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(Chapters 7 and 8, References and Appendix)

**RARE AND PROBLEMATIC TAXA FROM THE
MUCH WENLOCK LIMESTONE FORMATION**

by

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CHAPTER SEVEN

SHELL STRUCTURE, GROWTH AND BIOLOGICAL AFFINITIES OF THE PROBLEMATICAL GENUS *CORNULITES*

ABSTRACT. The genus *Cornulites*, type species *C. serpularius* Schlotheim, 1820, from the Much Wenlock Limestone Formation (Silurian) of England, comprises species with 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, so 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. scalariformis* Vine, 1882, and *C. cellulusus* sp. nov., from the Much Wenlock Limestone Formation, the shell structure of *Cornulites* is shown to be lamellar, but with prominent internal chambers at the apical end of the shell and, particularly in *C. cellulusus*, 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. cellulusus* probably a constructional feature relating to an upright life position. By comparison with shell structures seen in other taxa, it is shown that *Cornulites* shares the most characters with cnidarians, and the genus is interpreted as a stem-group anthozoan, possibly most closely related to rugose corals. The diversity of cornulitids in the Much Wenlock Limestone Formation is also reassessed, with four species recognized: *C. cellulusus*, *C. gremialis* sp. nov., *C. scalariformis* and *C. serpularius*.

TECHNIQUES for analysing molecular and genetic data (e.g. 18S rDNA) 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 of clades within the Metazoa, 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 e.g. Peterson and Eernisse 2001). However, even as a more stable classification of extant taxa is approached, the systematic position of many extinct metazoan groups remains poorly understood. Since 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.

Genetic material is not preserved in such ancient specimens, however, so exceptional preservation of soft parts or skeletal structure is required to enable accurate comparison with

living groups. Thus, the high quality preservation of shell structures seen in fossils from the Much Wenlock Limestone Formation (Silurian) of Britain has the potential to yield much information on the zoological affinities of problematical taxa. An excellent example of this is the genus *Cornulites*, the type species of which – *C. serpularius* Schlotheim, 1820 – is from the Much Wenlock Limestone Formation. 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 the affinities of *Cornulites* have never been reliably determined. In this study, the diversity of cornulitids in the Much Wenlock Limestone Formation has been reassessed, with four species of *Cornulites* recognized: *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 palaeoecology of cornulitids from the Much Wenlock Limestone Formation is also examined.

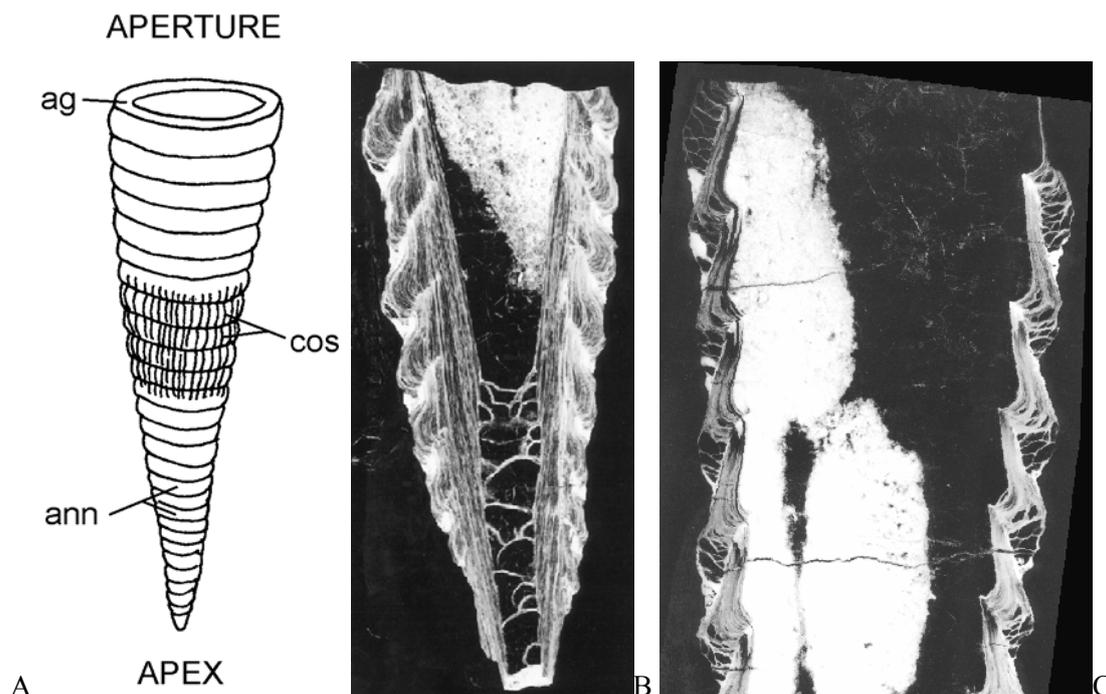
7.1 MATERIALS AND METHODS

The specimens studied are in the Lapworth Museum, University of Birmingham (prefix BU) and the Natural History Museum, London (NHM). The shell structure of *Cornulites* described in section 7.5 was based on existing thin sections of *C. cellulosus* – specimens NHM A455, A459 and A460, sectioned by Bather (1923), and BU 4386, 4388–4391 – and *C. scalariformis* (BU 4387). Additionally, two specimens of *C. cellulosus* (BU 4371 and 4378) were sectioned longitudinally, with one half of BU 4371 also cut into a series of transverse sections. The apertural end of the holotype of *C. cellulosus* (BU 4372) was polished, etched and stained, and studied as an acetate peel.

Thin sections were examined petrographically using a Zeiss Axioskop microscope, and the longitudinal and one transverse section of BU 4371 were etched for three hours using a saturated solution of EDTA in deionized water prior to examination under a Philips XL30 FEG environmental scanning electron microscope (ESEM).

7.2 TERMINOLOGY

No standardized system of cornulitid morphological terms has been defined previously. The following terms are used here:



TEXT-FIG. 7.1. Morphology of *Cornulites*. A, external morphology, showing apertural groove (ag), annulations (ann) and costae (cos). B, C, internal morphology in longitudinal section view. B, BU 4390, *C. cellulosus*, apical and mid-region, showing lamellar shell wall, with internal tabulae and camerae in apical region, x 6; C, BU 4388, *C. cellulosus*, apertural region, showing undulating lamellae and cellulae of shell wall, x 3.

External morphology (Text-fig. 7.1A) – *apex*, narrow, pointed end of shell; *aperture*, wide, round, open end of shell; *annulations*, transverse rings around body, parallel or sub-parallel to aperture; *costa*, longitudinal ornamentation, perpendicular to annulations.

Internal morphology (Text-figs 7.1B, c) – *lamellae*, continuous layers of calcite running round shell interior, parallel or sub-parallel 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-based groove around aperture, formed by undulation of lamellae, normally lenticular in plan view.

Additionally, in 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. 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 (see Text-figs 7.1B, c). These subdivisions are used for convenience of description and are not intended to indicate significant ontogenetic stages.

7.3 SYSTEMATIC PALAEOLOGY

CORNULITIDAE Fisher, 1962

Remarks. Fisher (1962) erected the Cornulitidae as a family containing four genera – *Cornulites*, *Conchicolites*, *Cornulitella*, and *Kolihaia*. Only Silurian species of *Cornulites* are described in this study, and a revision of the whole group is not attempted, but previously published descriptions and illustrations of other taxa suggest that cornulitids have been excessively subdivided at generic level. For example, *Cornulitella* (a name proposed by Howell (1952) to replace *Ortonia* Nicholson, 1872*b*, which Howell showed to be preoccupied) was originally described by Nicholson (1872*b*) 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, 1872*b*) – is compared with Schlotheim's illustration of *C. 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 seems to be an unreliable character upon which to found a new genus.

The grounds for the recognition of *Conchicolites* as a genus are similarly dubious. The genus was erected by Nicholson (1872*a*) to include taxa that were also 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, although Nicholson (1872*b*) separated *Conchicolites* from *Cornulitella* solely on ecological grounds, the latter being more completely attached to its substrate and never occurring in such large clusters.

The relationship of *Cornulitella* and *Conchicolites* to *Cornulites* is difficult to determine with certainty, but the available evidence suggests there are few convincing grounds for retaining the three taxa as separate genera. Hall (1888) regarded *Cornulitella* and *Conchicolites* as synonyms of *Cornulites*, and his approach is followed here. The fourth genus included in the Cornulitidae by Fisher (1962) – *Kolihaia* – was diagnosed as a tubular shell with 'radical [proximal] expansions that may bifurcate' (Fisher 1962, p. W138),

indicating a taxon quite unlike *Cornulites*; *Kolihaia* is now regarded as an epiplanktic anthozoan (Kříž *et al.* 2001).

In his brief account of Cornulitidae from the Silurian of Gotland, Larsson (1979b) identified four new genera, but did not describe, illustrate or propose names for any of the taxa. Thus, although *Cornulites* is the only cornulitid genus recognized here, other genera probably exist, and the diversity of the group throughout the Palaeozoic requires further assessment.

Genus CORNULITES Schlotheim, 1820

Type species. *Cornulites serpularius* Schlotheim, 1820. By monotypy.

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; 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 suitable material of *C. serpularius* for sectioning has not been found. If cellulae are absent from the type species, other taxa may be better placed in a separate genus.

Cornulites serpularius Schlotheim, 1820

Text-figs 7.2A, B

- * 1820 *Cornulites serpularius* Schlotheim, p. 378, pl. 29, fig. 7.
- ? 1859 *Cornulites serpularius* Schloth.; Murchison, p. 221, pl. 16, fig. 3 [only specimens illustrated by Murchison that resemble Schlotheim's syntypes].
- ? 1873 *Cornulites serpularius* Schloth.; Salter, pp. 85, 93, 128, 177.
- ? 1875 *Cornulites serpularius* Schlotheim; Baily, p. xlii.
- ? 1882 *Cornulites serpularius* Schlot.; Vine, p. 377.

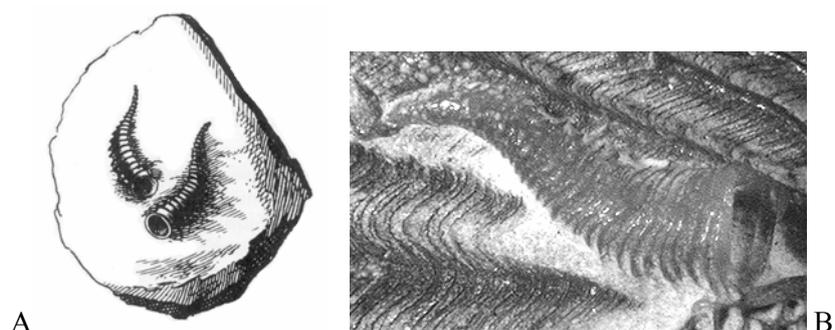
- 1888 *Cornulites serpularius* Schlotheim; Hall, p. 8.
- ? 1923 *Cornulites serpularius* Schlotheim; Reed, p. 269.
- 1962 *Cornulites serpularius* Schlotheim; Fisher, fig. 80 [reproduction of Schlotheim's original illustration].
- ? 1972 *Cornulites serpularius* Schlotheim; Blind, p. 5.
- 1979b *Cornulites serpularius* Schlotheim; Larsson, p. 208 [noted dissimilarity between Schlotheim's illustration of syntypes and material assigned to species by subsequent authors].

Material. The type specimens figured by Schlotheim (1820) cannot be located (Larsson 1979b; D. Korn, pers. comm. 2003). 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 NHM 58209, B8926 and B34691 (all from Dudley), B23134 (Aldridge, Staffs.), B34653 (Tickwood), and B3921 and B10115 (localities unknown), all of Wenlock age, are also referred to *C. serpularius*.

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

Description. Specimens of type species 6–7 mm long, with 20–25 annulations per shell. Annulations regular in shape, running parallel to circular shell 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 (1979b) 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: in fact, there are 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. Stubblefield (1938) noted that some illustrations in 19th century publications were restorative or interpretative, and lacked fine detail of imperfections in either the specimen or its matrix. Schlotheim's figure of *C. serpularius* shows the two syntypes to be unattached and resting free on an apparently homogenous substrate, whereas all small cornulitids from the Much Wenlock Limestone



TEXT-FIG. 7.2. *Cornulites serpularius* Schlotheim, 1820. A, reproduction of original figure of syntypes (Schlotheim 1820, pl. 29, fig. 7), x 3; B, Specimen attached to brachiopod BU 4376, Much Wenlock Limestone Formation, Dudley, x 10.

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.

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 in *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, which is 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. The possibility that the four species are ecophenotypes is discussed below.

Cornulites cellulosus sp. nov.

