricted here to small specimens that most closely resemble the material originally illustrated by Schlotheim (1820), but with the qualification that the exact morphology of the type material remains uncertain. All other specimens are transferred to different species.

**Figure 2.** A, B, *Cornulites serpularius* Schlotheim, 1820. A, reproduction of original figure of syntypes (Schlotheim, 1820, pl. 29, fig. 7; illustration rotated through 180° for convenient comparison with other specimens illustrated here), Silurian, Gotland, ×3. B, specimen attached to brachiopod BU 4376, Much Wenlock Limestone Formation, Dudley, ×7. C–H, ***Cornulites cellulossus* sp. nov.**, Much Wenlock Limestone Formation, Dudley. C, two paratypes on slab BMNH A230, ×0.8. D, close-up of apertural region of BMNH A845, showing irregular pattern of annulations, ×1. E, paratype BU 4369, ×0.8. F, paratype BU 4370, ×0.8. G, holotype BU 4372, ×1. H, paratype BMNH A846, ×0.8. I, BMNH A845, ×0.75. J, paratype BU 4371, ×1.2. K–O, ***Cornulites gremialis* sp. nov.**, Much Wenlock Limestone Formation, Dudley. K–M, cluster BMNH A470. K, view of 'top' surface of cluster, showing holotype (largest specimen, third from left) and six paratypes, ×1.25. L, 'bottom' surface of cluster, showing five paratypes, ×1.25. M, left lateral view of cluster, with holotype to right, ×1.25. N, cluster BMNH A483a, ×1.25. O, BMNH A483b, showing two paratypes attached to cephalopod, ×1.75. P, BU 4368, possible specimen of *C. gremialis*, ×1.5. Q, R, *Cornulites scalariformis* Vine, 1882, Much Wenlock Limestone Formation, Dudley. Q, specimen BMNH AN1177, ×0.5. R, BMNH A847, ×0.6.



The profound difference in size between *C. serpularius* and the three other species of *Cornulites* recognized here raises the possibility that the specimens of *C. serpularius* were juveniles of one of the other, larger species. The difference in spacing of the annulations does not support such a relationship between *C. serpularius* and *C. cellulosus* – the annulations are relatively broad even in the early growth stages of *C. cellulosus* – whilst the absence of costae from *C. serpularius* precludes it being an early ontogenetic stage of *C. scalariformis*. *C. gremialis* has close annulations quite similar to those of *C. serpularius*, but they are often irregular, a feature not illustrated in the syntypes of *C. serpularius* (Schlotheim, 1820: pl. 29, fig. 7). The presence of fine costae in *C. gremialis* also indicates that the taxa are not conspecific.

**CORNULITES CELLULOSUS SP. NOV.**

(FIGS 1B, 2C–J, 4A–M, 5A–G, 6A, B, 9A, B)

- 1859 *Cornulites serpularius* Schloth.; Murchison, p. 221, pl. 16, figs 3a, 4, 6–10 [various specimens described as from the Much Wenlock Limestone Formation of Ledbury, Herefordshire].
- ? 1859 *Cornulites serpularius* Schloth.; Murchison, pl. 10, fig. 2 [same figure of same two specimens in pl. 16, fig. 4, but described as from the Upper Llandovery].
- 1872a *Cornulites serpularius* Schlot.; Nicholson, p. 202, figs 1a, b [described and figured ‘*C. serpularius*’ as large taxon with thick, cellular shell walls].
- ? 1872b *Cornulites serpularius*; Nicholson, p. 449 [no illustrations, but again described ‘*C. serpularius*’ as being large].
- ? 1873 *Cornulites serpularius* Schloth.; Salter, pp. 85, 93, 128, 177.
- 1875 *Cornulites serpularius* Schlotheim; Baily, p. 41, pl. 19, figs 2a, b [copy of Murchison (1859)].
- ? 1882 *Cornulites serpularius* Schlot.; Vine, p. 377 [described as solitary form with ‘very thick’ shell walls, but no specimens figured].
- 1888 *Cornulites serpularius* Schlotheim; Hall, p. 21, pl. 116 A, figs 5–8.
- ? 1888 *Cornulites proprius* Hall; Hall, pl. 116, figs 15–21 [illustrated sectioned specimens showing thick shell walls formed solely of cellulae].
- ? 1923 *Cornulites serpularius* Schlotheim; Reed, p. 269 [summary of previous work on ‘*C. serpularius*’, without illustrations].
- 1923 *Cornulites serpularius* Schlotheim; Bather, p. 543, fig. 1.
- 1962 *Cornulites serpularius* Schlotheim; Fisher, figs 78.1a.

- ? 1962 *Cornulites serpularius* Schlotheim; Fisher, p. W137, figs 78.1b–e [figures described as sections of ‘*C. serpularius*’ but are copies of those figured by Hall (1888), pl. 116, figs 16–18, 20, 21) as *C. proprius* Hall, 1879.
- ? 1972 *Cornulites serpularius*; Blind, p. 5 [detailed description of shell structures similar to those seen in *C. cellulosus*, but without illustrations].
- 1974 ‘Unattached cornulitid’ Richards, p. 515, pl. 1, fig. 8.
- ? 1979a *Cornulitidae* gen. *b*, sp. *a*; Larsson, p. 210 [no illustrations, but described as conspecific with large, cellular forms previously placed in *C. serpularius*].
- ? 1991 *Cornulites serpularius* Schlotheim; Dzik, p. 126, pl. 2, figs 5, 6 [specimens probably examples of *C. cellulosus*].

*Derivation of name:* Latin *cellulosus*, full of small chambers, in reference to the distinctive shell structure.

*Holotype:* BU 4372, from the Much Wenlock Limestone Formation (Silurian: Wenlock: Homeric) of Dudley, England.

*Paratypes:* BU 4369, 4370, 4371 (with one longitudinal and five transverse sections), 4378 (with longitudinal section), 4380–84, 4386 (longitudinal thin section of specimen), 4388–91 (longitudinal thin sections of four separate specimens) and 4392; BMNH A230 (two specimens on same slab), A450, A455 (with one longitudinal and one transverse section), A459 (with transverse section), A460 (with transverse section), A845, A846, all from locality and horizon of holotype.

*Diagnosis:* Species of *Cornulites* with very broad annulations that are rounded in profile. Shell wall lamellar at apex, cellulae appearing between lamellae in mid-region, becoming dominant in apertural region; interior of apical shell region partitioned by tabulae running approximately perpendicular to lamellae, tabulae separated by dome-shaped camerae.

*Description:* Costae normally absent, very fine where present; annulations ~1 mm thick at apical end of shell, up to ~2 mm thick in mid- and apertural regions. Shell normally a straight-sided cone, but may show some sinuosity, particularly in early stages; aperture large, round. Specimens never found attached to shells of other organisms.

Specimens range in size from approximately 40 mm to at least 80 mm long, with maximum aperture diameter of around 25 mm. The largest specimen is BU 4392, which is 80 mm long, but with the apical region missing, indicating that it had a total length of approximately 95 mm. The holotype BU 4372 (Fig. 2G) is approximately 62 mm long and free of

matrix. The shell has 29 annulations, each of which can be traced around the entire shell exterior, although those closest to the aperture are somewhat irregular, with cellulae often visible in large numbers. The shell is straight-sided, but in cross-section changes from circular apically to elliptical aperturally; the aperture is oval, with a minimum diameter of 11 mm and a maximum of 16 mm. This may be due to crushing of the apertural region of the specimen, as the shell has longitudinal fractures on the plane running through the widest part of the aperture.

Towards the aperture of some specimens the annulations become obscure: the first 20 annulations of paratype BU 4369 (Fig. 2E) are very regular and similar, showing no sign of cellulae, but the remainder of the shell up to the aperture is extremely irregular, with annulations difficult to discern and numerous cellulae present on the external surface. A similar pattern is seen in paratype BU 4370 (Fig. 2F), with the first 20 or so annulations obvious, but those towards the aperture much harder to distinguish.

Not all specimens have continuously straight-sided shells: BU 4370 is straight-sided for the first 11 annulations (~15 mm) before changing growth direction (see Fig. 2F). The shell is then straight-sided again for the rest of its length. Paratype BMNH A846 (Fig. 2H) is very similar, showing a distinct change in growth direction after the 12th annulation, and with the annulations becoming difficult to identify in the apertural region. Paratype BMNH A845 (Fig. 2D, I), in contrast, has a distinctly curved apical shell region before becoming straight-sided in the mid-region and towards the aperture. It becomes expanded and extremely irregular close to the aperture (see Fig. 2D).

