

# CHITINOZOAN BIOSTRATIGRAPHY OF THE BASAL WENLOCK SERIES (SILURIAN) GLOBAL STRATOTYPE SECTION AND POINT

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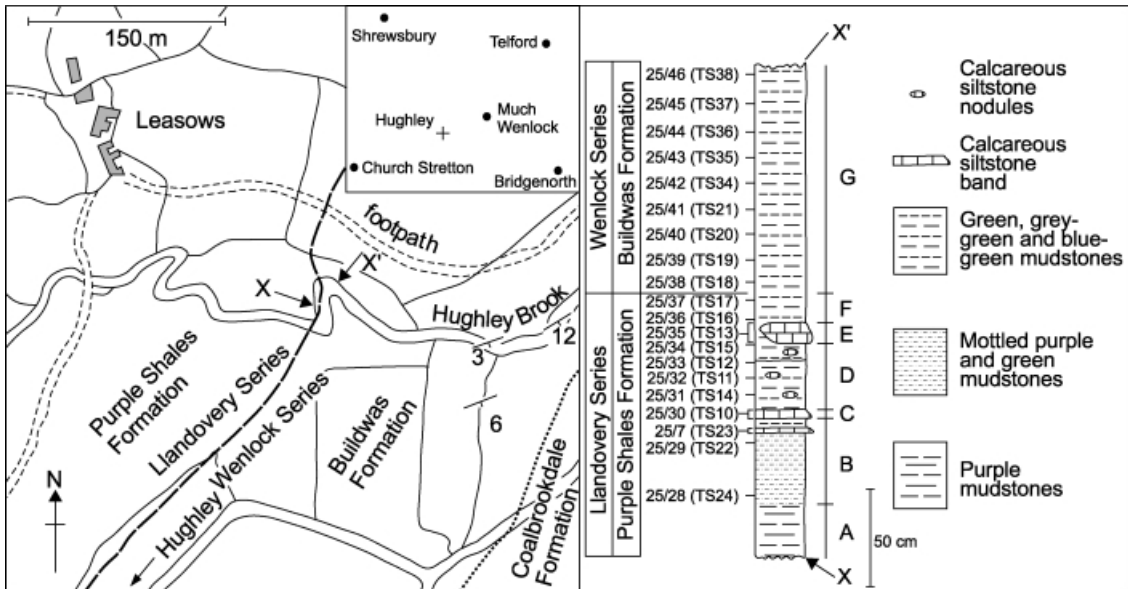
**ABSTRACT.** Diverse and abundant assemblages of chitinozoans allow the recognition of the upper part of the *Margachitina margaritana* Biozone in the uppermost Llandovery and lowermost Wenlock series of the Hughley Brook section. The *Cingulochitina bouniensis* and *Salopochitina bella* biozones are identified in the lower part of the Buildwas Formation, Wenlock Series. The chitinozoan data indicate that the base of the Wenlock Series most probably correlates with a level in the upper *centrifugus* or lower *murchisoni* graptolite biozones. Chitinozoans also indicate that the base of the *riccartonensis* graptolite Biozone may occur within the Buildwas Formation and not the overlying Coalbrookdale Formation.

**KEY WORDS:** Llandovery, Wenlock, Silurian, stratotype, chitinozoans.

THE international stratotype for the base of the Wenlock Series (Silurian) is defined in the Hughley Brook (or Leasows) section, approximately 200 m south-east of Leasows Farm, Hughley, Shropshire, United Kingdom (Bassett *et al.* 1975; Holland 1980; Martinsson *et al.* 1981). Initially, the correlation with graptolitic sequences was problematical and it was considered a disadvantage to retain the shelf succession of the Wenlock district as the 'type' Wenlock area (Cocks *et al.* 1971). However, a sequence of six Wenlock graptolite biozones through this succession was subsequently recognized (Bassett *et al.* 1975). Using these graptolite data, the base of the Wenlock Series was considered to correlate with the base of the *centrifugus* graptolite Biozone (Bassett *et al.* 1975; Holland 1980; Martinsson *et al.* 1981). Unfortunately there are no graptolites described from the Hughley Brook section and the correlation with the *centrifugus* Biozone is based on evidence from other sections and boreholes up to several kilometres away, and from stratigraphical horizons several metres above or below the boundary (Mabillard and Aldridge 1985; Loydell 1993; Mullins 2000). However, fragments of graptolites have been observed in this study in the palynomorph residues from samples 25/38, 25/39 and 25/43 of Mabillard and Aldridge (1985), indicating that they are present.