Text-figs 7.1B, C, 7.3A-H

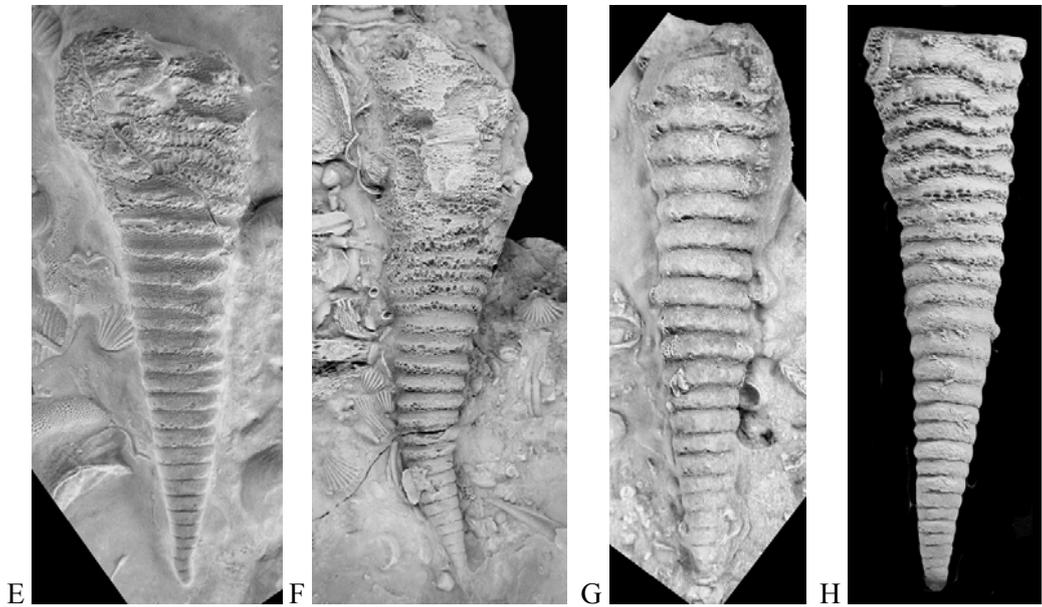
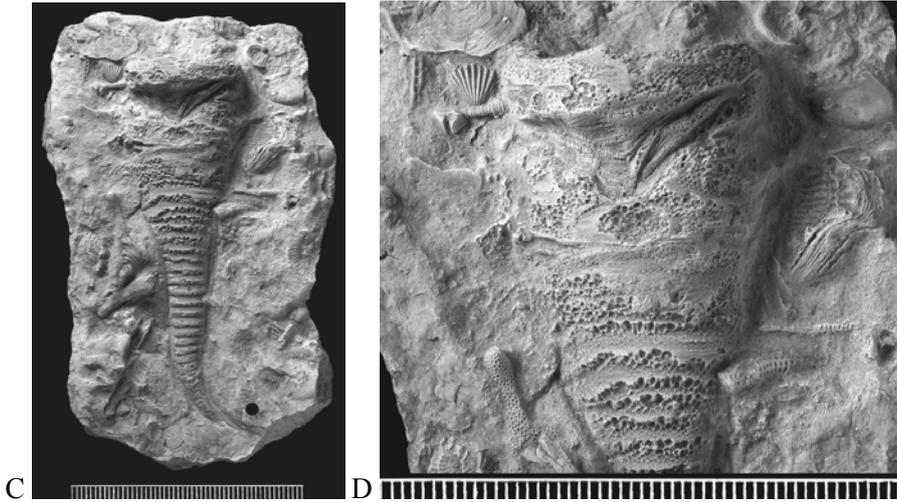
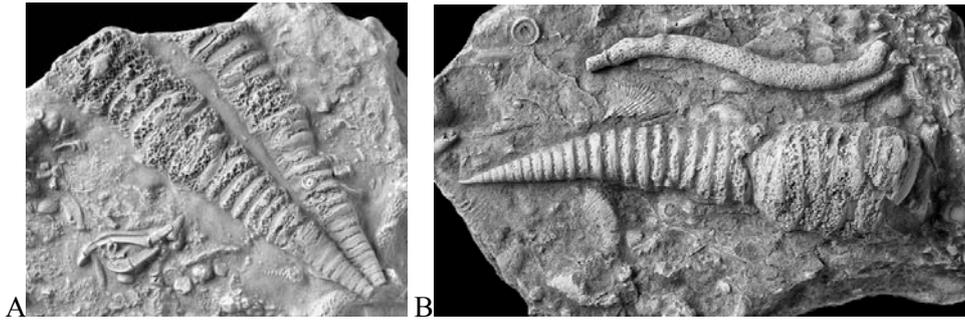
- 1859 *Cornulites serpularius* Schloth.; Murchison, p. 221, pl. 16, figs 3a, 4, 6–10 [various specimens described as from the Wenlock Limestone of Ledbury].
- ? 1859 *Cornulites serpularius* Schloth.; Murchison, pl. 10, fig. 2 [same figure of same two specimens in pl. 16, fig. 4, but described as from the Upper Llandovery].

- 1872a *Cornulites serpularius* Schlot.; Nicholson, p. 202, fig. 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, fig. 2a,b [kop. 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. 116A, 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, fig. 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.
- ? 1979b *Cornulitidae* gen. *b*, sp. *a*; Larsson, p. 210 [no illustrations, but described as conspecific with large, cellular forms previously placed in *C. serpularius*].

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

Holotype. BU 4372, from the Much Wenlock Limestone Formation 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; NHM 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 same locality as holotype.



TEXT-FIG. 7.3. *Cornulites cellulosus* sp. nov., Much Wenlock Limestone Formation, Dudley. A, two paratypes on slab NHM A230, x 0.75; B, paratype NHM A846, x 1; C, paratype NHM A845; D, close-up of apertural region of NHM A845, showing irregular pattern of annulations; scale bar increments in mm; E, paratype BU 4369, x1; F, paratype BU 4370, x1; G, paratype BU 4371, x2; H, holotype BU 4372, x1.2.

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 poorly preserved and incomplete with the apical region missing, indicating that it had a total length considerably greater than 80 mm. The holotype BU 4372 (Text-fig. 7.3H) is approximately 62 mm long and free of matrix, enabling the complete shell morphology to be seen. 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 to elliptical in shape, and the aperture is oval, with a minimum diameter of 11 mm and a maximum diameter 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 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 determine and numerous cellulae present on the external surface (see Text-fig. 7.3E). A similar pattern is seen in paratype BU 4370, with the first 20 or so annulations obvious, but those towards the aperture much harder to distinguish (Text-fig. 7.3F).

Not all specimens have continuously straight-sided shells: BU 4370 is straight-sided for the first 11 annulations (~15 mm) before abruptly changing growth direction (see Text-fig. 7.3F). The shell is then straight-sided again for the rest of its length. Paratype NHM A846 (Text-fig. 7.3B) is very similar, showing a distinct change in growth direction after the twelfth annulation, and with the annulations becoming difficult to identify in the apertural region. Paratype NHM A845 (Text-fig. 7.3C), in contrast, has a distinctly curved apical shell region before becoming straight-sided in the mid-region and towards the aperture, but, close to the aperture, it becomes expanded and extremely irregular (see Text-fig. 7.3D).

The apertural shell region is well-preserved in paratype BU 4371 (Text-fig. 7.3G) 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 revealed by examination of shell wall structure in longitudinal thin section, and is discussed in section 7.5. Detailed descriptions of the shell structure of *C. cellulusus* are also given in section 7.5.

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

Cornulites gremialis sp. nov.

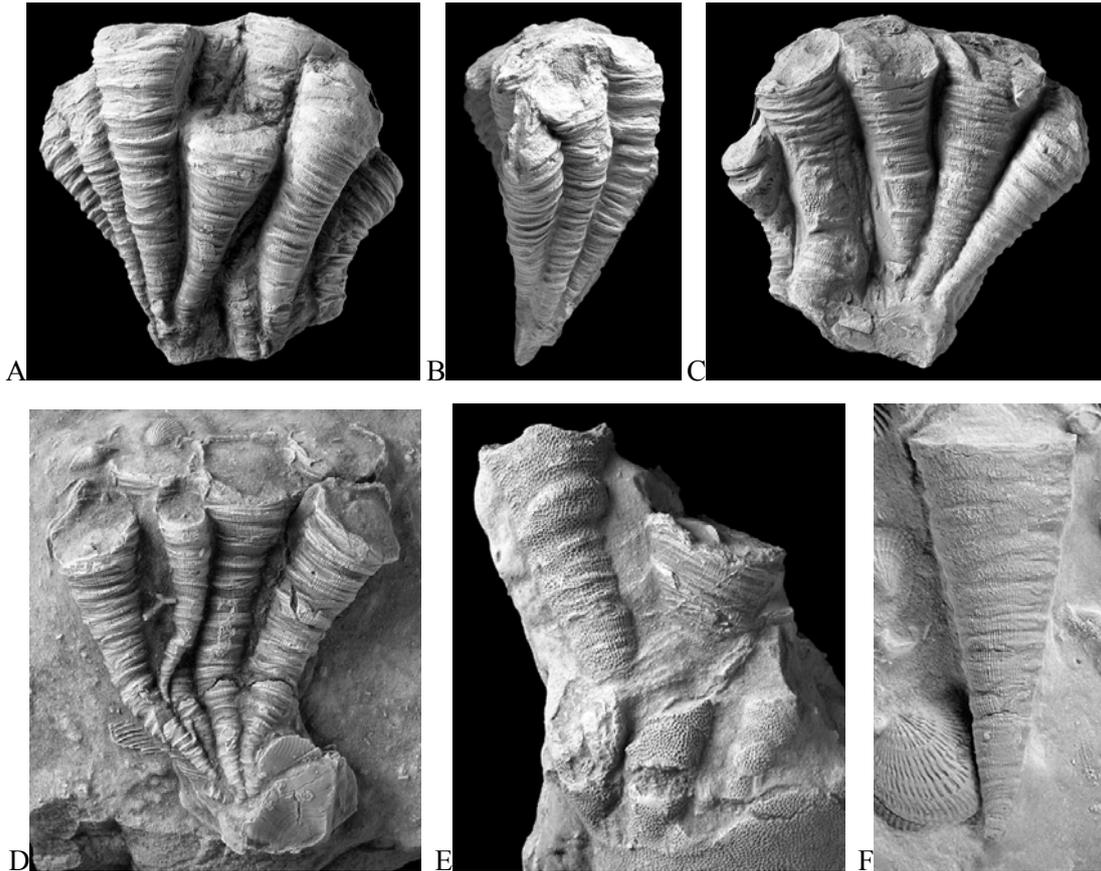
Text-figs 7.4A-F

Derivation of name. From the 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 NHM A470, attached to indeterminate shell fragment, from the Much Wenlock Limestone Formation of Dudley, England.

Paratypes. Ten other specimens in cluster NHM A470, NHM 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 same locality as 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.



TEXT-FIG. 7.4. *Cornulites gremialis* sp. nov., Much Wenlock Limestone Formation, Dudley. A-C, cluster NHM A470; A, view of top surface of cluster, showing holotype (largest specimen, third from left) and five paratypes; B, left lateral view of cluster, with holotype to right; C, bottom surface of cluster, showing five paratypes, all x 1.25; D, cluster NHM A483a, x 1.5; E, NHM A483b, showing two paratypes attached to cephalopod, x 2; F, BU 4368, possible specimen of *C. gremialis*, x 1.75.

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

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

The holotype is the largest specimen on cluster NHM A470 (see Text-fig. 7.4). 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 5 costae per millimetre.

Remarks. BU 4368 (Text-fig. 7.4F) is a solitary, unattached cornulitid approximately 33 mm in length, with a circular aperture of ~13 mm diameter. In some aspects, particularly the arrangement of annulations and costae over much of the shell surface, it resembles specimens of *Cornulites gremialis*. However, at the apex, the annulations are thicker, and there is a suggestion that cellulae are present, making it much more like *C. cellulosus*. 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.

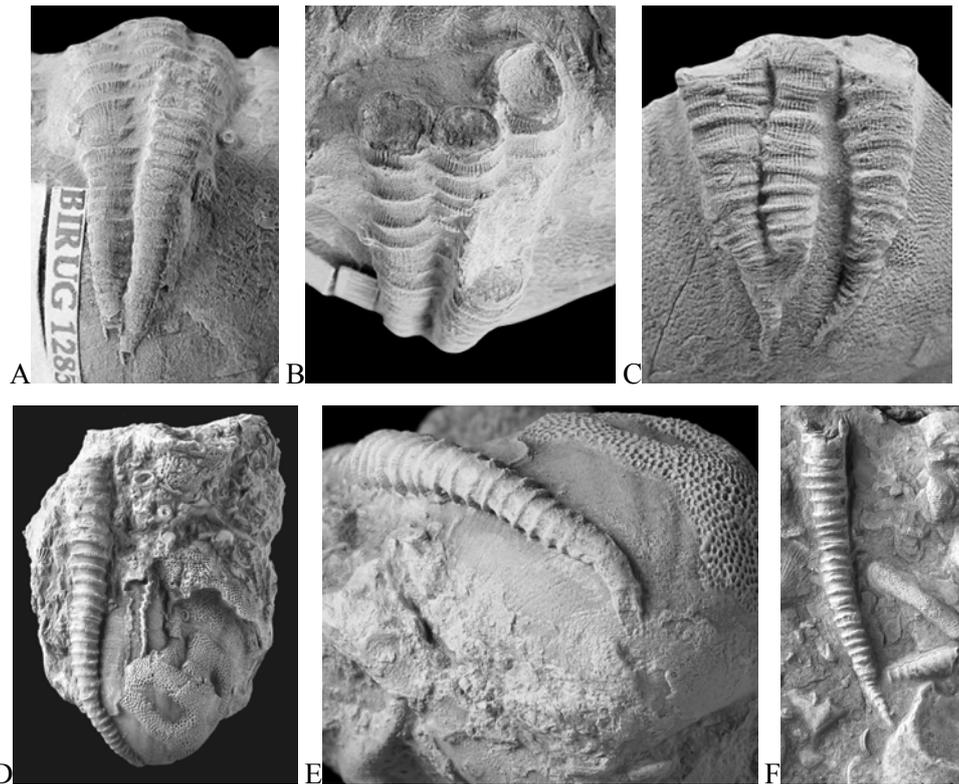
The overall shell shape, and closely spaced, irregular annulations that normally alternate between prominent and less prominent make *C. gremialis* easy to distinguish from *C. scalariformis*. The conical shell morphology of *C. gremialis* is similar to that of *C. cellulosus*, but the two taxa can be separated by the differences in annulation and costae 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* do not support the two taxa being interpreted as conspecific.