The apertural shell region is well preserved in paratype BU 4371 (Fig. 2J) and has a morphology not seen in other specimens: after consistently increasing in diameter up to the annulation closest to the aperture, the shell then begins to close again, such that the aperture is narrower in diameter (~11 mm) than the final annulation (~13 mm). The origin and development of this apertural constriction is discussed below.

*Remarks:* *Cornulites cellulatus* is the largest species of *Cornulites* in the Much Wenlock Limestone Formation. This, combined with the size of the annulations, their convexity in profile, and the thick, cellular walls, makes it easy to distinguish from *C. serpularius*, *C. gremialis* and *C. scalariformis*. *C. cellulatus* is most similar to *C. proprius* Hall, 1879 from the Niagara Group (Silurian) of Indiana. *C. proprius* reached shell lengths of up to 80 mm and also had a thick, cellular shell wall, but differs from *C. cellulatus* in that the cellulae of *C. proprius* form the entire thickness of the wall (see Hall, 1888: pl. 116, figs 1–21), and are not divided into zones by the lamellae, as in *C. cellulatus*

(see below). The annulations of *C. proprius* are also much finer and more irregular.

### ***CORNULITES GREMIALIS* SP. NOV.**

(FIG. 2K–O, ?2P)

*Derivation of name:* Latin, *gremialis*, growing in a cluster from a stump, in reference to the species often occurring in clusters attached to a shell fragment.

*Holotype:* Largest specimen of cluster BMNH A470, attached to indeterminate shell fragment, from the Much Wenlock Limestone Formation of Dudley, England.

*Paratypes:* Ten other specimens in cluster BMNH A470, BMNH A483a (six specimens attached to ?brachiopod shell fragment) and A483b (two specimens attached to cephalopod); BU 4378 (cluster of six specimens) and 4385 (two fused specimens), all from locality and horizon of holotype.

*Other material:* BU 4368, a solitary specimen from the Much Wenlock Limestone Formation of Wren's Nest Hill, Dudley, is questionably assigned to the species.

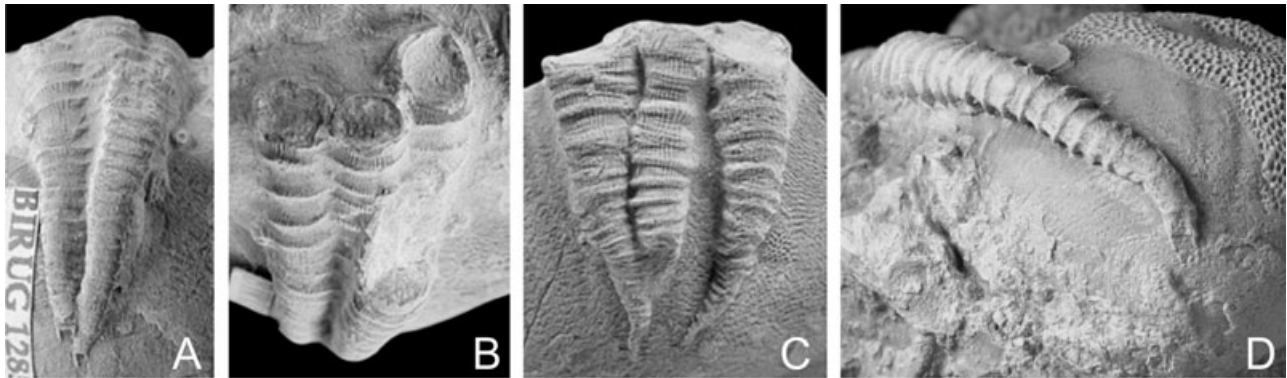
*Diagnosis:* Closely, rather irregularly annulated species of *Cornulites*, annulations alternating between pronounced and less pronounced. Costae fine but prominent; closely spaced.

*Description:* Shell normally slightly sinuous or twisted, particularly in early growth stages. Aperture increases regularly in size; aperture sometimes ovoid rather than circular. Specimens normally found in clusters, with apices attached to shell fragments; smaller specimens often using larger ones as substrate. Pronounced annulations not normally obvious in apical region of shell.

The holotype is the largest specimen on cluster BMNH A470 (see Fig. 2K–M). It is approximately 32 mm long, with an aperture diameter of around 10 mm. The shell surface has pronounced annulations spaced approximately 1 mm apart, and around five costae per millimetre.

*Remarks:* BU 4368 (Fig. 2P) is a solitary, unattached cornulitid approximately 33 mm long, with a circular aperture ~13 mm across. In some respects, particularly the arrangement of annulations and costae over much of the shell surface, it resembles specimens of *Cornulites gremialis*. At the apex, however, the annulations are thicker, and there is a suggestion that cellulae are present, making it much more like *C. cellulatus*. Its specific assignation is thus uncertain, but if cellulae are a feature of all cornulitids then there are sufficient similarities to *C. gremialis* for it to be questionably included in the species.

The overall shell shape, and closely spaced, irregular annulations that normally alternate in prominence



**Figure 3.** *Cornulites scalariformis* Vine, 1882, Much Wenlock Limestone Formation, Dudley. A, B, four specimens attached to brachiopod BU 4373. A,  $\times 2.25$ , B,  $\times 3$ . C, three specimens attached to brachiopod BU 4374,  $\times 3$ . D, NHM A847,  $\times 0.75$ .

make *C. gremialis* easy to distinguish from *C. scalariformis*. The conical shell morphology of *C. gremialis* is similar to that of *C. cellulosus*, but the two taxa can be separated by the differences in annulation and costal morphology. As noted above, the closest similarity of *C. gremialis* is to *C. serpularius*, but the irregularity of the annulations and prominence of costae in *C. gremialis* suggest they are not conspecific.

*CORNULITES SCALARIFORMIS* VINE, 1882  
(FIGS 2Q, R, 3A–D, 7A, B)

- ? 1859 *Cornulites serpularius* Schloth.; Murchison, pl. 16, fig. 5 [illustration of three specimens similar to *C. scalariformis*].
- \* 1882 *Cornulites scalariformis* Vine, p. 379, pl. 15, figs 1, 9, 10.
- 1974 'Cornulitid transitional between attached and free-living forms Richards, p. 515, pl. 1, fig. 7.
- 1979a *Cornulites? scalariformis* Vine; Larsson, p. 208.
- ? 1979a *Cornulites? cf. scalariformis* Vine; Larsson, p. 208 [no illustrations].

**Material:** The type specimens of *C. scalariformis* have not been traced. However, Vine's illustrations (1882: pl. 15, figs 1, 9 and 10) are sufficiently clear to enable material to be identified with greater certainty than for *C. serpularius*. Four specimens attached to brachiopod BU 4373, three specimens attached to brachiopod BU 4374, and two specimens attached to brachiopod BU 4375, BU 4377a–d (four separate, unattached specimens), BU 4387 (longitudinal thin section of specimen), BMNH A847, and BMNH AN1177, all from the Much Wenlock Limestone Formation of Dudley, are placed in *C. scalariformis*.

**Emended diagnosis:** Species of *Cornulites* with widely spaced, narrow annulations separated by concave areas with thin, prominent costae. Aperture width expands slowly, particularly in later growth stages, producing essentially tubular shell morphology. Shell wall predominantly lamellar, but with occasional cellulae present adjacent to external annulations.

**Description:** *Cornulites scalariformis* has a shell length of up to at least 45 mm, as seen in BMNH AN1177 (Fig. 2Q) and BMNH A847 (Figs 2R, 3D), with an aperture diameter of up to 5 mm. Annulations of BMNH A847 approximately 0.5 mm thick, separated by 1-mm bands in which costae are present; costal density around 5 per mm. The type specimen illustrated by Vine (1882: pl. 15, fig. 1) is incomplete, being around 15 mm long, with a diameter of  $\sim 3$  mm at apical end and  $\sim 4$  mm at apertural end, and shows eight annulations. The shell microstructure of *C. scalariformis* seen in thin section BU 4387 is described below.

**Remarks:** *Cornulites scalariformis* is easily distinguishable from *C. serpularius* and *C. cellulosus* by having a narrow, almost tubular shell even when large (aperture width approx. 3 mm at specimen length 12 mm, and 5 mm at length 45 mm) and well-spaced, prominent annulations separated by areas containing pronounced costae. Some smaller specimens, such as those attached to brachiopod BU 4374 (Fig. 3C), show similarities to *C. gremialis*, but the two species can be separated by the prominence of the costae and consistency of annulation morphology: *C. scalariformis* always has more pronounced costae than *C. gremialis*, whilst its annulations are generally very similar, and do not show the variation of *C. gremialis*.