The use of microfossils to correlate the base of the Wenlock Series was investigated by Mabillard and Aldridge (1985), who described rich microfossil assemblages of acritarchs, conodonts, chitinozoans and ostracods from the type section. They noted that the base of the Wenlock Series is not coincident with the base of any microfossil biozone, but occurs within the *Pterospathodus amorphognathoides* conodont interval (Mabillard and Aldridge 1985). Using these conodont data and the correlation of the conodont and graptolite biozones in Loydell *et al.* (1998), it has been suggested that the base of the Wenlock Series could only be reliably constrained as somewhere within the interval of the *lapworthi* to *murchisoni* graptolite biozones (Mullins 2000, p. 369). Mabillard and Aldridge (1985) also highlighted the use of the acritarchs *Deunffia brevispinosa* Hill, *Deunffia ramusculosa* Downie and *Domasia amphora* Martin in recognizing the uppermost Llandovery Series. They also showed that the base of the Wenlock Series occurred within the range of the ostracod *Craspedobolbina interrupta* (Jones), with several typical ostracod species also being identified from the Wenlock Series (Mabillard and Aldridge 1985).

The first occurrence of the chitinozoan *Margachitina margaritana* (Eisenack) was reported to be in sample 25/38, 67 mm above the base of the Wenlock Series (Mabillard and Aldridge 1985, text-fig. 5).



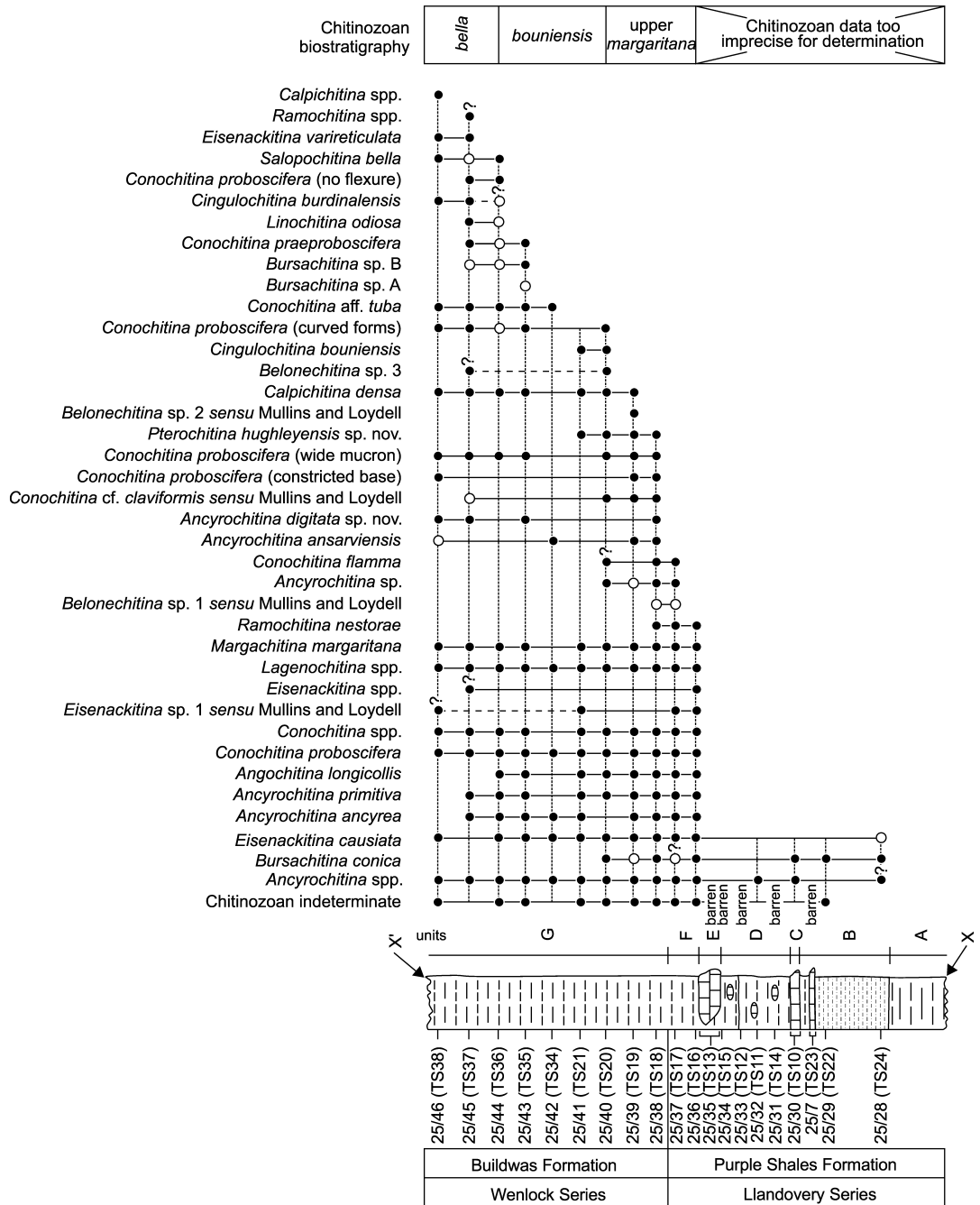
TEXT-FIG. 1. Geographical map and stratigraphical log showing the location of the GSSP for the base of the Wenlock Series, Silurian, in the Hughley Brook section, Hughley, Shropshire (Mabillard and Aldridge 1985; Bassett 1989). The sample numbers (prefix 25/) of Mabillard (1981) and Mabillard and Aldridge (1985) are shown together with the original slide and organic residue sample numbers (prefix TS). The location of the studied section (X–X') is shown. The sample heights above and below the base of the Wenlock Series are based on Mabillard (1981, fig. 5): 25/28, –956 mm; 25/29, –681 mm; 25/7, –622 mm; 25/30, –525 to –572 mm; 25/31, –467 mm; 25/32, –372 mm; 25/33, –306 mm; 25/34, –242 mm; 25/35, –144 to –219 mm; 25/36, –125 mm; 25/37, –31 mm; 25/38, 67 mm; 25/39, 161 mm; 25/40, 256 mm; 25/41, 350 mm; 25/42, 447 mm; 25/43, 636 mm; 25/44, 825 mm; 25/45, 1017 mm; 25/46, 1211 mm.