Cornulites scalariformis Vine, 1882

Text-figs 7.5A-F

- ? 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.
- 1979b *Cornulites? scalariformis* Vine; Larsson, p. 208.
- ? 1979b *Cornulites? cf. scalariformis* Vine; Larsson, p. 208 [no illustrations].

Material. As with *Cornulites serpularius*, the type specimens of *C. scalariformis* have not been traced. However, Vine’s illustrations (1882, pl. 15, figs 1, 9, 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), NHM A847, and NHM Aunreg1 [unregistered specimen], all from the Much Wenlock Limestone Formation of Dudley, are placed in *C. scalariformis*.



TEXT-FIG. 7.5. *Cornulites scalariformis* Vine, 1882, Much Wenlock Limestone Formation, Dudley. A, B, four specimens attached to brachiopod BU 4373; A, x 2.5, B, x 3; C, three specimens attached to brachiopod BU 4374, x 3; D, E, specimen NHM A847, D, x 0.5, E, x 0.75; F, specimen NHM Aunreg1, x 0.5.

Diagnosis. *Cornulites* with widely spaced, narrow annulations separated by concave areas containing thin, prominent costae. Width of aperture increases slowly, particularly in later growth stages, giving shell morphology of very gradually tapering cone. 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 NHM A847 (Text-figs 7.5D, E) and NHM Aunreg1 (Text-fig. 7.5F), with an aperture diameter of up to 5 mm. Annulations of NHM A847 approximately 0.5 mm thick, separated by 1 mm bands in which costae are present; costae have density of 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 ~3 mm at apical end and ~4 mm at apertural end, and shows eight annulations. The shell microstructure of *C. scalariformis* seen in thin section BU 4387 is described in section 7.5.

Remarks. *Cornulites scalariformis* is easily distinguishable from *C. serpularius*, and *C. cellulosus* by having a very narrow, conical shell even when large, and well-spaced, prominent annulations separated by areas containing pronounced costae. Some smaller specimens, such as those attached to brachiopod BU 4374 (Text-fig. 7.5c) 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*.

7.4 CORNULITID PALAEOECOLOGY

Richards (1974) recognized four types of cornulitid palaeoecology: solitary commensal taxa, gregarious commensal taxa, free-living forms and parasites. Commensal and parasitic species were always attached to the hard-parts of other organisms, with their ecological distinction being based on whether they ‘cause[d] injury to the host’ (Richards 1974, p. 519). Free-living cornulitids show no sign of ever having been attached, although Richards (1974) interpreted some taxa as transitional, the apical part of the shell being fixed to a host organism, and the apertural end growing freely away from the substrate (e.g. Richards 1974, pl. 1, fig. 7).

Of the four cornulitid species from the Much Wenlock Limestone Formation, two (*Cornulites serpularius* and *C. scalariformis*) are always found attached to other organisms, one (*C. gremialis*) normally occurs in clusters growing upon one another, with only the apical part of the shells fixed to a foreign object, and one (*C. cellulosus*) is solitary and unattached. None of the attached species show any sign of having damaged their host, so are not parasitic in the sense of Richards (1974). However, *C. scalariformis* is commonly found attached to brachiopods in a very specific orientation, growing radially from umbo to commissure, terminating close to the valve margin in most cases (Text-figs 7.5A-C) but occasionally outgrowing the host (e.g. Text-fig. 7.5D). A near-identical pattern was described in Devonian cornulitids attached to the brachiopod *Mucrospirifer* (Schumann 1967), their apertures being clustered around the lateral parts of the commissure, which were the areas closest to the inhalant current (Rudwick 1970). It is probable that the cornulitids were utilizing the current to obtain nutrients, and a similar interpretation can be applied to the specimens of *C. scalariformis*. Furthermore, if they were intercepting food particles at the expense of the host, the cornulitids could be regarded as ectoparasites, despite not injuring the host in any visible way. In contrast, many of the specimens of *C. serpularius* attached to brachiopods do not show a pattern of preferential orientation, growing across the shell obliquely or away from the

commissure, indicating that they did not rely on the host as a food source or were attached to dead organisms.

There can be little doubt that cornulitids found attached to the hard-parts of other organisms, living or dead, were suspension feeders or predators of microscopic animals. However, Richards (1974) raised the possibility that large, solitary, unattached forms were mobile, enabling them to deposit-feed as well as filter-feed. At least with regard to *C. cellulusus*, such behaviour is highly improbable. No soft-tissues are preserved, so the original presence or absence of locomotory body parts cannot be determined, but its skeletal morphology suggests that *C. cellulusus* was sessile. The shell is structurally heterogenous, being densely lamellar towards the apex, and becoming more and more cellular towards the aperture (see section 7.5.1 for details), rather than having the homogeneity and uniform thickness typical of the shells of mobile taxa. The most plausible orientation for its shell structure is that *C. cellulusus* lived in a fixed position, approximately upright, with the thicker apical part of the shell anchored in the sediment and the aperture facing upwards into the water column. As with other cornulitids, it was either a filter-feeder or a predator of small planktonic and nektonic organisms.

The possibility cannot be entirely discounted that the four species of *Cornulites* from the Much Wenlock Limestone Formation are ecophenotypes, with the variations in morphology reflecting adaptations to different ecological niches. However, the differences in ornamentation and shell shape appear to be profound, and the groups are regarded as separate, species-level taxa here.

7.5 CORNULITID SHELL STRUCTURE

The microstructure of *Cornulites* was first examined by Salter (*in* Murchison 1859, p. 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 listed as examples of *C. serpularius* but are evidently specimens of *C. cellulusus*. Further illustrations of the microstructure of *Cornulites*, based on both longitudinal and transverse sections, were provided by Hall (1888), and showed that the cellular structure comprised almost the entire shell wall, but resolved little clear pattern. Fisher (1962, fig. 78,1b-e) reproduced Hall’s 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.

Bather (1923) sectioned three specimens of *C. cellulusus* (NHM A455, A459 and A460), showing that the shell was composed of cellulae and lamellae, and that there was a

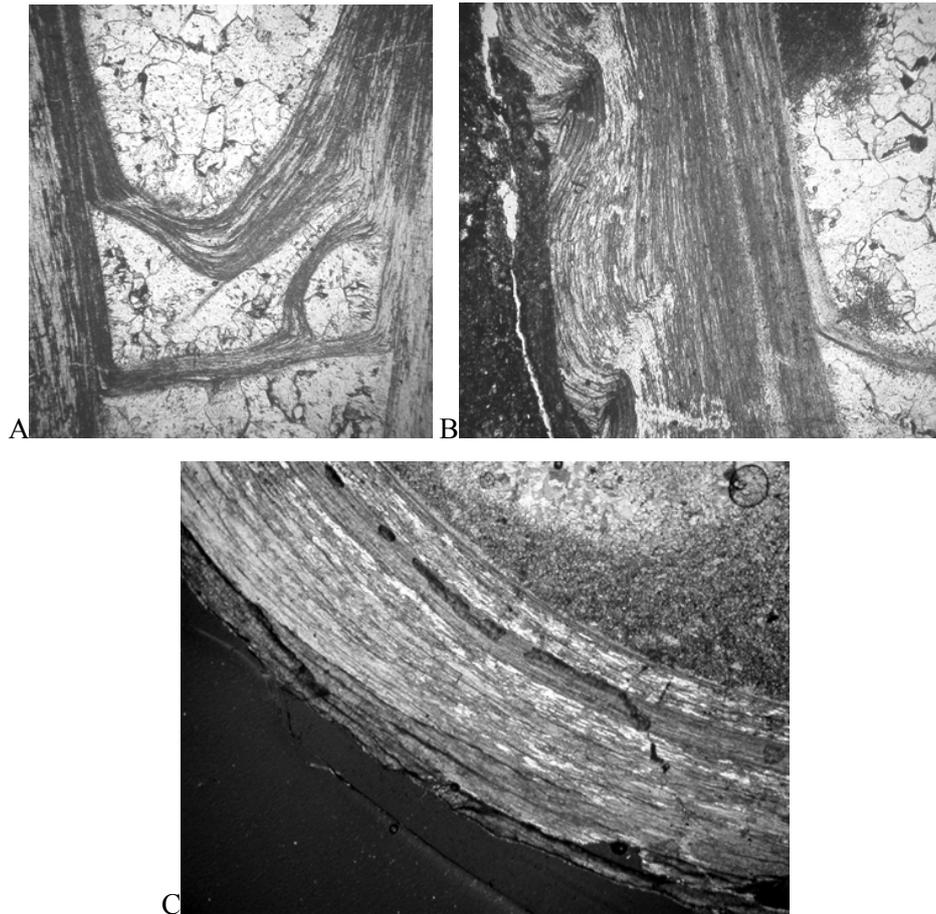
clear pattern. In transverse section, the lamellae were seen to separate the cellulae into narrow, approximately concentric bands around the aperture, whilst in longitudinal view, the lamellae were ‘essentially continuous’ (Bather 1923, p. 544) and ran in an undulating fashion along the shell interior, with the cellulae present between lamellae towards the external surface (see Bather 1923, fig. 1). Blind (1972) also described the shell of *C. serpularius* as being composed of both cellulae and lamellae, but did not include any supporting illustrations, either of specimens or sections.

In this study, the thin sections of *C. cellulusus* made by Bather (1923) have been re-examined, previously undescribed thin sections of *C. cellulusus* and *C. scalariformis* in the Lapworth Museum studied, and two further specimens of *C. cellulusus* sectioned.

7.5.1 STRUCTURE OF *CORNULITES CELLULOSUS*

The longitudinal and transverse sections of *Cornulites cellulusus* show that the shell can be divided into three parts – the apical region, mid-region, and apertural region (see section 7.2 for definitions). The very apex of the shell is not preserved in any of the specimens studied, so it cannot be determined whether the egg-shaped initial chamber described by Blind (1972) is present. The most prominent features of the apical region are the tabulae, which run across the shell interior approximately perpendicular to the surface of the shell wall. The tabulae closest to the apex lie directly upon one another (Text-fig. 7.1A), but aperturally they become separated by dome-shaped vacuities (camerae) of various sizes (Text-fig. 7.6A). The shell wall in the apical region is bipartite, with undulating lamellae towards the exterior, and straight lamellae towards the interior (Text-fig. 7.1A). Each straight lamella is connected to a tabula, and the connection occurs on both sides of the shell interior (Text-fig. 7.6A), such that in longitudinal view, the tabulae and lamellae take on the appearance of stacked, elongate cups. In transverse view, the apical region is formed of concentric zones of lamellae (Text-fig. 7.6C).

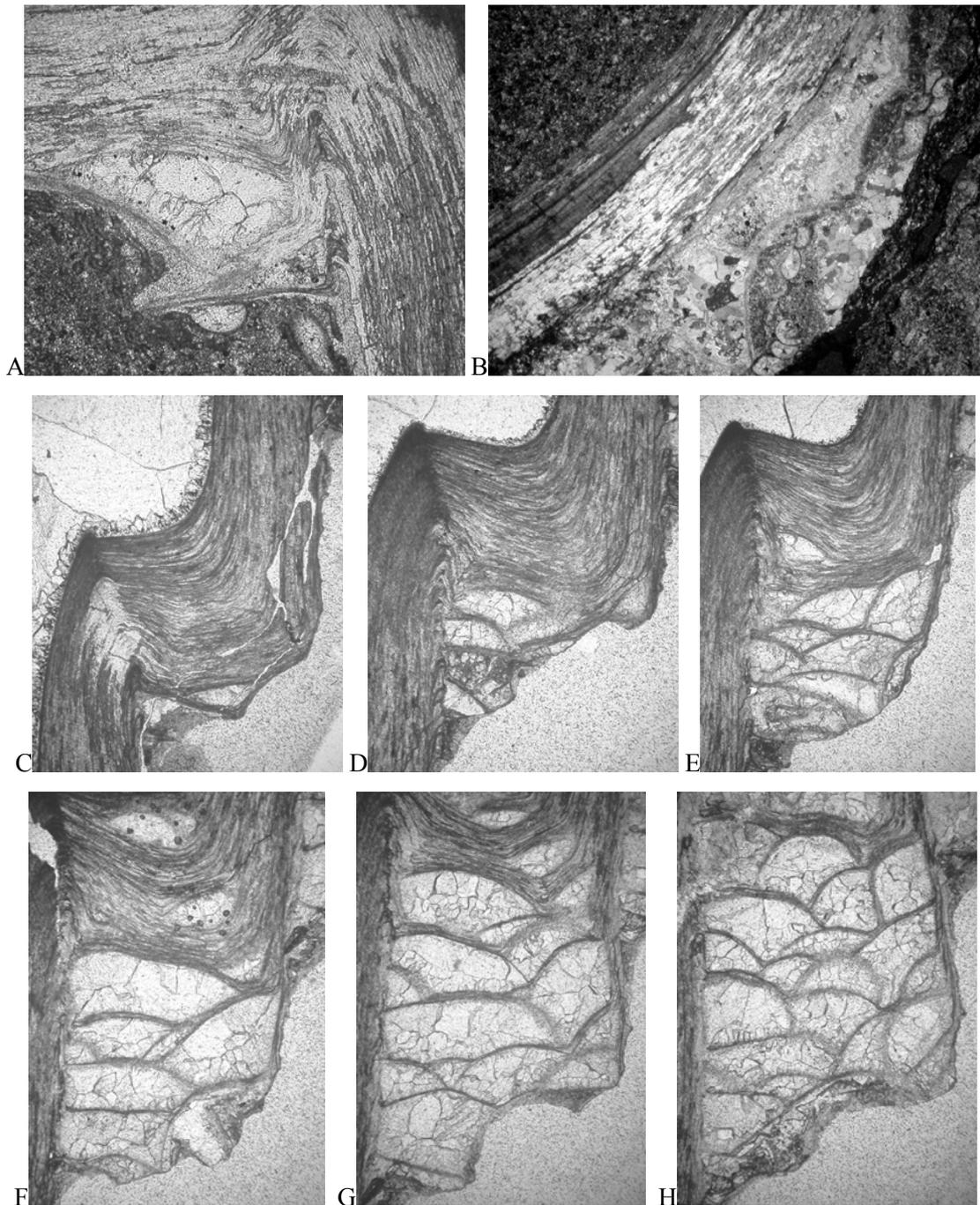
In the mid-region, beyond the most distal tabula, the interior of the shell is of simple, straight-sided shape in longitudinal section, expanding in width from apex to aperture (see e.g. Text-fig. 7.1A). At approximately the point where the tabulae stop, the shell exterior begins to become cellular, with the first cellulae (Text fig. 7.7A) 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 (Text-fig. 7.6B), but towards the aperture, the undulating lamellae become more and more prominent until, at the apertural end of the mid-region, they comprise the entire thickness of the shell wall (Text-fig. 7.1B). Cellulae are more abundant at the exterior surface of the mid-region shell wall towards the