The possibility cannot be discounted entirely that the species of *Cornulites* described here are ecophenotypes, with the variations in morphology reflecting adaptations to different ecological niches. However, the differences in ornamentation and shell shape appear



to be significant and consistent, and the morphologies are therefore regarded as representing species.

### CORNULITID SHELL STRUCTURE

The microstructure of *Cornulites* was first examined by Salter (in Murchison, 1859: 221), who described the shell as having 'a highly complex cellular structure'. His description was presumably based on the longitudinally sectioned specimens illustrated by Murchison (1859: pl. 16, figs 8–10), which were described as *C. serpularius* but are evidently *C. cellulosus*. Further illustrations of the microstructure of *Cornulites*, based on both longitudinal and transverse sections of specimens from the Silurian of North America, were provided by Hall (1888). He showed shell walls composed almost entirely of cellulae, with little clear pattern to the structure.

In contrast, Bather (1923) sectioned three specimens of *C. cellulosus* (BMNH A455, A459 and A460) and revealed a shell wall composed of cellulae and lamellae with a clear pattern to their distribution. In transverse section, the lamellae were seen to separate the cellulae into narrow, approximately concentric bands around the aperture, while in longitudinal view the lamellae are 'essentially continuous' (Bather, 1923: 544), running in an undulating fashion along the shell interior, with cellulae present between lamellae towards the external surface (see Bather, 1923: fig. 1). Fisher (1962: figs 78, 1b–e) reproduced Hall's (1888) figures, and described the cellulae as being scarce in the lower part of the shell, but developing rapidly in the mid-region and towards the aperture. Blind (1972) described (but did not illustrate) the shell of *C. serpularius* as being composed of both cellulae and lamellae.

The most recent study (Vinn & Mutvei, 2005) was a detailed account of shell structure and ontogeny based on Ordovician cornulitids from Anticosti Island, Canada, and Silurian specimens from Gotland and Estonia. They described all cornulitids as having lamellar, calcite shells with cellulae, and showed a variety of cellular-lamellar patterns (see Vinn & Mutvei, 2005: figs 4, 5). *Conchicolites* was shown to differ from *Cornulites* in lacking cellulae ('vesicles' of Vinn & Mutvei, 2005) in the shell wall, and having tabulae that were not connected to the lamellae of the shell wall.

Specimens of *Cornulites* from the Much Wenlock Limestone Formation show a well-preserved internal structure comparable with the preservation seen in brachiopods and trilobites (Wilmot & Fallick, 1989), known to have had original low-magnesian calcite exoskeletons. Under cathodoluminescence *Cornulites* shows no sign of microdolomite inclusions such as are seen in crinoid ossicles from the same formation (Wilmot & Fallick, 1989). This excludes an originally high-

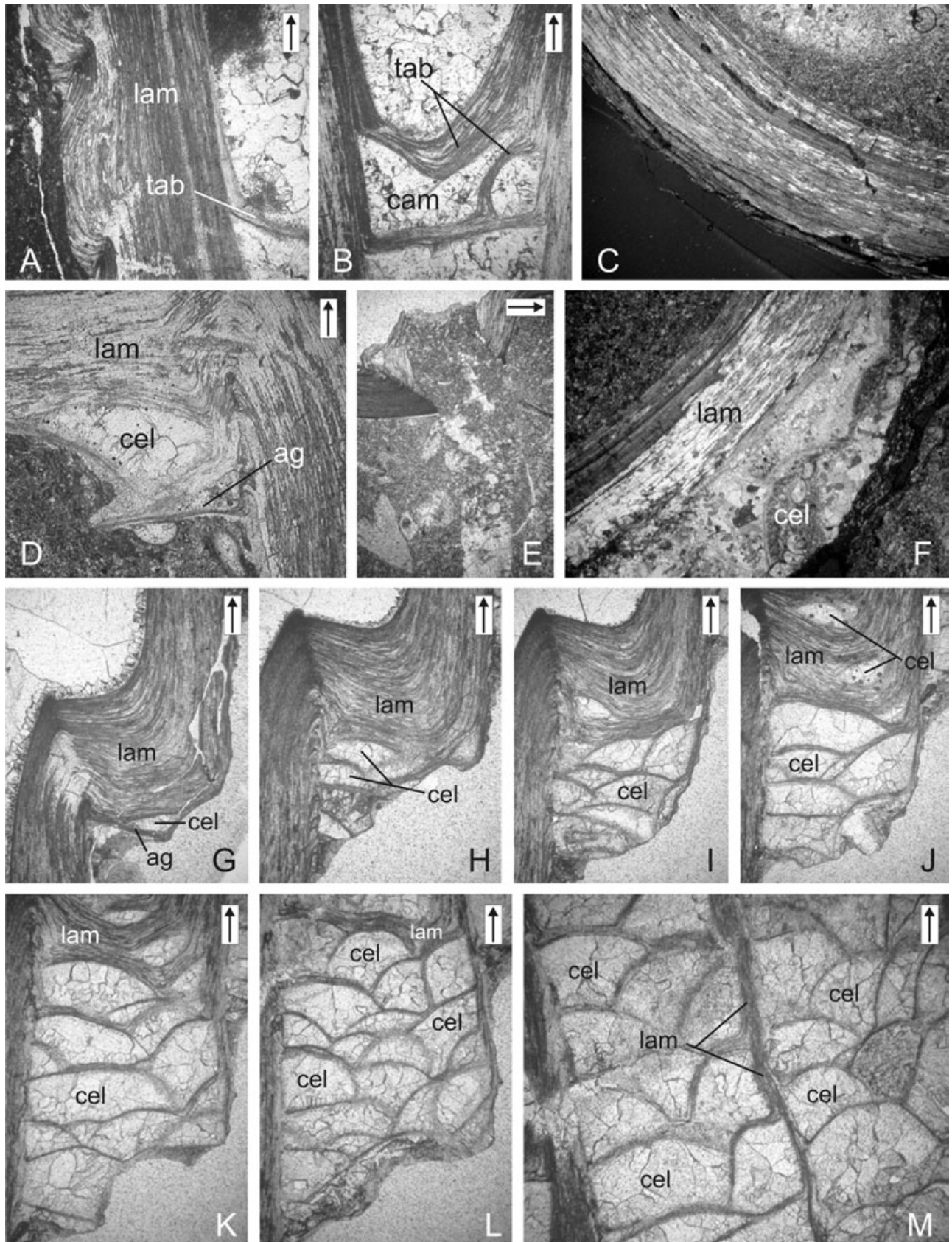
magnesian calcite composition. Original aragonite shells in the Much Wenlock Limestone Formation are invariably preserved as neomorphic calcite spar (Wilmot & Fallick, 1989).

### SKELETAL STRUCTURE OF *CORNULITES CELLULOSUS*

The longitudinal and transverse sections of *Cornulites cellulosus* show that the shell can be divided into three parts – the apical region, mid-region and apertural region (see above for definitions). The actual apex is not preserved in any of the specimens studied, so it cannot be determined whether the egg-shaped initial chamber described in various cornulitids by Blind (1972) and Vinn & Mutvei (2005) is present. The most prominent internal features of the apical region are the tabulae, which are approximately perpendicular to the surface of the shell wall. The tabulae closest to the apex are stacked directly upon one another (Fig. 1B), but aperturally they become separated by dome-shaped vacuities (camerae) of various sizes (Figs 1B, 4B). In the apical region, the shell wall is bipartite, with undulating lamellae towards the exterior, and non-undulate lamellae towards the interior (Fig. 4A). Each tabula is connected to a lamella, and the connection occurs on both sides of the shell interior (Fig. 4B). In transverse view the apical region is formed of concentric zones of lamellae (Fig. 4C), such that, in three dimensions, the tabulae and lamellae take the form of stacked, elongate cups.