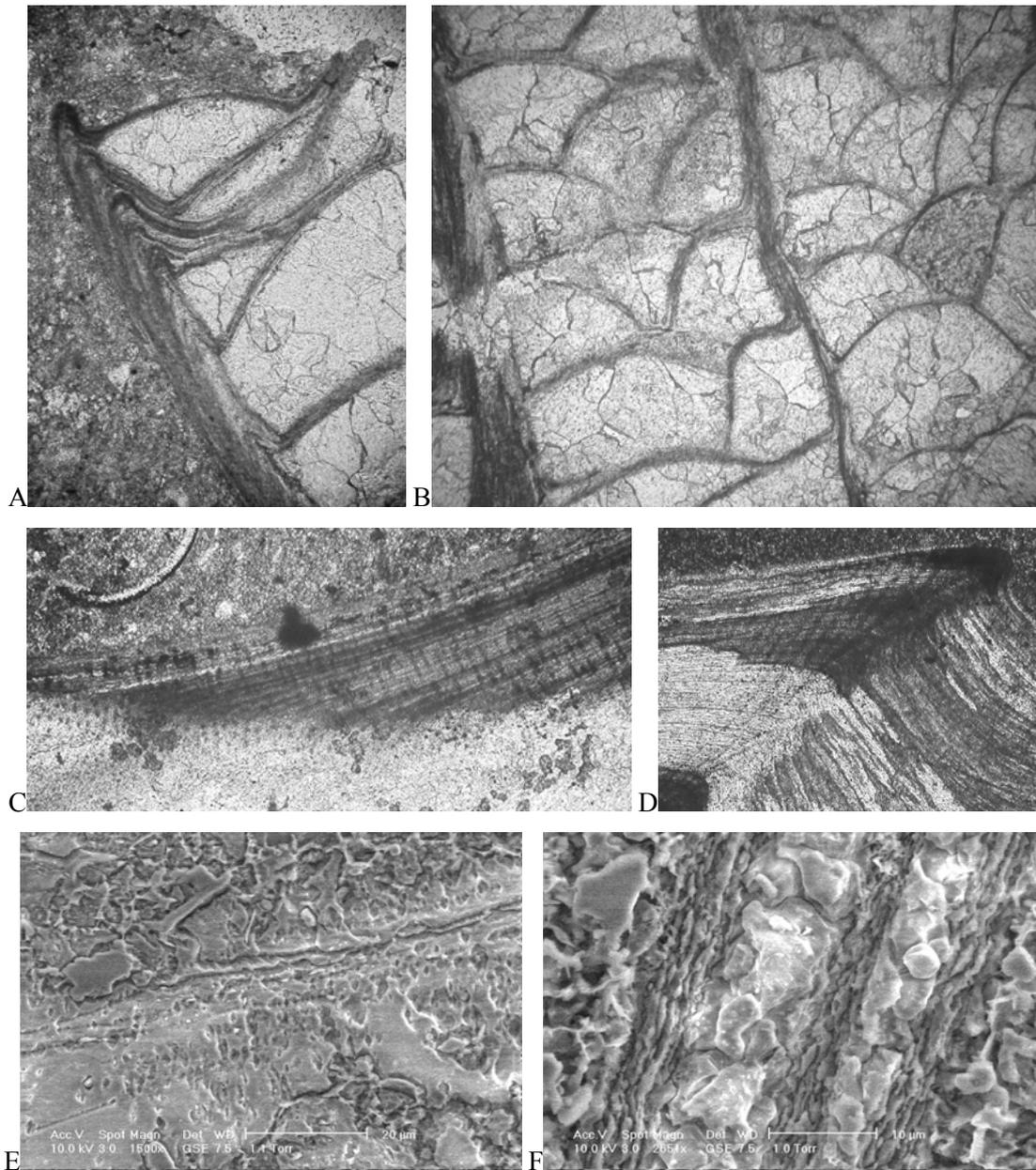
TEXT-FIG. 7.6. Shell wall structures in apical region of *Cornulites cellulosisus* sp. nov, BU 4371. A, longitudinal section showing tabulae and camerae, aperture towards top, x 30; B, longitudinal section showing undulating lamellae, straight lamellae and tabula, aperture towards top, x 30; C, transverse section showing concentric lamellae, shell interior to top right, x 30.

aperture, but are still relatively scarce (see e.g. Text-figs 7.7A, B). In transverse view, the undulating lamellae and cellulae form a somewhat irregular band around the exterior of the shell, with concentric lamellae inside (Text-fig. 7.7C).

In the apertural region, the undulating lamellae run along the interior surface of the shell, giving it an annulated appearance exactly the same as that of the shell exterior. 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, but the cellulae rapidly increase in number closer to the aperture (see Text-figs 7.7C-H). At the aperture of well-preserved specimens, they form almost the entire shell wall, with the lamellae reduced to a thin layer covering the shell interior (Text-fig. 7.8A). The longitudinal section of BU 4378 shows the change from one annulation to the next moving towards the aperture: the transition begins with an increased number of cellulae to the exterior of the undulating lamellae (Text-figs 7.7C, D),

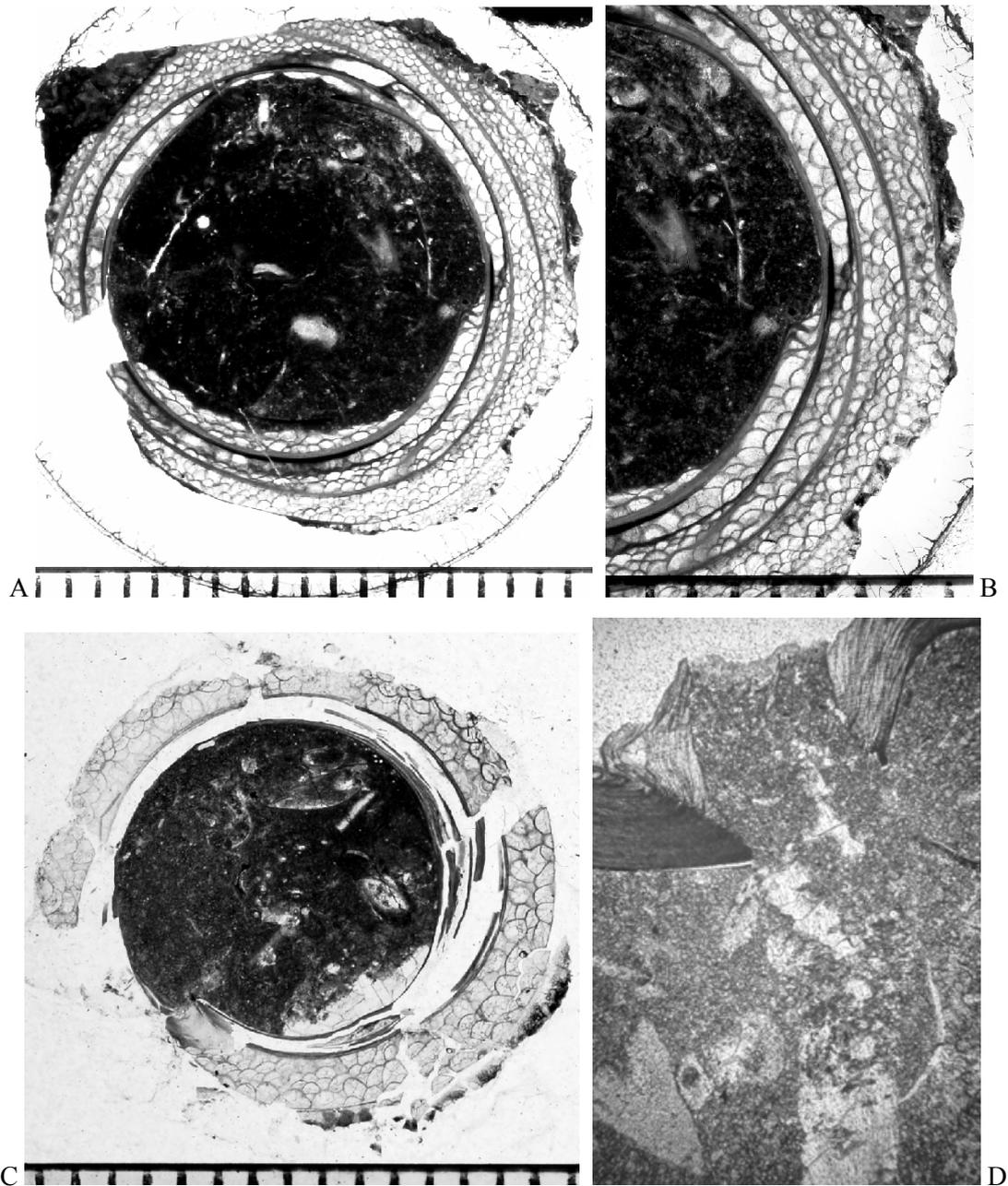


TEXT-FIG. 7.7. Development of cellulae in *Cornulites cellulosis* sp. nov. A, BU 4371, longitudinal section through annulation in mid-region of shell, showing overgrowth of apertural groove by undulating lamellae, with single cellula present; aperture towards top of image, x 30; B, BU 4371, transverse section through shell wall, showing concentric lamellae and cellulae; shell interior to top left, x 30; C-H, BU 4378, development of cellulae seen in longitudinal sections through annulations from mid- (C) to apertural (H) shell regions, x 20.

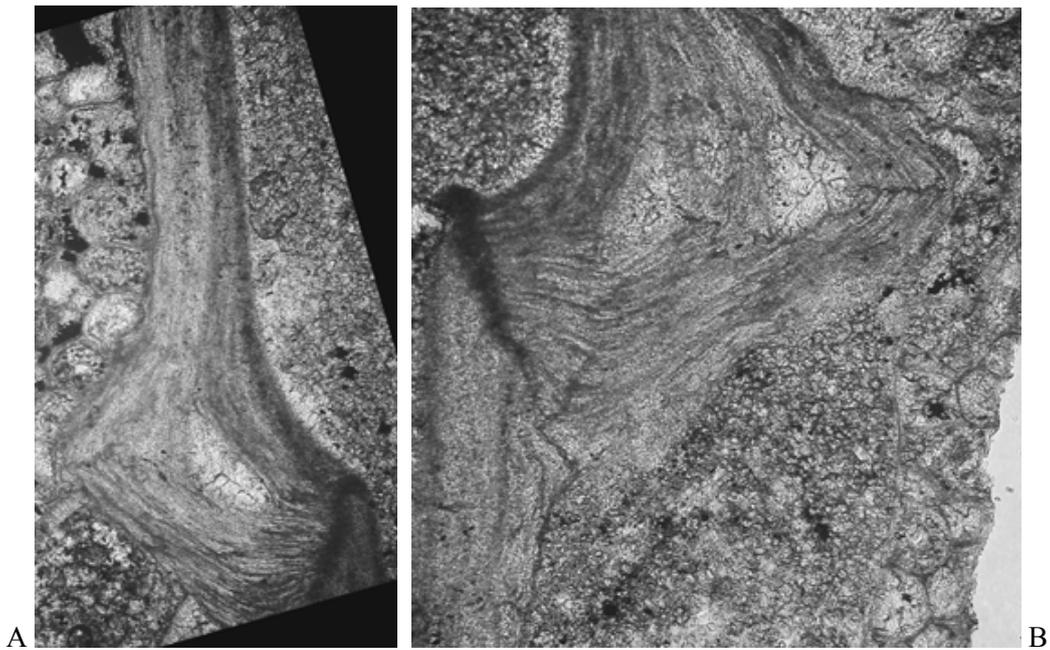


TEXT-FIG. 7.8. Shell structures of *Cornulites cellulusus* sp. nov. A, B, BU 4378, longitudinal sections through apertural region of shell, showing development of cellulae into zones; A, stacked lamellae separated by cellulae, x 40; B, zones, x 40; C-E, BU 4371, pseudopunctae; C, transverse view, x 40, D, longitudinal view, x 40; E, ESEM image of transverse section, shell interior towards top in all images; F, BU 4371, ESEM image of transverse section across mid-region shell wall, showing bipartite structure within lamellae.

then occasional additional cellulae between bands of lamellae (Text-figs 7.7E, F), and finally almost every lamella is separated by cellulae (Text-figs 7.7G, H). In transverse view, a section cut at the apical end of the apertural region is composed of a thick band of cellulae around the



TEXT-FIG. 7.9. A, NHM A459, transverse section close to aperture of *C. cellulosis*; B, close-up of concentric lamellae, separated by zones of cellulae, scale bar increments in mm; C, NHM A455, transverse section across apertural region of *Cornulites cellulosis*, showing concentric lamellae and apertural groove filled with cellulae; scale bar increments in mm; D, *Trypanites* boring, *C. cellulosis*, BU 4378, longitudinal section, aperture towards right, x 10.



TEXT-FIG. 7.10. A, B, BU 4387, *C. scalariformis*, longitudinal sections through shell wall, showing lamellar structure separated by occasional cellulae, aperture towards top in both images; A, shell interior to right, x 30; B, shell interior to left, x 40.

shell perimeter, and a thin band of lamellae around the interior (Text-fig. 7.9C), whereas sections cut closer to the aperture show numerous bands of cellulae being separated by occasional very thin bands of lamellae (Text-figs 7.9A, B). Significant here is that the cellular bands are not wholly concentric, but pinch out in both directions around the shell, giving them a lenticular shape (Text-figs 7.9A, B). The other significant feature of the cellulae in the area around the aperture is that they form ‘zones’ in longitudinal view – thin, elongate, almost rectangular areas bounded either side by thin bands of lamellae – in which the cellulae appear to be stacked (Text-fig. 7.8B).

Examined under ESEM, the transverse, mid-region section of BU 4371 shows an alternating pattern of thinly foliated lamellae and blocky crystalline lamellae (Text-fig. 7.8F). This may represent an original shell wall in which the foliated lamellae were formed of low-magnesian calcite and have original structures preserved, whereas the blocky lamellae were formed of aragonite that has subsequently been remineralized. Conversely, the shell wall may have originally been formed of alternating organic and inorganic lamellae.

7.5.2 STRUCTURE OF *CORNULITES SCALARIFORMIS*

In the original description of *Cornulites scalariformis*, Vine (1882, p. 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 broadly supported by the structures seen in the longitudinally sectioned specimen of *C. scalariformis* (BU 4387; Text-figs 7.10A, B). The specimen is incomplete, with nothing of the apical region preserved, but as with *C. cellulosus*, 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, the distribution of the cellulae is slightly different from that of *C. cellulosus*, with them normally occurring in the centre of the shell wall rather than towards the external surface (Text-figs 7.10A, B; compare with *C. cellulosus*, Text-figs 7.7D-F). Furthermore, they do not show a pronounced increase in abundance towards the aperture, remaining relatively large but few at each annulation.

7.5.3 OTHER SHELL FEATURES

7.5.3.1 Pseudopunctae

The longitudinal thin section of *Cornulites cellulosus* (BU 4371) shows that many of the lamellae, both straight and undulating, have small but distinct crenulations that align to form linear structures running perpendicularly through the shell wall (Text-fig. 7.8D). In a slightly oblique transverse section through the same specimen, the crenulations are also seen, but the linear structures change in morphology across the shell. Closest to the interior, they are straight and elongate, but towards the exterior they become elliptical and then circular (see Text-fig. 7.8C), indicating that they are long, thin tubes. To further investigate the microstructure, both the longitudinal and one transverse section of BU 4371 were etched and examined under ESEM, but the results were inconclusive. The transverse section studied has one region in which possible tubular structures are preserved (Text-fig. 7.8D), but they cannot be accepted with certainty as evidence that the shell wall was perforate.

7.5.3.2 Borings

Close examination of 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, Text-fig. 7.9D), but the even distribution of borings on both the buried and exposed external surfaces of the fossil indicates that many were formed whilst the cornulitid was alive. Had all borings occurred after death, one would expect to see a greater number on the shell interior and a more uneven distribution on the exterior (unless all different parts of the shell exterior were exposed for similar lengths of time). The proportion of *in vivo* borings suggests that the cornulitid might have retained relatively high levels of nutrients or soft tissue between the lamellae, even after they had been overgrown by later increments of shell material, although the density could also be a function of time.

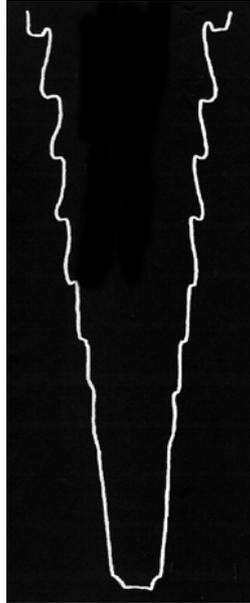
7.6 CORNULITID GROWTH

The first detailed study of cornulitid ontogeny was produced by Hall (1888). He stated that all cornulitids began as a 'simple point...[attached to] the surface of some other organism' (Hall 1888, p. 16), before forming thin, coiled tubes that straightened or retained a slight sinuosity as they grew. Finally, in most cases, cornulitids outgrew the substrate, with the shell taking on 'a constantly expanding tubular form' (Hall 1888, p. 16). In terms of shell structure, Hall (1888) described the inner and outer walls as being in contact initially, with the development of the cellular structure between the walls coinciding with the expansion of the shell as it grew away from the substrate.

The investigation of shell structures in *Cornulites cellulosis* by Bather (1923) revealed that, at least in some cornulitids, the change in shell structure during growth was more complex than described by Hall (1888). Rather than simply having inner and outer walls separated by cellulae, Bather (1923) showed that *C. cellulosis* deposited successive sets of lamellae, between which were the cellulae. The lamellae, he argued, were laid down by 'a periodical shrinkage and sloughing of the outer membrane' (Bather 1923, p. 544) and the cellulae possibly by a liquid or a gas.

Fisher (1962) based his hypothesis of cornulitid growth almost entirely on the work of Hall (1888), with a few minor modifications. He argued that cornulitids began life as free-swimming larvae, and remained mobile until the shell had begun to straighten, when the cornulitid attached itself to a substrate. Four growth stages, distinguished by changes in the morphology and ornamentation of the external shell surface, were defined: early, intermediate (juvenile), advanced (adult) and advanced (gerontic). In the early stage, cornulitids had smooth shells, then annulations in the intermediate stage, annulations and costae in the adult stage, and finally just costae in the gerontic stage. In terms of changes in shell structure, Fisher (1962) described the cellulae as rare in the early stage, but rapidly appearing in the intermediate stage and being abundant in the advanced stages.

Most recently, Blind (1972) defined a three-stage model, with cornulitids having 'an egg-shaped, orally constricted initial chamber' (Blind 1972, p. 6), then a thick-walled juvenile shell, followed by a cellular adult shell, although no supporting illustrations were included. The shell layers deposited early in life were described by Blind (1972) as very irregular, being gradually levelled out by the deposition of subsequent layers, the function of which, Blind (1972) suggested, was to reduce the volume of the living chamber.



TEXT-FIG. 7.11. Simplified longitudinal section view of *Cornulites* body morphology, based on shell structures seen in *C. cellulatus*. Narrow apical end of shell with tabula; shell wall formed of straight then undulating lamellae; apertural region with apertural groove; approximately x 1.

The very apex of the shell is not preserved in the specimens of *Cornulites cellulatus* and *C. scalariformis* studied, so the earliest growth stages are not seen. Fisher's (1962) hypothesis that cornulitids were free-swimming as larvae, then mobile until the shell straightened, is possible but very difficult to test, whilst the presence of an egg-shaped initial chamber (Blind 1972) cannot be confirmed.

Since the shell of *Cornulites* is a hollow cone or tapering cylinder with relatively thick walls, it is most parsimonious to interpret it as having been the protective external skeleton of a soft-bodied organism that had an overall growth direction of apex (small) to aperture (large). Thus, the shell structures described in section 7.5 can be interpreted chronologically. As noted above, the earliest stages of cornulitid ontogeny are unknown, but the connection of each tabula to the lamellae that form the shell wall indicates that growth was by the addition of calcite increments over the whole shell surface. Accepting that the shell was an external skeleton, the addition of each new increment must have been over the *interior* shell surface, such that the tabulae and lamellae became stacked upon each other in the growth direction, from apex to aperture (see e.g. Text-figs 7.1A, 7.6A, B). Moreover, the concentric pattern of the lamellae seen in transverse section (Text-fig. 7.6C) shows that the structure is essentially that of cones being deposited within cones. 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. There is a variation in the thickness of the tabulae, however, with some comprising numerous calcite increments

deposited directly upon one another (see Text-fig. 7.6A), so this camera-forming separation may only have occurred at specific (major?) growth stages.

Towards the aperture, away from the tabulae, the lamellae gradually developed undulations, which terminated aperturally with the development of an apertural groove (see Text-fig. 7.11). As each lamella was overgrown by subsequent lamellae, so the apertural groove was closed off. This is illustrated in Text-figs 7.7A and 7.7C. The external annulations must thus represent the changing position of the aperture as the cornulitid grew in size. The development of cellulae towards the aperture of large specimens produces a complex pattern, with the cellulae forming distinct 'zones' (Text-fig. 7.8B). It is difficult to trace the lamellae across the zones, but the sequence of cellulae development illustrated in Text-figs 7.7C-H and the relationship of lamellae to cellulae seen in Text-fig. 7.8A shows that they were stacked upon each other in exactly the same way as the lamellae. The complex appearance of these cellular areas is simply the result of the undulating lamellae not accreting directly upon one another, but leaving small spaces between each other. As the lamellae became more and more undulate, so the cellulae became more abundant and prominent, and the structural relationship between them more complex. The cellulae are spaces between lamellae and, as the lamellae were stacked from apex to aperture, making (in transverse view) the lamellae closer to the surface of the shell older than those nearer the interior, so it is likely that the cellulae are stacked in the same arrangement, with those closer to the shell exterior being older than those closer to the interior.

Although cellulae are abundant in the shell wall of all specimens of *C. cellulusus* studied, they are most numerous at the apertural end of large specimens. As *C. cellulusus* was a solitary, unattached cornulitid, growing vertically away from the substrate, it is probable that the development of cellulae represents a means of constructing a lightweight shell as the animal increased in size. If the lamellae were not separated by cellulae in the more apertural parts of the shell, they would create a pronounced thickening of the shell wall and the cornulitid would become increasingly top-heavy. Even allowing for the apical part of the shell sinking into the substrate, the organism would have been in danger of being knocked over, particularly under high-energy conditions. By contrast, cornulitids such as *C. scalariformis* that were attached to other organisms would have had the weight of their shell supported by the host, and consequently did not develop the extensively cellular wall structure.

The change in shell growth direction seen in some specimens of *C. cellulusus* (e.g. BU 4370 and NHM A846) is perhaps due to the cornulitid having been dislodged from its optimal life position at an early stage in ontogeny, and then growing in a different direction to correct this. The loss of obvious annulations, coupled with the appearance of cellulae on the external surface of the apertural region of many large specimens of *C. cellulusus* is probably

an artefact of preservation, either due to abrasion or compaction of the shell post-mortem. The cellular shell wall of the apertural region would have been more vulnerable to damage than the densely lamellar shell structure of the apical region, as indicated by the fractured, irregular apertural region of BU 4369 (Text-fig. 7.3E). However, it is possible that some of the irregularities seen in the apertural region might be the result of shell repair. NHM A845, for example, shows an apparent cross-cutting relationship of annulations close to the aperture (Text-fig. 7.3D), the morphology of which is very similar to conch regeneration structures described in Silurian tentaculitids by Larsson (1979a, fig. 18). The cellular shell wall of the apertural region of cornulitids may thus have been vulnerable to damage during life as well as after death.

7.7 BIOLOGICAL AFFINITIES

Cornulites is perhaps the most enigmatic of all problematica from the Much Wenlock Limestone Formation. When erecting the genus, Schlotheim (1820) was uncertain of its systematic position, but suggested that it possibly belonged to the Annelida, presumably by comparison with the mineralised tubes of serpulids. This was developed by Murchison (1859), who diagnosed *Cornulites* as a tubicolous annelid on the basis of its segmentation and shell structure. Many authors (e.g. Nicholson 1872a, 1872b, 1873; Baily 1875; Vine 1882; Reed 1923) followed this interpretation, although Nicholson (1872a, p. 202) described the structure of *Cornulites* as ‘wholly unlike’ that of serpulids, and noted a general resemblance to corals. As described above, Bather (1923) showed the shell of *C. cellulusus* to be continuous rather than segmented, and argued that cornulitids were more similar structurally to cephalopods and the Ordovician stromatoporoid *Aulacera* than tubicolous annelids. There were clear differences between cornulitids and those taxa too, and Bather (1923, p. 545) regarded both the shell growth and zoological position of *Cornulites* as ‘problems for future solution’.