In the mid-region, beyond the most distal tabula, the interior of the shell has in longitudinal section a simple, straight-sided shape, expanding in width from apex to aperture (see, for example, Fig. 1B). At approximately the point where the tabulae stop, the shell exterior begins to become cellular, with the first cellulae (Figs 1B, 4D, G) appearing between the undulating lamellae. At this apical end of the mid-region, the straight lamellae and undulating lamellae form half the thickness of the shell wall each (Fig. 4A), but towards the aperture the undulating lamellae become increasingly prominent until, at the apertural end of the mid-region, they comprise the entire thickness of the shell wall (Fig. 1B). From this point, cellulae are more abundant on the exterior surface of the shell wall, increasing in number towards the aperture, but are still relatively scarce (see, for example, Fig. 4G, H). In transverse view, the undulating lamellae and cellulae form a somewhat irregular band around the exterior of the shell, with concentric lamellae inside (Fig. 4F).

In the apertural region the undulating lamellae run along the interior surface of the shell, giving it an annulated appearance virtually indistinguishable from that of the shell exterior (e.g. Fig. 4G). The lamellae form the bulk of the shell wall in the apical part of



the apertural region, with cellulae in small numbers close to the external surface. The cellulae increase rapidly in number closer to the aperture (see Fig. 4I–K) and at the aperture form almost the entire shell wall (Fig. 4L, M) with the lamellae reduced to a thin layer covering the shell interior (Figs 5E, 6A). The longitudinal section of BU 4378 shows how the change from one annulation to the next occurs moving aperturally. The transition begins with an increased number of cellulae to the exterior of the undulating lamellae (Figs 4G, H), then occasional additional cellulae appear between bands of lamellae (Fig. 4I, J), and finally almost every lamella is separated by cellulae (Fig. 4K, L). Each cellula is orientated with its convex surface directed towards the aperture. Although the cellulae increase the total shell wall thickness, the quantity of skeletal calcite remains constant. The increased wall thickness is simply a consequence of lamellae bifurcating to accommodate the cellulae.

In transverse view, a section cut at the apical end of the apertural region is composed of a thick band of cellulae around the shell perimeter, and a thin band of lamellae around the interior (Fig. 5E), whereas sections cut closer to the aperture show numerous bands of cellulae separated by occasional very thin bands of lamellae (Fig. 5F, G). The cellular bands are not wholly concentric but pinch out in both directions, giving them a broadly fusiform shape (Fig. 5F, G). In addition, the cellulae are orientated with their convex surfaces directed towards the interior of the shell. In longitudinal view the cellulae in the area around the aperture are stacked in ‘zones’ – thin, elongate, almost rectangular areas bounded on either side by thin bands of lamellae (Fig. 4M). Examined under ESEM, the transverse, mid-region section of BU 4371 shows an alternating pattern of thinly foliated lamellae and blocky crystalline lamellae (Fig. 5D).

In the original description of *Cornulites scalariformis*, Vine (1882: 380) stated that the shell wall was laminar, with ‘circular, oval or angular cavities’ in the shell wall adjacent to each annulation (see Vine, 1882: pl. 15, fig. 9). This is supported broadly by the structures seen in the longitudinally sectioned specimen of *C. scalariformis* (BU 4387; Fig. 7A, B). The specimen

is incomplete, with nothing of the apical region preserved, but as with *C. cellulatus*, the mid- to apertural regions are composed of lamellae that are straighter towards the apex and increasingly undulate towards the aperture, and which are separated by cellulae. However, their distribution is slightly different from that of *C. cellulatus*, with the cellulae normally occurring in the centre of the shell wall rather than towards the external surface (Fig. 7A, B; compare with *C. cellulatus*, Fig. 4G–I). Furthermore, they do not show a pronounced increase in abundance towards the aperture, remaining relatively large but few at each annulation. A closely comparable pattern of cellulae distribution was described in the contemporaneous Gotland taxon *C. aff. scalariformis* (see Vinn & Mutvei, 2005: figs 4.7, 4.8).

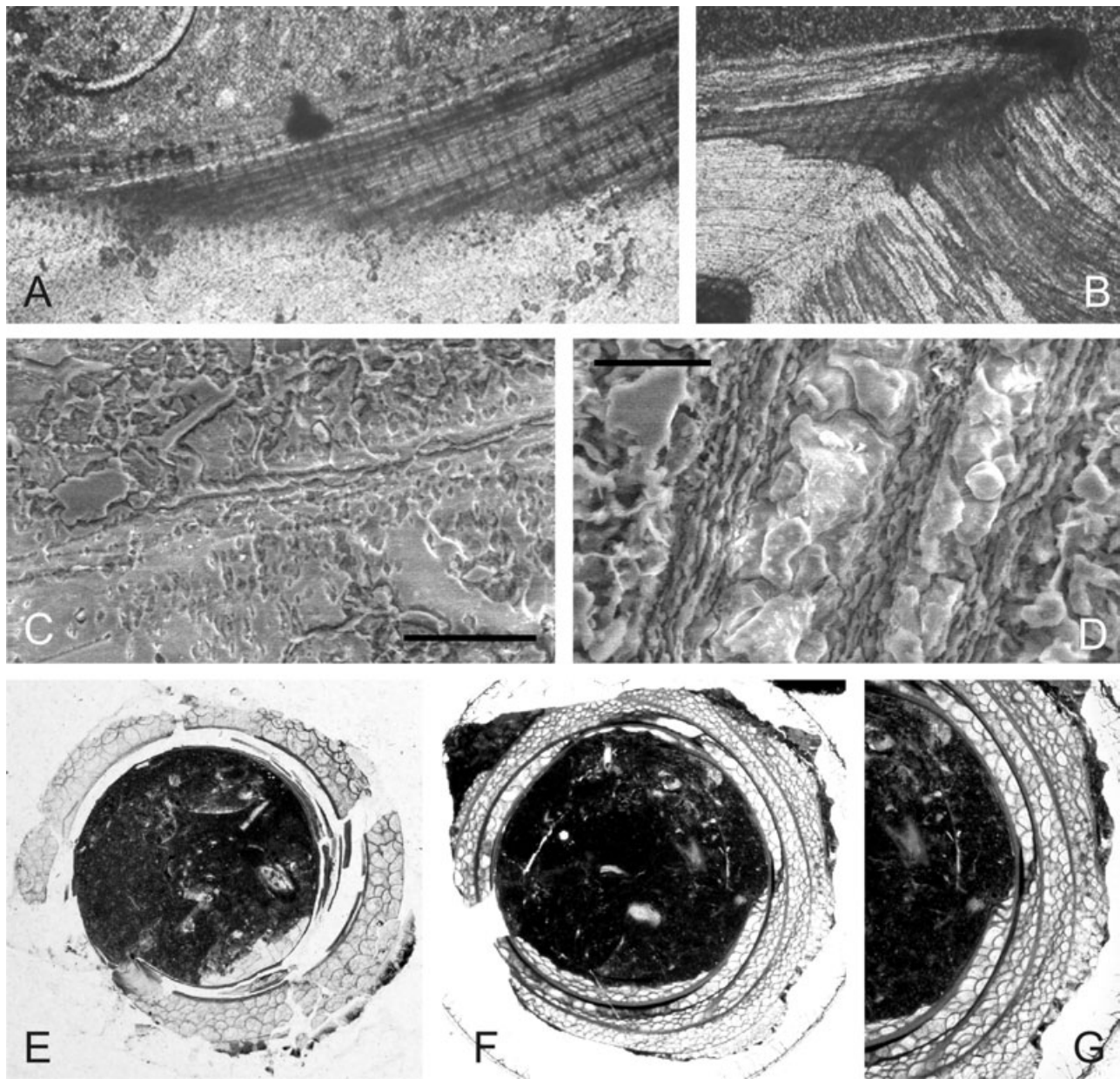
The longitudinal thin section of *Cornulites cellulatus* (BU 4371) shows that the lamellae have small but distinct crenulations that form linear structures running perpendicularly through the shell wall (Fig. 5B). They are seen also in a slightly oblique transverse section through the same specimen (Fig. 5A). Vinn & Mutvei (2005: fig. 4.1) illustrated morphologically identical crenulations in *Cornulites aff. scalariformis* from the Wenlock of Estonia, the surface representation of which is a series of minute protuberances (Vinn & Mutvei, 2005: fig. 4.2). Caused by point inflections in the cornulitid lamellae these features are referred to as ‘pseudopuncta’ (sing. pseudopunctum).

The longitudinal section of BU 4371 shows that the shell is extensively bored, particularly across the exterior surface. Some examples are clearly post-mortem (e.g. *Trypanites* boring, Fig. 4E), but an even distribution of borings on both the buried and the exposed external surfaces of the fossil indicates that many were formed while the cornulitid was alive, possibly by boring organisms ‘mining’ organic material present between the lamellae.