Fisher (1962) did not place cornulitids in a phylum, but reiterated the fact that their cellular shell structure was quite unlike that of tubicolous annelids, being more akin to some cnidarians, poriferans and fusulinids. Blind (1972, p. 5) found ‘striking correspondences in the shells of cornulitids and molluscs’, based on specimens of *Cornulites* from the Silurian of Gotland, and suggested they might be primitive members of that phylum. Most recently, Dzik (1991, 1993) raised the possibility that cornulitids were lophophorates, having interpreted the Ordovician taxon *Cornulitozoon* as a form of solitary bryozoan. Thus, in nearly two centuries since the first diagnosis, *Cornulites* and its putative relatives have been allied with a wide variety of invertebrate phyla, but no consensus has been reached as to their

true affinities. The microstructure and shell growth outlined above, combined with new information on the ontogeny and skeletal structure of invertebrates, enable the matter to be reassessed.

7.7.1 COMPARISONS WITH OTHER TAXA

The relationship of extinct taxa to living groups is often difficult to determine, and it can be tempting to simply erect a new phylum or other high-level taxon. However, this does little to further our understanding of the biology or phylogeny of such groups: problematical organisms must be more closely related to some living taxa than others (Budd and Jensen 2000) and a comparison with members of extant clades should always be made. Using the shell structures and growth patterns described above, it is possible to assess the affinities of *Cornulites*, particularly with regard to previous interpretations of its systematic position.

Fisher (1962) commented on similarities in the cellular shell structure of cornulitids and that of some fusulinid foraminiferans. Foraminiferans are unicellular organisms, and although macroscopic forms are known (e.g. *Nummulites*), none are of the scale of taxa such as *Cornulites cellulusus*, examples of which reached at least 80 mm in length. Furthermore, no protists are known that have a morphology like that of *Cornulites*, so the genus cannot be referred to that clade. Cornulitids are interpreted here as metazoans.

The phylogenetic relationships of taxa within the Metazoa are contentious, with many different models having been proposed. The most comprehensive recent analysis is that of Peterson and Eernisse (2001; Text-fig. 7.12), which combines developmental, molecular (18S rDNA) and morphological evidence and, as with the machaeridians (Chapter 6), is used here to assess the likely relationships of cornulitids to extant taxa. Choanoflagellates and placozoans are tiny, extremely simple organisms, which do not secrete calcareous skeletons, whilst ctenophores are exclusively soft-bodied, so a close relationship of cornulitids to any of those groups cannot be supported. Similarly, all ecdysozoans grow by moulting their exoskeleton, rather than by adding new increments of shell material to existing hard-parts, and no deuterostomes form external skeletons of lamellar, low-magnesian calcite, so the referral of *Cornulites* to either of those clades can be ruled out. That leaves sponges, lophotrochozoans, and cnidarians as the three clades of extant metazoans with which cornulitids are most comparable.

7.7.1.1 Cornulitids as sponges

The Porifera are divided into three extant classes – Calcarea, Hexactinellida, and Demospongia – all of which include taxa with mineralized skeletons. Hexactinellid and demosponge skeletons, however, are formed of silica spicules, making them quite unlike the

non-spiculate calcite shell of *Cornulites*. Calcarea, as their name suggests, have skeletons composed of calcium carbonate, but are also spiculate, again separating them from cornulitids. However, one extinct group of poriferans, the Stromatoporoidea, includes Palaeozoic forms that had non-spiculate skeletons of calcium carbonate (Kershaw 1998; Stearn *et al.* 1999). The calcium carbonate was normally deposited in distinct laminae, and some stromatoporoids had a cellular microstructure (Stearn 1993), which led Bather (1923) and Fisher (1962) to suggest that they might be closely related to cornulitids. Certainly, there are similarities between the two groups, but closer examination shows that there are also fundamental differences.

In stromatoporoids, the soft tissues covered a flat or slightly convex external surface, with calcium carbonate being deposited in sheets beneath (see e.g. Stearn and Pickett 1994), so that in section view the outer laminae are younger than the inner laminae. The opposite is true in cornulitids – the soft tissues covered the internal surface and the inner lamellae are younger than the outer lamellae. More significantly, although the pseudopunctae seen in cornulitids may have given the shell a degree of porosity, they are not part of an intricate, interconnected series of wall chambers, canals and pores of the kind found in poriferans. The restriction of abundant cellulae to the more apertural parts of large specimens of *Cornulites cellulosis*, and their total enclosure by subsequent lamellae, shows that they were not an integral part of cornulitid soft-part organization, and were more probably a late ontogenetic constructional feature (see section 7.5.2). If cornulitids were sponges, one would expect the entire shell of all forms to have pores, canals and chambers, which is not the case. Furthermore, studies on stromatoporoids from the Ordovician (Yoo and Lee 1993) and Devonian (Rush and Chafetz 1991) indicate that many Palaeozoic forms had skeletons composed of high-magnesian calcite: examination under cathodoluminescence shows that cornulitid shells were formed of low-magnesian calcite. The combination of all lines of evidence, therefore, does not support a poriferan affinity for *Cornulites*.

7.7.1.2 Cornulitids as lophotrochozoans - annelids

The commonest interpretation of the biological affinities of cornulitids has been that they were tubicolous annelids, probably most closely related to the Serpulidae. Within the Annelida, tube-building is seen in many polychaetes of the Terebellida and Sabellida, but serpulids (Order Sabellida) are the only group that normally construct tubes of calcium carbonate (ten Hove and van den Hurk 1993). Despite the regularity with which the two groups have been allied, a detailed comparison of structures and growth patterns in annelids and cornulitids has never been carried out. Previous studies have tended to rely on broad morphological similarities rather than close examination of taxa, with a high possibility of comparing analogous rather than homologous characters. Reed (1923), for example,

described *Cornulites* as having a segmented shell structure, which he regarded as clear evidence for placing the genus in the Annelida. However, Bather (1923) pointed out that neither *Cornulites* nor tubicolous annelids have segmented shells. The study of cornulitid shell structure and growth described here, combined with recent work on the structure of serpulid tubes, enables the relationship of the two groups to be re-evaluated.

Ten Hove and van den Hurk (1993, p. 27) stated that most serpulid tubes are composed of a thin, hyaline inner layer and a thicker outer layer formed of ‘anteriorly directed chevron-like lamellae’, although some forms have three-layered tubes. Fischer *et al.* (1989, 2000) indicated that there was greater variation – the tube walls of the Oligocene polychaete *Diplochaetetes mexicanus* could be formed of one or several layers of lamellar calcite (Fischer *et al.* 1989). They showed also that all tubes of *D. mexicanus* had internal tabulae, some of which were multilamellar. This lamellar-tabular tube structure is similar to the shell structure of cornulitids, but there are also profound differences. The lamellae of serpulid tubes are formed of agglutinated calcite grains, separated by thinner, micritic lamellae (Fischer *et al.* 1989), or of micrite and peloids with ‘intercalated lenses of fibrous calcite/aragonite’ (Fischer *et al.* 2000, p. 35), whilst the tabulae apparently form randomly, rather than being structures formed at distinct growth stages (Fischer *et al.* 1989). In contrast, cornulitid shells are not composed of agglutinated calcite grains, micrite or peloids, and the tabulae were formed at distinct growth stages, each tabula being the apical representation of a lamella. Furthermore, the combination of tabulae, lamellae, apertural grooves, cellulae and pseudopunctae gives the cornulitid shell a complexity far beyond that of serpulid tubes. There are thus no grounds for interpreting *Cornulites* as a member of the Annelida.

7.7.1.3 Cornulitids as lophotrochozoans - molluscs

Blind (1972) argued that the microstructure of ‘*Cornulites serpularius*’ from the Silurian of Gotland resembled the nacreous layer of mollusc shells. As he included no supporting illustrations, the accuracy of his comparison cannot be determined, and it is also unclear whether he was describing specimens that would be placed in *C. serpularius* as defined here. However, nacre is always formed of aragonite, and the shell of *Cornulites* is composed of low-magnesium calcite: in the Much Wenlock Limestone Formation, originally aragonitic shells are invariably replaced by clear neomorphic calcite spar. Also, the microstructure of cornulitid lamellae (e.g. Text-fig. 7.8F) does not convincingly resemble the distinctive layered tablets that form nacre (see e.g. Carter and Lutz 1990, pls 1–4). Instead, it is more like the lamellar (foliated) shell structures described by Wendt (1990, p. 45) as normally being formed of calcite, and found in taxa belonging to the Hydrozoa, Tabulata, Rugosa, Serpulidae, Brachiopoda, Bryozoa, Gastropoda and Bivalvia.

On a more general level, the growth of mollusc shells by marginal accretion is quite different from the whole shell, cone-in-cone accretion of calcite increments seen in cornulitids. Although the tabulae of cornulitids are comparable with the septa of cephalopods, the latter do not close off the apical part of the cephalopod shell as cornulitid tabulae do, but are perforated by the siphuncle, which interconnects all chambers. Cornulitid camerae were not interconnected. Additionally, cephalopod septa are solely transverse across the shell, and do not continue along the interior to form lamellae as seen in cornulitids.

7.7.1.4 Cornulitids as lophotrochozoans - bryozoans

Dzik (1991, 1993) suggested that cornulitids were lophophorates, probably the sister group of bryozoans, with which they shared characters of a ‘subspherical protoecium...and tubular, initially creeping but later erect peristome, which is frequently funnel-like’ (Dzik 1993, p. 350). He also noted (Dzik 1991) that there were similarities in the tube microstructure of some bryozoans and the putative Ordovician cornulitid *Cornulitozoon*, and hypothesized 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. Ignoring the question of whether *Cornulitozoon* is a true cornulitid, the characters upon which Dzik based his hypothesis are somewhat general. An upright, tubular or funnel-shaped skeleton is not unique to bryozoans, and neither are the laminar structures as seen in the zooid walls of calcareous bryozoans. More significantly, bryozoan skeletons are not known to contain chambers or grow by cone-in-cone accretion, making them fundamentally unlike the cellular shell of *Cornulites*.

7.7.2 RELATIONSHIP OF *CORNULITES* TO *TENTACULITES*

In addition to *Cornulites*, Schlotheim (1820) erected the genus *Tentaculites* to include a different group of annulated, conical, calcareous shells from the Palaeozoic. Two species of *Tentaculites* were described, *T. scalaris* and *T. annulatus*, but as with *Cornulites serpularius*, the specimens figured by Schlotheim (1820) cannot be traced (Larsson 1979a). Based on the original illustrations of Schlotheim (1820), *Tentaculites* and *Cornulites* are morphologically similar, with the most obvious differences being that the shell of *Tentaculites* is more slender than that of *Cornulites*, with a narrower aperture, rarely shows any sinuosity, and normally lacks obvious longitudinal ornamentation. However, whilst suggesting that *Cornulites* might be most closely related to annelids, Schlotheim (1820) interpreted *Tentaculites* as a crinoid appendage. Subsequent assessments of the biological affinities of *Tentaculites* have been varied (see Larsson 1979a for summary): some authors (e.g. Nicholson 1872a, 1872b, 1873; Fisher 1962) have followed Schlotheim in regarding *Tentaculites* and *Cornulites* as belonging

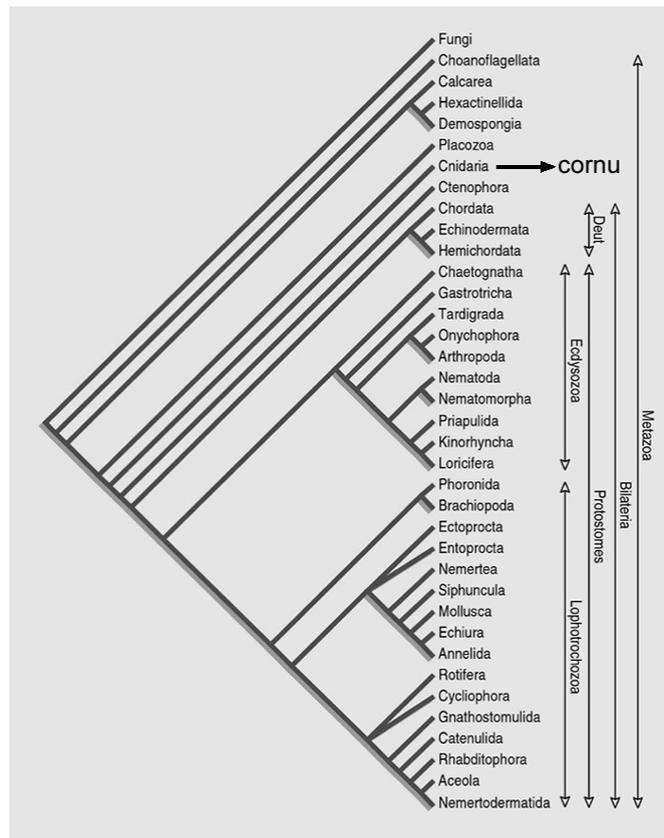
to separate phyla, while others (e.g. Murchison 1859; Vine 1882; Dzik 1991, 1993) have argued that the two genera are closely related. Larsson (1979a) provided a detailed analysis of tentaculitid shell structure and growth, which, with the greater understanding of shell structure and growth of cornulitids described above, enables the relationship of the two groups to be reassessed.

As with cornulitids, the earliest growth stages of the tentaculitid shell are very rarely preserved (Larsson 1979a), but near-complete specimens of tentaculitids show a number of structural similarities, particularly towards the apex of the shell. Most prominent are the transverse shell layers (septa) that, in many tentaculitids, divide the apical region into distinct chambers, or camerae (see Larsson 1979a, fig. 12). These are remarkably close in arrangement to the tabulae and camerae of cornulitids, but the septa do not continue up the interior shell surface to form lamellae in the same way as the tabulae do in *Cornulites*. Instead, they taper distally, and the shell wall is formed of separate lamellae, unconnected to the septa, producing a bipartite division of primary (outer) and secondary (inner) layers. Larsson (1979a, p. 27) also noted 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 pseudopunctae oriented perpendicular to the surface of the wall.

The phylogenetic position of tentaculitids is unresolved, but Towe (1978) found striking similarities in the shell microstructure of some species and that of brachiopods, and tentatively suggested that tentaculitids were most closely related either to the brachiopods, or their sister group, the phoronids. Larsson (1979a, p. 59) suggested that tentaculitids were perhaps most closely related to phoronids, but noted that extant members of that clade do not have a mineralized external skeleton, making direct comparison with tentaculitids impossible, and that the lophophorate feeding system of phoronids was incompatible with the planktonic mode of life proposed for some tentaculitids. Whether the shell structures shared by both cornulitids and tentaculitids are homologous or homoplastic remains to be seen.

7.7.3 CORNULITIDS AS CNIDARIANS

As sessile, conical or tubular organisms with radially symmetrical calcite skeletons, cornulitids share many similarities with members of the Cnidaria. Cnidarians are simple metazoans, divided into four major clades: Anthozoa, Cubozoa, Hydrozoa and Scyphozoa (Bridge *et al.* 1995). With scyphozoans and cubozoans being soft-bodied, normally free-swimming, and having tetradial symmetry, cornulitids cannot be closely related to either group, but both hydrozoans and anthozoans include sedentary taxa with a calcareous skeleton



TEXT-FIG. 7.12. Phylogenetic tree of metazoan relationships (Peterson and Eernisse 2001) showing possible position of cornulitids within the Cnidaria.

and a conical or cylindrical body shape. Of the hydrozoans, however, only one group – the hydrocorallines – forms mineralized skeletons, and these are formed of numerous vertical tubes connected by horizontal canals, with soft tissues present only close to the surface (see e.g. Oliver and Coates 1987, p. 189). Anthozoans are the cnidarian clade with which cornulitids are most comparable, and taxa such as *Cornulites scalariformis* and *C. gremialis*, in particular, show a close resemblance to the extinct rugose corals. Cornulitid annulations are much like the growth lines seen in many Palaeozoic corals, whilst the cellulae and tabulae are morphologically very close to the dissepiments and tabulae of Rugosa. Internally, cornulitids do not have any structures analogous or homologous to the septa of rugosans, and a columella is also absent, but this does not preclude an anthozoan affinity for the group, as most members of the other major clade of Palaeozoic corals, the Tabulata, have neither septa nor a columella.

Although cornulitids are often found as clusters, taxa such as *C. scalariformis* are found also as solitary forms, showing that they were not colonial in the sense of forming integrated, interconnected groups. The clusters were probably controlled by availability of suitable substrate and nutrients, with numerous cornulitids attaching themselves to the same

host organism where beneficial to the individual cornulitid. Within the Anthozoa, solitary taxa are seen most prominently in the Palaeozoic clades Rugosa and Heterocorallia, but it is unclear whether anthozoans are primitively solitary or colonial: the Tabulata are exclusively colonial, whereas Rugosa include colonial and solitary taxa.

The precise phylogenetic position of cornulitids remains problematical, but the detailed information on the shell structure and growth of *Cornulites* provided by the thin sections of *C. cellulusus* and *C. scalariformis* suggests that they are anthozoans, most closely related to rugose corals. Cornulitids were undoubtedly metazoans, and a close affinity with poriferans, annelids and molluscs can be ruled out, whilst a close relationship to bryozoans is not supported. They share a considerable number of characters with cnidarians, particularly solitary rugose corals, and although a lack of septa indicates that they cannot belong to the Rugosa as presently defined, it is proposed here that they represent a clade of stem-group anthozoans.

CHAPTER EIGHT

CONCLUSIONS

Asteroidea

The low preservation potential of starfish makes their true abundance and diversity in Silurian ecosystems difficult to assess, but the variety of body morphologies seen in the Wenlock taxa described shows that they were more diverse than has been previously thought (Chapter 2). This diversity of body shape, with multiradiate species, cushion stars, and long-rayed forms, indicates that asteroids had begun to exploit a variety of ecological niches, in particular different methods of feeding to the morphologically conservative taxa present in the Ordovician. Ecologically, the appearance of *Lepidaster grayi*, the first asteroid with supernumerary rays, would have been particularly significant, since extant multiradiate forms commonly have very specialized methods of feeding. Their additional rays are used to capture and subdue active prey, or manipulate irregularly shaped organisms that five-rayed starfish cannot and, by functional convergence, a similar interpretation is invoked for *L. grayi*. At least some Palaeozoic asteroids were active predators, rather than detritivores and scavengers.

The presence of supernumerary rays in *L. grayi* is also a significant development in both asteroid and echinoderm phylogeny, as it shows that plasticity of the asteroid body plan has been present for most, if not all, of the evolutionary history of the clade. How exclusively five-rayed Ordovician taxa gave rise to a thirteen-rayed Silurian species is unclear, but the development of supernumerary rays in extant starfish allows two hypotheses to be proposed – the ‘all-in-one’ model, and the ‘quadrants’ model. The ‘all-in-one’ model of ray addition is normally seen in living taxa with a relatively small number of supernumerary rays, so it would seem more probable that *L. grayi* added its rays in that fashion, but the existence of a specimen possibly having only nine rays suggests that addition may have followed the ‘quadrants’ model.

Calyplocymba mariae

The crinoid fauna of the Much Wenlock Limestone Formation was comprehensively reviewed by Widdison (2002), but the delicate, slender camerate *Calyplocymba mariae* is a particularly unusual discovery. With a small calyx, long, cirriated stem and long, pinnulate rays, *C. mariae* was uniquely adapted to the low energy environment in which it lived, but the most unusual aspect of its morphology are the thinly mineralised calycal plates. This possibly

reflects an energy-saving mechanism for a crinoid living in conditions in which nutrients were in poor supply, and in which the risk of predation was relatively low.

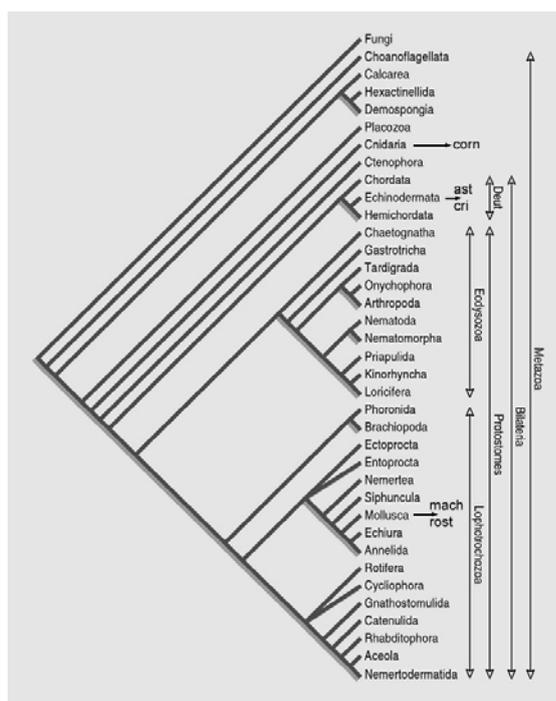
Rostroconchs

British Silurian rostroconchs have received almost no attention in studies of the group, but the four species of conocardiceans recognized in the Much Wenlock Limestone Formation indicate that they were not uncommon, at least locally. The fauna shows close similarities to contemporaneous assemblages previously described from the Silurian of Canada and Gotland. Species are placed in two genera – *Mulceodens* and *Redstonia* – which have previously been placed in separate family-level clades: the Bransoniidae and Hippocardiidae, respectively. However, the autecology of *R. sima* and *M. aedicula* from the Much Wenlock Limestone Formation indicates that morphological differences between the genera can be better explained as the result of ecological specialization within closely related rostroconchs. Ecologically, *Redstonia* lived in low energy conditions, having a large primary carina and rostrum for the separation of inhalant and exhalant currents, whereas *Mulceodens* is found in sediments deposited under much higher energy. This is reflected by its more robust shell ornamentation, shorter rostrum and pronounced denticles in the anterior gape. Following the work of Wagner (1997), who showed that the bransoniids and hippocardiids were polyphyletic, *Mulceodens* and *Redstonia* are here placed in the same clade.

Machaeridians

By examination of the sclerite structure of the machaeridian *Turrilepas wrightiana* (de Koninck, 1857) and comparison with previously published studies on other taxa, it is evident that machaeridians grew by marginal accretion of their sclerites, rather than moulting. The original composition of the sclerites was low-magnesian calcite, and they formed a dorsal, external skeleton. Thus, an affinity with echinoderms, arthropods and annelids is excluded. The two groups with which machaeridians share the most characters are brachiopods and molluscs, but, as the plane of bilateral symmetry in machaeridians ran longitudinally along the body, with serially repeated sclerites arranged as opposing units either side of this axis, an affinity with the former group is not supported. Machaeridians are interpreted as total-group molluscs, most closely related to aplacophorans and polyplacophorans.

The presence of outer sclerites in *Lepidocoleus? extraplax* sp. nov. shows that Adrain's (1992) classification of machaeridians into a quadriseriate group (Turrilepadomorpha) and a biseriata group (Lepidocoleomorpha) is invalid, and a tripartite division of the clade into Plumulitidae, Turrilepadidae and Lepidocoleidae is followed, pending further study.



TEXT-FIG. 8.1. Probable phylogenetic relationships of rare and problematical taxa from the Much Wenlock Limestone Formation, based upon phylogenetic analysis of Metazoa (Peterson and Eernisse 2001). Abbreviations as follows: *ast*, asteroids; *cri*, crinoids; *corn*, cornulitids; *mach*, machaeridians; *rost*, rostroconchs.

Cornulitids

Serial transverse and longitudinal sections of *Cornulites cellulusus* sp. nov. and *C. scalariformis* Vine, 1882, show that cornulitids grew by the cone-in-cone accretion of increments of low-magnesian calcite. The shell wall is lamellar, with cellulae present, most prominently in the apertural region of large specimens of *C. cellulusus*, and internal chambers are present in the apical region. This pattern of shell structure and growth, combined with overall morphology and mineralogy, suggests that cornulitids were stem-group anthozoans, possibly most closely related to rugose corals.

Ecologically, most taxa attached themselves to the hardparts of other organisms early in life and many show preferential orientation, growing towards the feeding currents generated by their hosts. *C. cellulusus* is unusual in never being found attached to the substrate, and having an upright mode of life, and it is argued that the extensively cellular shell structure present is a form of lightweight shell construction.

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APPENDIX

PROVENANCE OF SPECIMENS

THE Much Wenlock Limestone Formation fossils studied in this project are exclusively from museum collections, and detailed information on the horizons from which they were collected is often lacking, particularly for those collected in the 19th Century in the outcrops around Dudley. Commonly, specimens are described only as having come from ‘Dudley’, ‘Wren’s Nest’ or ‘Sedgley’, and though these terms probably refer in turn to each of the Silurian inliers of the area – Castle Hill, Dudley, Wren’s Nest Hill, and Hurst Hill, Sedgley – this is by no means certain. Additionally, a wide variety of lithologies are present in each of the inliers, not all of them of Wenlock age, so palaeoecological interpretations are difficult to make without closer examination of specimen provenance.

The lithofacies of the Much Wenlock Limestone Formation in the West Midlands were described by Ratcliffe and Thomas (1999), whilst sedimentological studies of the formation were made by Butler (1939), Shergold and Bassett (1970), Scoffin (1971) and Bassett (1974, 1989). By making thin sections of the matrix surrounding various museum specimens and comparing them with the lithologies previously described, it has proved possible to determine the likely provenance of the specimens, and thus produce better-supported interpretations of their palaeoecology.

MATERIAL AND METHODS

The thin sections described here were made from the matrix of specimens in the Lapworth Museum, University of Birmingham (prefix BU), Natural History Museum, London (NHM), and Wollaton Hall Natural History Museum, Nottingham (NOTNH), as follows:

1. NHM 40215, holotype of the asteroid *Lepidaster grayi* Forbes, 1850, from Castle Hill, Dudley;
2. NOTNH FS03795, specimen of *L. grayi* from Dudley;
3. NOTNH FS03800, specimen of *L. grayi* from Dudley;
4. NHM E53614, holotype of *Doliaster brachyactis* gen. et sp. nov., from Coates Quarry, Wenlock Edge;
5. BU 4350, holotype of the asteroid *Hudsonaster? carectum* sp. nov., from Sedgley;

Petrographical analysis was carried out using a Zeiss Axioskop MC100 microscope, and photomicrographs taken using a Nikon Coolpix digital camera.

DESCRIPTION OF THIN SECTIONS

Thin section 1 (BMNH 40215)

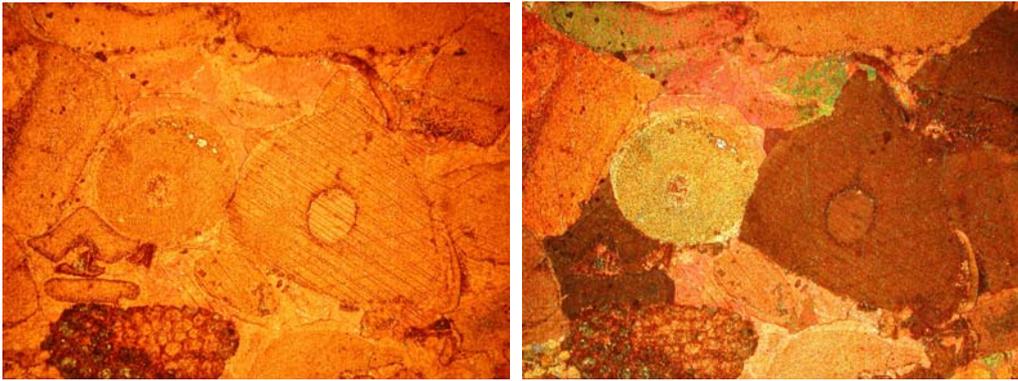
Thin section 1 (Text-fig. A1) shows the lithology to be an homogenous limestone, with shell fragments of non-ferroan calcite forming the bulk of the rock. Abraded crinoid ossicles are the dominant bioclasts, with other skeletal fragments (e.g. bryozoans, brachiopods) forming a minor component. Very little finer-grained, non-bioclastic material is present; most of the space between the bioclasts is filled by non-ferroan calcite cement, often as syntaxial overgrowths.