#### COMPARISON OF *CORNULITES* WITH OTHER PROBLEMATICA

The likely position of *Cornulites* within the Metazoa is discussed below, but there are other problematical

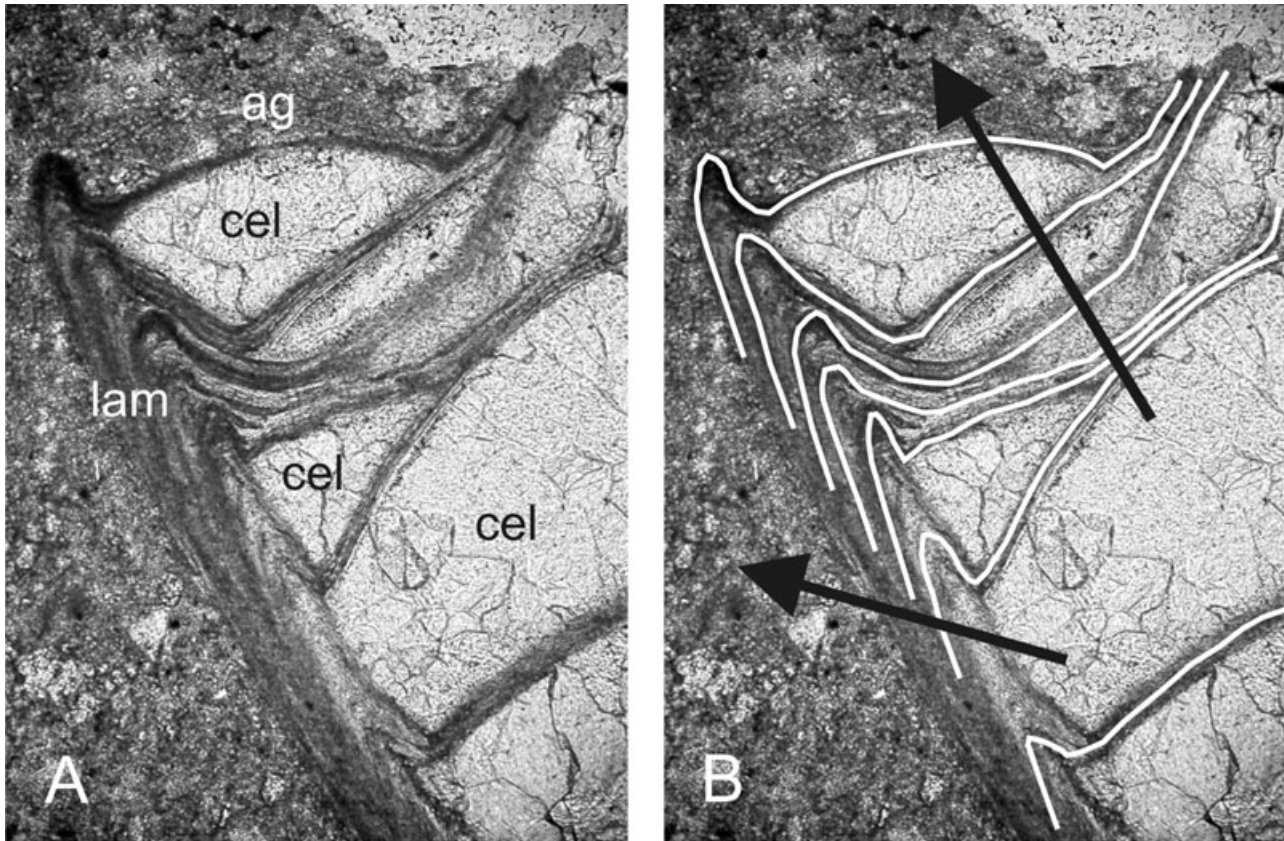
**Figure 4.** A–C, E, shell wall structures in apical region of *Cornulites cellulatus* sp. nov., BU 4371. A, longitudinal section showing undulating and straight lamellae (lam) and tabula (tab), aperture towards top,  $\times 25$ . B, longitudinal section showing tabulae (tab) and camerae (cam), aperture towards top,  $\times 25$ . C, transverse section showing concentric lamellae, shell interior to top right,  $\times 25$ . E, *Trypanites* boring in BU 4378, longitudinal section, aperture towards right,  $\times 6$ . D, F–M, development of cellulae in *Cornulites cellulatus* sp. nov. D, BU 4371, longitudinal section through annulation in mid-region of shell, showing overgrowth of apertural groove (ag) by undulating lamellae (lam), with single cellula (cel) present,  $\times 25$ . F, BU 4371, transverse section through shell wall, showing concentric lamellae (lam) and cellulae (cel); shell interior to top left,  $\times 25$ . G–L, BU 4378, development of cellulae seen in longitudinal sections through annulations from mid- (G) to apertural (L) shell regions; G–J,  $\times 18$ , K and L,  $\times 20$ . M, BU 4378, longitudinal section through apertural region of shell, showing development of cellulae into zones separated by thin lamellar bands,  $\times 35$ . Arrows indicate direction of aperture in longitudinal sections.



**Figure 5.** Shell structures in *Cornulites cellulosus* sp. nov. A–C, BU 4371, pseudopuncta. A, transverse view,  $\times 45$ , B, longitudinal view,  $\times 45$ . C, ESEM image of transverse section (scale bar = 20  $\mu\text{m}$ ), shell interior towards top in all images. D, BU 4371, ESEM image of transverse section across mid-region shell wall, showing bipartite structure within lamellae, scale bar = 10  $\mu\text{m}$ . E, BMNH A455, transverse section across apertural region showing concentric lamellae and apertural groove filled with cellulose,  $\times 4$ . F, G, BMNH A459. F, transverse section close to aperture,  $\times 3.25$ . G, close-up of concentric lamellae, separated by zones of cellulose,  $\times 4$ .

taxa, notably *Tentaculites* Schlotheim, 1820, and *Cloudina* Germs, 1972, with which it shares distinct similarities. Schlotheim (1820) erected *Tentaculites* to include a different group of annulated, conical, calcareous shells from the Palaeozoic and described two species, *T. scalaris* and *T. annulatus*. As with *Cornulites serpularius*, the specimens figured by Schlotheim (1820) cannot be traced (Larsson, 1979b), but based on

the original illustrations the two genera are morphologically similar. Like *Cornulites*, *Tentaculites* is radially symmetrical about its long axis, but the shell is more slender, with a narrower aperture, rarely shows any sinuosity, and normally lacks obvious longitudinal ornamentation. However, having suggested that *Cornulites* might be most closely related to annelids, Schlotheim (1820) interpreted *Tentaculites* as a



**Figure 6.** Shell structures in *Cornulites cellulosus* sp. nov. A, B, BU 4378,  $\times 60$ . Longitudinal section through apertural version of shell showing continuity between lamellae (lam) in the shell wall and partitions bounding cellulae (cel): selected lamellae are highlighted in B, 'ag' indicates the apertural groove. The pattern of overlap in the lamellae shows that growth occurred in the direction indicated by the arrows.

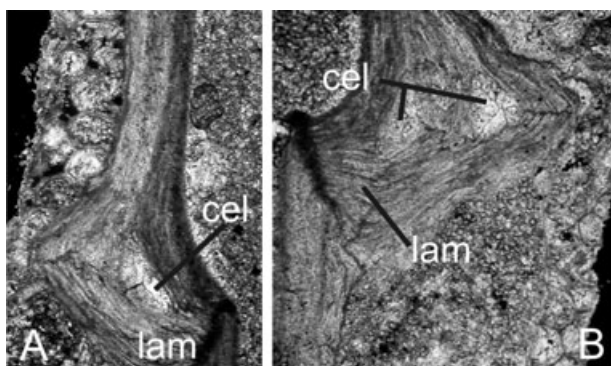
crinoid appendage. Subsequent assessments of the biological affinities of *Tentaculites* have been varied (for a summary see Larsson, 1979b): whilst some authors (e.g. Nicholson, 1872a, b, 1873; Fisher, 1962) have followed Schlotheim in regarding *Tentaculites* and *Cornulites* as belonging to separate phyla, others (e.g. Murchison, 1859; Vine, 1882; Bouček, 1964; Dzik, 1991, 1993) have argued that the two genera are closely related. Indeed, Bouček (1964) erected the Order Cornulitida as a constituent group of his Class Tentaculita, a classification followed by Vinn (2005).

As with cornulitids, the earliest growth stages of the tentaculitid shell are very rarely preserved (Larsson, 1979b), but the shell structures of some tentaculitids show a number of similarities to *Cornulites*, particularly towards the shell apex. Most prominent are the transverse shell layers that, in many tentaculitids, divide the apical region into distinct chambers, or camerae (see Larsson, 1979b: fig. 12). These are similar in arrangement to cornulitid tabulae and camerae, although the transverse layers do not continue up the interior shell surface to form lamellae. Instead, they

taper distally, and the shell wall is formed of separate lamellae, unconnected to the transverse layers, producing a bipartite division of primary (outer) and secondary (inner) layers (Bouček, 1964; Larsson, 1979b). Larsson (1979b: 27) noted also that tentaculitid lamellae were 'not persistent along or around the conch', making them unlike the continuous lamellae of cornulitids. However, he did show that the lamellar part of the conch contained pseudopuncta orientated perpendicular to the surface of the wall. The phylogenetic position of tentaculitids is unresolved but, based on similarities in shell microstructure, Towe (1978) raised the possibility that they were most closely related either to the brachiopods or their sister group, the phoronids. Larsson (1979b: 59) suggested that tentaculitids were perhaps more closely related to phoronids, but noted that the lophophorate feeding system of phoronids was incompatible with the planktonic mode of life proposed for some tentaculitids. Vinn (2005) and Vinn & Mutvei (2005) have interpreted cornulitids and tentaculitids as closely related groups of probable lophophorates but, as discussed

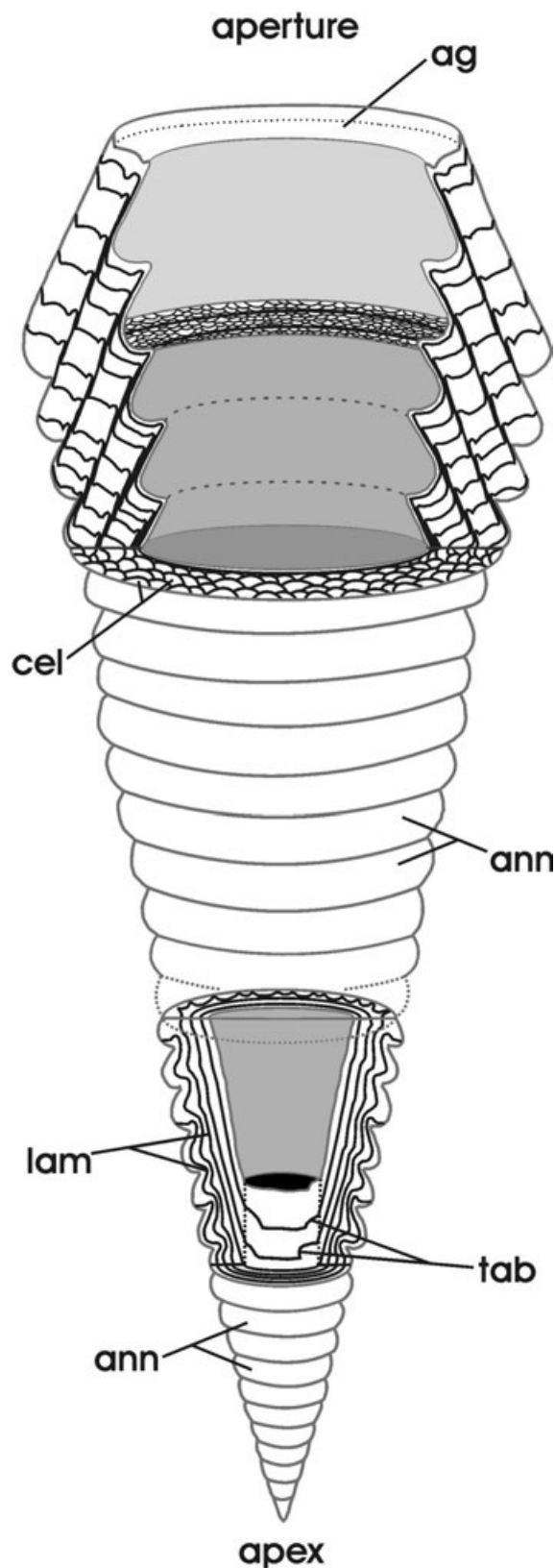
below, comparable morphologies and shell structures are found also in cnidarians. Further work is required to resolve both the affinities of *Tentaculites* and its systematic relationship to *Cornulites*.

*Cloudina* is a genus of tubular, calcareous fossils found in rocks of Ediacaran age. The first detailed study of the shell structure of *Cloudina* was that of Grant (1990), who described a cone-in-cone structure of stacked tubes, a layer of calcium carbonate having been deposited over the entire surface at each growth stage, and the presence of vacuities between the layers both apically and aperturally (see Grant, 1990: figs 5, 7, 9). He described also that each new tubular cone of calcium carbonate was deposited eccentrically within



**Figure 7.** A, B, BU 4387, *C. scalariformis*, longitudinal sections through shell wall, showing lamellar structure (lam) separated by occasional cellulae (cel), aperture towards top in both images. A, shell interior to right,  $\times 20$ . B, shell interior to left,  $\times 23$ .

**Figure 8.** Schematic reconstruction of *Cornulites* shell morphology, based on shell structures seen in *C. cellulosus* (approximately  $\times 5$ ). Transverse annulations (ann) are visible externally; cutaway sections show major aspects of internal morphology. Narrow apical end of shell possesses tabulae (tab) internally (upper surface of most apertural tabula shaded black; more apical tabulae shown only in section). Shell wall in apical region composed of internally straight, but externally undulating, lamellae (lam). Towards aperture, convex-inwards cellulae (cel) become abundant outside inner lamellar layer; in vertical section, cellulae are convex-upwards and bounded by well-separated undulating lamellae. In this orientation, the undulating lamellae form a shell wall of outwardly and downwardly dipping zones. Towards aperture, cellulae are arranged in crescentic transverse arcs, indicating an eccentricity to the cone-in-cone growth pattern. In upper cut-away, pale grey shading represents inner surface of outermost shell layer; medium grey indicates inner surface of whole skeleton with faint transverse annulations visible (broken lines). Apertural region has prominent apertural groove (ag).



earlier layers, and stated that he was unaware 'of any Cambrian or younger fossils that share features of the *Cloudina* shell structure' (Grant, 1990: 286). However, although simpler and lacking such features as pseudopuncta and cellulae, the overall pattern of shell growth and structure in *Cloudina* is very similar to that of *Cornulites*. In particular, the placement of each layer eccentrically within earlier layers gives *Cloudina* a transverse section view similar to that of *Cornulites cellulossus* (compare Fig. 5F with Grant, 1990: fig. 5E). It is possible therefore that the more complex skeleton of *Cornulites* developed from that of a *Cloudina*-like ancestor.

### CORNULITID ONTOGENY

Relatively few previous studies have considered the ontogeny or skeletal development of *Cornulites*, particularly its earliest growth stages. Hall (1888) stated that all cornulitids began as a 'simple point . . . [attached to] the surface of some other organism' (Hall, 1888: 16), whilst Bather (1923) suggested that the lamellae were laid down by 'a periodical shrinkage and sloughing of the outer membrane' (Bather, 1923: 544) and the cellulae possibly by a liquid or a gas. The growth diagram produced by Fisher (1962: W136, fig. 79) is extremely dubious and appears to be an amalgam of several disparate taxa.

Blind (1972: 6) described cornulitids as having 'an egg-shaped, orally constricted initial chamber' but no illustrations were provided. However, Vinn & Mutvei (2005: figs 5.4, and 6) figured a number of small cornulitids in which the apical region is well preserved, confirming the presence of globular or ovoid initial shell chambers. They interpreted cornulitid shell growth as having been controlled by a secretory epithelium which covered the entire cornulitid body. The epithelium deposited thin layers of calcite, which at the aperture formed the external annulations, costae and the cellular wall, and deposited over the internal shell surface a thin layer that covered previous cellulae and lamellae. Apically, 'the epithelium secreted a compact lamellar inner layer' (Vinn & Mutvei, 2005: 731) forming the shell wall, with the internal chamber being partitioned periodically by the deposition of tabulae.

The very apex of the shell is not preserved in the specimens of *Cornulites cellulossus* and *C. scalariformis* studied, so the earliest growth stages are not seen. Thus, although it has been identified in small, attached cornulitids (Vinn & Mutvei, 2005), the initial morphology of large, unattached forms remains unknown.