The rock is best described as a crinoidal biosparite or crinoidal grainstone and can thus be interpreted with a high degree of certainty as being from the crinoidal grainstone lithofacies of the Upper Quarried Limestone Member (Ratcliffe and Thomas 1999). Sedimentary structures such as grading or laminations are absent, and there is no geopetal evidence of way up, so it cannot be ascertained whether the surface containing the holotype of *Lepidaster grayi* is at the top or the base.

Thin section 2 (NOTNH FS03795)

Two lithologies are seen within the thin section (Text-fig. A2), but both are quite different from thin section 1. Most of the rock is bioclastic limestone, but the specimen of *Lepidaster grayi* is found in a thin veneer of parallel-laminated siltstone that covers one surface. The contact between the two units is sharp and relatively flat, with most of the largest bioclasts concentrated in the section of the limestone directly against or close to the siltstone and the fauna present in the limestone is much more diverse than that of thin section 1, with brachiopods, gastropods, bryozoans, bivalves and crinoids all seen. The limestone has a micritic matrix and becomes finer-grained away from its contact with the siltstone, changing from packstone to wackestone.

The siltstone is composed mainly of angular quartz fragments, along with pyrite framboids that are often elongate and oriented parallel to the contact with the limestone. Clay minerals (muscovite and probably illite) are present in small quantities. The combination and



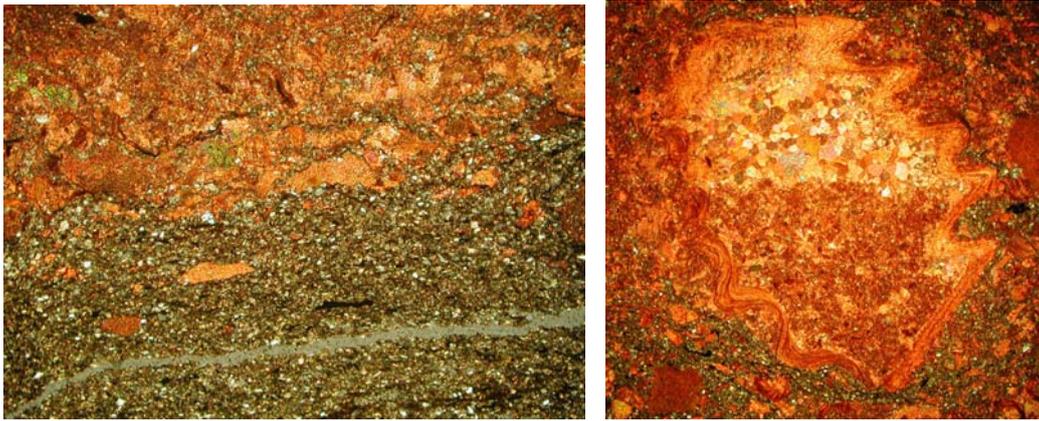
TEXT-FIG. A1. Photomicrographs of thin section 1; matrix of NHM 40215, holotype of *Lepidaster grayi* Forbes, 1850, from Castle Hill, Dudley. Images taken under plane- (left) and cross-polarized light (right), both x 15. See text for further details.

composition of the two lithologies in the thin section make it likely that the specimen came from the interbedded limestone and silty mudstone lithofacies that comprises the upper part of the Nodular Beds Member (Ratcliffe and Thomas 1999).

The sharp nature of the siltstone-limestone contact, coupled with the grading of clasts within the limestone, suggests that the siltstone lies at the base, overlain by the limestone. This is supported by geopetal structures – a brachiopod close to the contact between the limestone and siltstone has cavity infill that gives the same way up direction (see Text-fig. A2). Thus the specimen of *L. grayi* is preserved at the base of the unit.

Thin section 3 (NOTNH FS03800)

Containing very little calcite compared to either of the previous two, thin section 3 (Text-fig. A3A) at first appears to be another distinct lithology. However, closer examination reveals that its composition is in fact very similar to that of the siltstone in thin section 2. Angular, silt-sized grains of quartz are the dominant clasts, with pyrite framboids, muscovite and other clay minerals making up the remainder of the rock. The muscovite and pyrite often form very obvious laminae, with occasional fragments of non-ferroan calcite also found lying parallel to those laminations. No geopetal structures are seen, but the quartz clasts appear to be slightly gradational in a direction perpendicular to the laminations, with grainsize decreasing away from the surface containing the specimen of *Lepidaster grayi*.



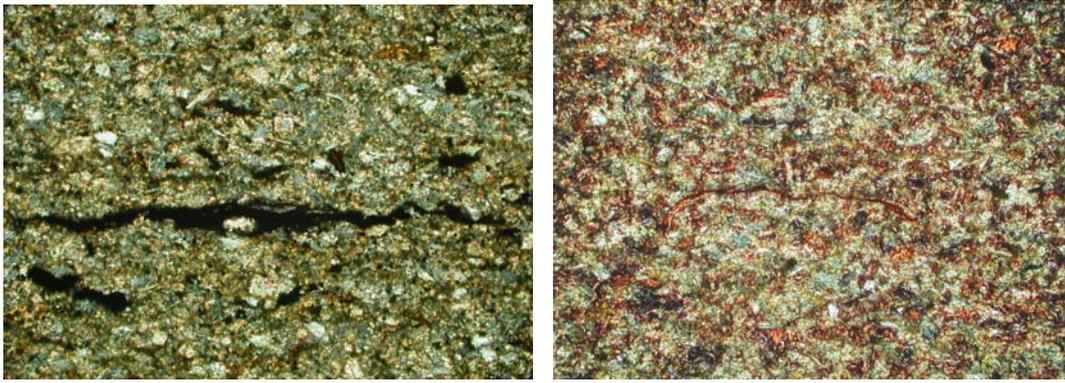
TEXT-FIG. A2. Photomicrographs of thin section 2; matrix of NOTNH FS03795, *Lepidaster grayi* Forbes, 1850, from Dudley. Images taken under cross-polarized light, showing contact of limestone and siltstone (left) and cavity infill of brachiopod (right), both images x 15. Surface containing specimen of *L. grayi* towards base of both images, see text for further details.

The strong resemblance of thin section 3 to the siltstone horizon in thin section 2 implies that it was collected from the same interbedded limestone and silty mudstone lithofacies, although the lack of bioclastic material could also be explained by the specimen of *L. grayi* having been found in the underlying, generally finer-grained nodular limestone lithofacies (Ratcliffe and Thomas 1999). Either way, the sample was unequivocally collected from the Nodular Beds Member.

Thin section 4 (BMNH E53614)

A strong similarity to thin section 2 is observed in thin section 4 (Text-fig. A4) with the bulk of the matrix being formed by bioclastic limestone and the remainder being parallel-laminated quartz siltstone. The main difference is that thin siltstones are present on both top and bottom surfaces of thin section 4, meaning that one cannot apply the way up interpretation of thin section 2 and determine the base of the bed using the presence of a siltstone horizon. However, sedimentological evidence indicates that the surface bearing the holotype of *Doliaster brachyactis* is the top – the contact between the bioclastic limestone and the quartz siltstone on the opposite surface is sharp and scoured with the limestone containing more silt and fewer large bioclasts as one moves away from that contact. The siltstone layer containing *D. brachyactis* has a more gradational contact with the limestone.

Once again, it is likely that the lithology seen in thin section 4 is from the interbedded limestone and silty mudstone lithofacies, particularly as this unit is predominant in the Much Wenlock Limestone Formation of Wenlock Edge (Scoffin 1971; Ratcliffe and Thomas 1999), where the fossil was found.



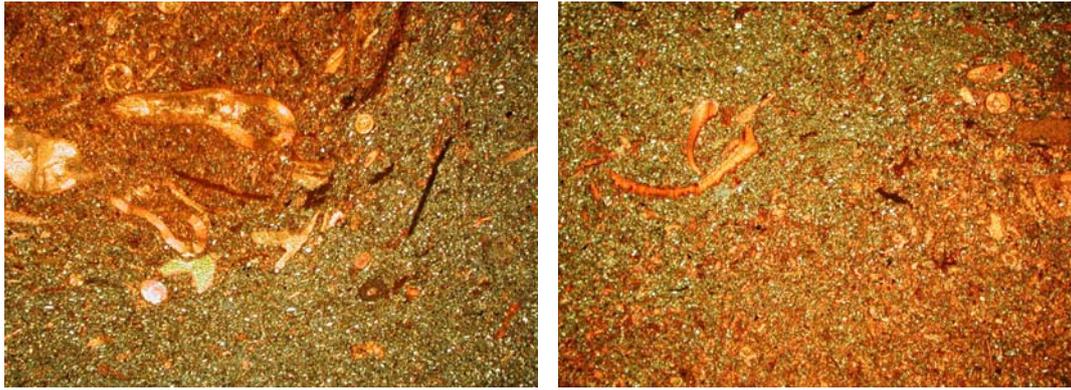
TEXT-FIG. A3. Comparative photomicrographs of A, thin section 3, and B, thin section 5 (right). Both images x 20.

Thin section 5 (BIRUG 12473)

In almost every aspect thin section 5 (Text-fig. A3B) is quite different from the previous four. It is much finer-grained – clay- rather than silt-sized clasts – with very little quartz and few bioclasts of non-ferroan calcite. Tiny crystals of pale green or yellow-brown clay minerals, probably illite and chlorite, are dominant, together with interconnected patches of very fine-grained, amorphous non-ferroan calcite. Pyrite is present only in occasional small clumps.

The lithology is also devoid of laminations, but shows some heterogeneity in the change in ratio of clay minerals to calcite that can be traced from one surface to the other. The surface containing the holotype of *Carectum tessellatum* is underlain by sediment richest in clay minerals, with relatively little amorphous non-ferroan calcite, but this changes as one moves towards the opposite surface, calcite gradually becoming more abundant. The occasional calcitic bioclasts, however, tend to occur in the clay-dominated part of the section.

The rock seen in thin section 5 does not fit into any of the lithofacies of the Much Wenlock Limestone Formation defined by Ratcliffe and Thomas (1999). However, it bears a strong resemblance to the ‘pale green calcareous mudstone’ of Shergold and Bassett (1970, p. 127) that forms part of their limestone/siltstone lithofacies at the base of the Lower Elton Formation, immediately overlying the Much Wenlock Limestone Formation. Additionally, Hurst (1975, p. 312) noted that the appearance of green-coloured beds was indicative of the units directly on top of the Much Wenlock Limestone Formation, whilst Bassett (1976, p. 211) observed that ‘fine, mid-grey to olive-green siltstones [are] typical of the beds above the Much Wenlock Limestone’. More recently, in defining the type Wenlock-Ludlow boundary at Pitch Coppice Quarry, near Ludlow, Lawson and White (1989) documented olive-coloured calcareous shaly siltstones in the lower part of the Lower Elton Formation (bed ‘F4’, Lawson and White 1989, p. 81). It is likely, therefore, that this specimen is from the Lower Elton Formation.



TEXT-FIG. A4. Limestone-siltstone contacts at bottom (left) and top (right) of thin section 4, both x 15.

DISCUSSION

The finer-grained, green-coloured Sedgley mudstone is almost certainly from the Lower Elton Formation. Were Sedgley located in the Welsh Borderlands, this would necessitate the specimens being interpreted as of Ludlow age as the Lower Elton Formation there is defined as the first unit of the Gorstian (Lawson and White 1989). However, extensive research (e.g. Shergold and Bassett 1970; Bassett 1974, 1976; Hurst 1975; Ratcliffe and Thomas 1999) on the Wenlock-Ludlow boundary suggests this may not be the case in the West Midlands. Graptolite evidence published by Bassett (1974) convincingly supports the argument that the contact between the Much Wenlock Limestone Formation and the Lower Elton Formation is diachronous, such that although it defines the Wenlock-Ludlow boundary on Wenlock Edge, it does not do in the Dudley area. This is the result of the crinoidal grainstones of the Upper Quarried Limestone Formation being part of a sandbody that migrated from the West Midlands out to Wenlock Edge, with the transition from Much Wenlock Limestone Formation to Lower Elton Formation (marked by the top of the Upper Quarried Limestone Member) occurring earlier in the West Midlands, as outlined by Ratcliffe and Thomas (1999). Thus it is shown that the Lower Elton Formation in Dudley and Sedgley is actually Wenlock in age.

With regard to the difference in lithology, it would appear likely that the green-coloured silty claystones of Lower Elton Formation were deposited in lower energy conditions than the blue-grey siltstones of the Nodular Beds Member, although reduced terrestrial input of sediment would also explain the lack of siliciclastic material in the claystones. The reduced laminations seen in the Sedgley specimens may be the result of more intense bioturbation and the increased clay mineral content could be explained by increased volcanic activity at that time.