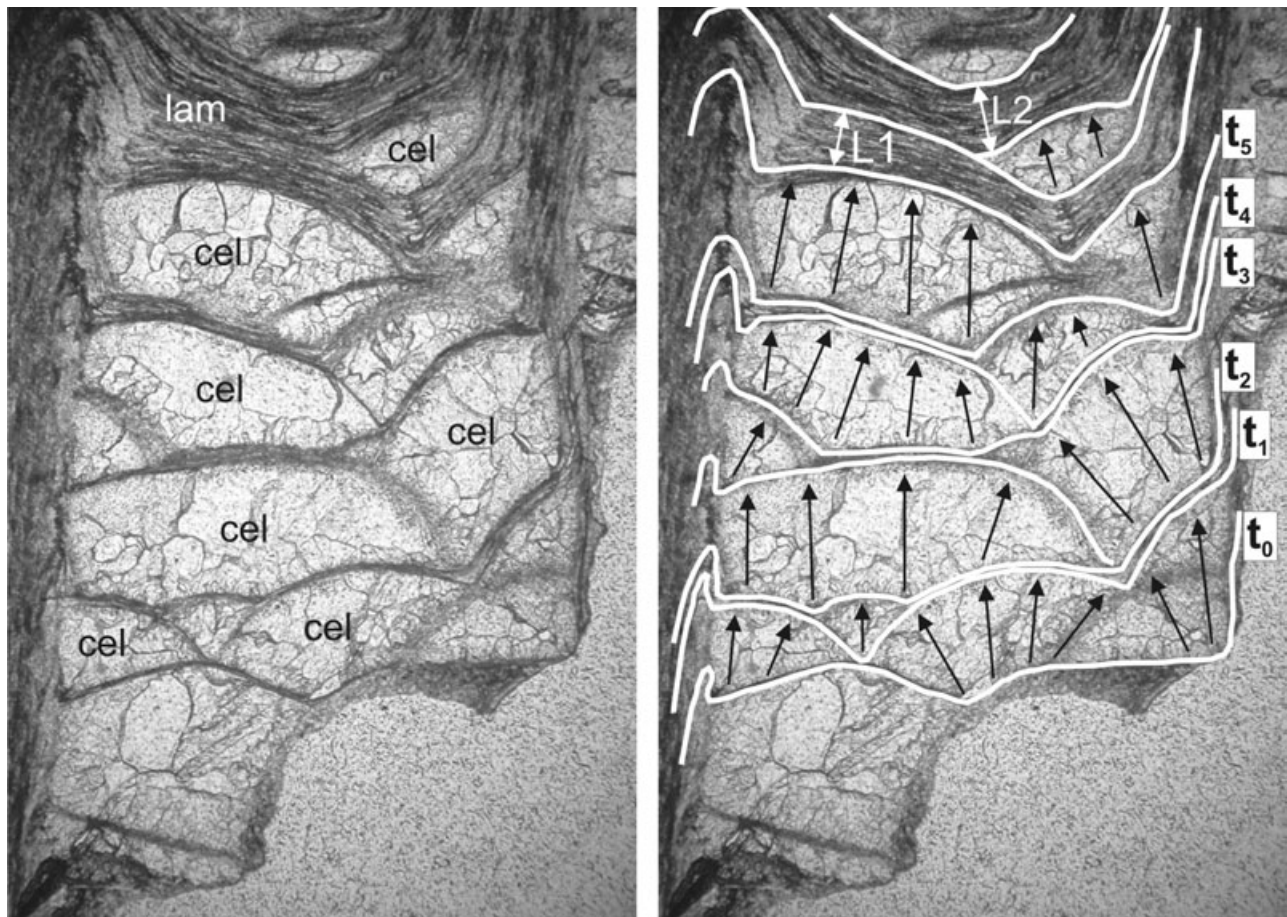
Shell formation in *Cornulites* was by accretionary growth, with the tabulae and lamellae stacked upon each other in the growth direction from apex to aperture (see, for example, Figs 1B, 4B, 8). The concentric

pattern of lamellae seen in transverse section (Fig. 4C) shows that the structure is essentially cone-in-cone, although a more eccentric pattern is seen aperturally in transverse sections of *C. cellulossus* (Fig. 5F, G). This suggests that there was a degree of growth axis rotation between periods of deposition, similar to that described in *Cloudina* (Grant, 1990). Each tabula represents the base of a cone, with the camerae indicating that the soft tissues were lifted up, away from pre-existing tabulae, prior to the deposition of the next tabula. A plausible analogue for this process is that described by Tavener-Smith & Williams (1972) for the deposition of bryozoan diaphragms. Based on studies of mantle translation in living brachiopods, they suggested that when a bryozoan zooid migrated distally within its tube 'the basal part of the epithelial cover must have secreted a transverse organic membrane, which sealed off that segment of the zooecial tube just vacated . . . [and then] acted as a seeding sheet for the secretion of the mineral constituents of the diaphragm' (Tavener-Smith & Williams, 1972: 142).

Aperturally, away from the tabulae, the lamellae gradually develop undulations, terminating with the development of an apertural groove (see Fig. 6A, B). As each lamella was overgrown by subsequent lamellae, so the apertural groove was closed off (see Fig. 4D, G). The external annulations thus represent the position of the aperture at particular growth stages, whilst the zones seen in longitudinal section (Fig. 4M) are the structural expression of an increase in lamellar undulation towards the aperture (see Fig. 8). This increase in undulation is combined with an increase in lamellar bifurcation: towards the aperture every undulating lamella bifurcates from the lamella beneath to accommodate a cellula (compare Fig. 4G, L). The overall growth pattern of *Cornulites*, based on *C. cellulossus*, is shown in Figure 8, whilst Figure 9 illustrates the apertural development of the cellulae.

Cellulae are most numerous towards the aperture of large cornulitids such as *C. cellulossus*. In such solitary, unattached taxa, probably growing vertically away from the substrate (see below), the increase in cellulae might have assisted in the maintenance of an upright life position. In such an orientation, an increase in cellulae would have minimized the density of the apertural shell region as the cornulitid grew, with the non-cellular apex of the shell serving to 'anchor' the animal to the substrate. This is supported by the fact that the shells of smaller, attached cornulitids, such as *C. scalariformis* (Fig. 7A, B) and *C. aff. scalariformis* (Vinn & Mutvei, 2005: figs 4.7, 4.8), have considerably fewer cellulae.

The change in shell growth direction seen in some specimens of *C. cellulossus* (e.g. BU 4370, Fig. 2F, and BMNH A846, Fig. 2H) is perhaps due to the cornulitid



**Figure 9.** Development of cellulae in *Cornulites cellulosis* sp. nov. A, B, BU 4378,  $\times 60$ . Longitudinal section through annulation in apertural region of shell, showing stacking of cellulae (cel) and lamellae (lam). Lamellae deposited at selected time intervals  $t_0$ – $t_5$  are highlighted in B; black arrows represent growth directions within and between cellulae. L1 and L2 are thickened series of lamellae without cellulae, and represent later shell layers that closed off and overgrew the lamellae and cellulae of an earlier growth stage.

having been dislodged from its life position, and then growing in a different direction to compensate. Such changes in growth direction would also explain the lamellar eccentricity seen in transverse sections.

The loss of obvious annulations in many large specimens of *C. cellulosis* (e.g. BU 4369, Fig. 2E) is probably a consequence of either irregularities in late-stage shell growth or post-damage shell repair. The distorted annulations close to the aperture of BMNH A845 (Fig. 2D), for example, are very similar to conch regeneration structures described in Silurian tentaculitids by Larsson (1979b: fig. 18).

#### ZOOLOGICAL AFFINITIES OF *CORNULITES*

Given that the available data relate only to skeletal morphology, problematical fossils like *Cornulites* are difficult to assign zoologically. However, such organ-

isms must necessarily be more closely related to some living taxa than to others (Budd & Jensen, 2000), and the exceptional preservation of cornulitid shell structures seen here provides the best basis for comparison presently available.

The size, skeletal structure and growth of *Cornulites* preclude Fisher's (1962) suggestion of a relationship to fusulinid foraminiferans and indicate strongly that cornulitids were metazoans. Five major grades of organization are recognized within the Metazoa: Porifera, Cnidaria, Lophotrochozoa, Ecdysozoa and Deuterostomia (see Peterson & Eernisse, 2001; Halanych, 2004). The lack of skeletal porosity rules out cornulitids being poriferans, whilst their morphology and ontogeny also excludes any affinity with ecdysozoans and deuterostomes. Of the lophotrochozoan clades with which cornulitids have been compared previously, there are no molluscs, living or



fossil, with a shell structure or development like that of *Cornulites*.

The commonest interpretation of the biological affinities of cornulitids has been that they were tubicolous annelids, probably most closely related to the Serpulidae (see, for example, Murchison, 1859; Nicholson, 1872a, b, 1873; Baily, 1875; Vine, 1882; Reed, 1923). Serpulids (Order Sabellida) are the only group that normally construct tubes of calcium carbonate (ten Hove & van den Hurk, 1993). Most serpulid tubes are composed of a thin, hyaline inner layer and a thicker outer layer formed of 'anteriorly directed chevron-like lamellae' (ten Hove & van den Hurk, 1993: 27), although some forms have three-layered tubes. The lamellae are formed of agglutinated calcite grains separated by thinner, micritic lamellae (Fischer, Galli & Reitner, 1989) or of micrite and peloids with 'intercalated lenses of fibrous calcite/aragonite' (Fischer, Pernet & Reitner, 2000: 35). In addition, the internal partitions of serpulid tubes apparently form randomly, rather than being structures formed at distinct growth stages (Fischer *et al.*, 1989). These and serpulid lamellae are thus profoundly unlike the tabulae and lamellae of cornulitids, and the combination of tabulae, lamellae, apertural grooves, cellulae and pseudopuncta gives the cornulitid skeleton a complexity far beyond that of serpulid tubes (for further discussion see Vinn & Mutvei, 2005; Vinn, 2005): there are thus no grounds for interpreting *Cornulites* as a member of the Annelida.

Recent studies (Dzik, 1991, 1993; Vinn & Mutvei, 2005; Vinn, 2005) have suggested that cornulitids were probably lophophorates, related most closely either to bryozoans (Dzik, 1991, 1993) or phoronids (Vinn, 2005). However, phylogenetic analyses (e.g. Peterson & Eernisse, 2001; Halanych, 2004) have cast doubt on the monophyly of the lophophorates (see also Nielsen, 2002), suggesting instead that brachiopods and phoronids form a clade, with bryozoans the sister-group of all other lophotrochozoans. Until this has been resolved, the skeletal features of *Cornulites* should be compared with individual taxa rather than 'lophophorates' as a group. Secondly, the structure and development of the cornulitid shell can be analogized closely with that of some zoantharians (Cnidaria: Anthozoa), particularly rugose corals. Thus, *Cornulites* is compared separately with phoronids, bryozoans and cnidarians.

#### *CORNULITES* – SHELLED PHORONID, SOLITARY BRYOZOAN OR ASEPTATE CNIDARIAN?

Vinn (2005) hypothesized that phoronids were perhaps the closest living relatives of *Cornulites* and the tentaculitids, but the supporting evidence is slight. Morphologically, phoronids have a bulbous apex from

which a thin, straight tube arises, quite unlike the gradually expanding morphology of *Cornulites*. More significantly, the phoronid tube is unmineralized, being formed of polymeric mucopolysaccharides (Emig, 1982; Cohen, 2000) arranged as a central basophilic layer and two peripheral acidophilic layers. The central layer is formed of 'numerous very thin parallel coats' (Emig, 1982: 39) but the hypothesis that this 'microlamellar structure... secreted by the entire body surface' (Vinn, 2005: 210) is homologous with the lamellar calcite skeleton of *Cornulites* is unconvincing. Phoronid tubes have neither the growth pattern nor the complexity of the cornulitid skeleton and, while brachiopods are accepted by most researchers as their sister-group and can have lamellar, pseudopunctate shells, using these features to create a composite suite of lophophorate shell characters and reconstruct cornulitids as 'skeletal phoronids' is entirely speculative. The only two groups with which *Cornulites* can be compared directly are bryozoans and cnidarians.

Dzik (1991, 1993) first raised the possibility that cornulitids were 'close to the extinct ancestors of the Bryozoa' (Dzik, 1991: 128), having noted similarities between the putative Ordovician cornulitid *Cornulitozoon* and corynotrypid bryozoans. The characters upon which the hypothesis was based were that *Cornulitozoon* was of similar size and shape to corynotrypids, had the same non-porous wall structure and 'funnel-like apertural collars' (Dzik, 1991: 122), and an apical morphology virtually identical to that of the bryozoan ancestrula. He argued also that Siluro-Ordovician members of the two groups showed a closely similar original shell microstructure (Dzik, 1991) and speculated that cornulitids diverged from bryozoans after the acquisition of a tubular, mineralized skeleton but prior to the development of small zooid size and a colonial life habit. This was supported broadly by Vinn & Mutvei (2005: 733–735), who noted that some bryozoans have a 'vesicular wall structure... and an egg-shaped embryonic shell' similar to *Cornulites*.

Although the initial chamber of *Cornulites* certainly resembles that of bryozoans, its morphology is similar also to that seen in some corals (e.g. Stolarski, 2000: fig. 2D) and molluscs (Vinn & Mutvei, 2005). Hence, the shape is more likely to reflect functional constraints than being indicative of a close phylogenetic relationship. Similarly, there are groups other than bryozoans that have lamellar low-magnesian calcite skeletons, including rugose corals (Sandberg, 1975). Of the skeletal characters listed by Vinn (2005) as present in both cornulitids and bryozoans, pseudopuncta are the only feature for which a close analogue is lacking in zoantharians.

Tavener-Smith & Williams (1972) argued that the distribution of bryozoan pseudopuncta, which are developed most strongly in trepostomes, cystoporates

and cryptostomes, indicated they are 'restricted to [bryozoan] skeletons of coelocystic origin' (Tavener-Smith & Williams, 1972: 156). From this it was deduced that pseudopuncta functioned as muscle bases that 'improved the attachment of a highly folded, hypostegal epithelium to the skeletal surface' (Tavener-Smith & Williams, 1972: 156). Nothing is known of cornulitid soft tissues, but it is likely that their pseudopuncta served a similar function. Although no analogous microstructures have been described in corals, Wise (1970) and Muscatine, Tambutte & Allemand (1997) noted small pits and spines on the inner surface of some scleractinian skeletons, interpreted as the skeletal surface impressions of desmocytes that attached the soft tissues to the coral skeleton. The means by which the soft parts were attached to the lamellar calcite skeleton of Palaeozoic corals requires further investigation.

In terms of overall skeletal structure, cornulitid cellular and tabulae are comparable with both the dissepiments and tabulae of corals and the cystiphragms and diaphragms of bryozoans. Their method of formation is comparable also, based on the studies of bryozoans by Tavener-Smith & Williams (1972) and of zoantharians by Wells (1969). There are no structures in cornulitids analogous to zoantharian septa, but this does not negate the possibility of a cnidarian affinity. Stolarski (2000) showed that the scleractinian species *Guynia annulata* was initially aseptate, whilst Fedorowski (1991: 417) argued it was 'very probable' rugose corals also lacked septa early in ontogeny. Additionally, septa are extremely weakly developed in early taxa such as *Tabulaconus* (see Debrenne, Gangloff & Lafuste, 1987).

Cornulitids were solitary organisms. Solitary taxa are known in many cnidarian groups, fossil and extant (Scrutton, 1997), but not within the Bryozoa. While accepting that the ancestral bryozoan was probably solitary (Dzik, 1991), it is more parsimonious to compare *Cornulites* with cnidarians. Furthermore, cornulitid shell symmetry is clearly radial, suggesting also a closer affinity to cnidarians. The pseudopuncta of *Cornulites* do resemble those of bryozoans, but we interpret this character as having been acquired convergently.

#### ACKNOWLEDGEMENTS

Olev Vinn, Euan Clarkson and Ivan Sansom are thanked for useful discussions and advice, and two anonymous reviewers for their constructively critical comments on an earlier version of this manuscript. Paul Hands (Earth Sciences, University of Birmingham) is thanked for his preparation of thin sections and Jon Clatworthy (Lapworth Museum of Geology) and Paul Jeffery (Natural History Museum, London)

for their assistance in locating cornulitid specimens. Photographs of specimens BMNH A230, A450, A455, A459-60, A470, A483a-b, A845-7 and Aunreg1 were taken by Mr Phil Hurst and are provided courtesy of the Natural History Museum. L.G.H. acknowledges a School of Earth Sciences, University of Birmingham, Research Studentship.

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