This first appearance of this taxon has subsequently been used to define the base of the 'global' *M. margaritana* Biozone (Verniers *et al.* 1995). *M. margaritana*, however, has also been recovered 31 mm below the base of the Wenlock Series in sample 25/37 (Mabillard 1981, pl. 6, fig. 21). This occurrence was used to suggest that the base of the Wenlock Series could occur within the interval of the *insectus* to *centrifugus* graptolite biozones (Mullins 2000; Mullins and Loydell 2001).

A re-examination of the chitinozoans described by Mabillard (1981) and Mabillard and Aldridge (1985) is presented here. This study has recognized a more diverse fauna, which provides the potential for more accurate correlation of other sections with the international stratotype. A revision of the position of the base of the Wenlock Series within the graptolite biostratigraphical scheme can now be suggested, using several studies that have correlated the graptolite and chitinozoan biostratigraphical schemes (Loydell *et al.* 1998, 2003; Verniers 1999; Mullins 2000; Mullins and Loydell 2001, 2002).

#### LOCALITY AND MATERIAL

The Global Stratotype Section and Point (GSSP) for the base of the Wenlock Series and Sheinwoodian Stage is defined in the Hughley Brook section, Hughley, Shropshire (NGR SO5688 9839; Text-fig. 1). A transitional boundary between purple and grey-green mudstones occurs and the series boundary is defined at the base of Bed G of the Buildwas Formation, which overlies the Llandoverly Purple Shales Formation (Text-fig. 1; Bassett *et al.* 1975; Bassett 1989). Twenty samples were collected bed-by-bed through the sequence by John Mabillard (JM) and RJA and processed using standard palynological techniques (see Mabillard and Aldridge 1985, pp. 90–91 and references therein). The palynological residues were sieved



TEXT-FIG. 2. Stratigraphical distribution of chitinozoans across the type Llandoverly-Wenlock series boundary in the Hughley Brook section, Hughley, Shropshire. ●, chitinozoans observed on John Mabillard's original microscope slides; ○, chitinozoans recovered only from John Mabillard's remaining palynomorph residues.

at 10  $\mu\text{m}$  and 53  $\mu\text{m}$  and the latter fraction was examined for chitinozoans. We have re-examined the strew mounted slides made by JM for transmitted light microscopy and the remainder of the palynological residues to enable more reliable determination of species by scanning electron microscopy.

#### CHITINOZOAN BIOSTRATIGRAPHY

Of the 20 samples studied, five from the Purple Shales Formation were barren of chitinozoans (25/7, 25/31, 25/33, 25/34, 25/35; Text-fig. 2). From the uppermost green to grey-green mudstones of the Purple Shales Formation, only samples 25/36 and 25/37 yielded significant numbers of chitinozoans (308–586 per 100 grams of sample). Chitinozoans are generally abundant in the Buildwas Formation (586–1660 per 100 grams), except in sample 25/42, which yielded only 28 chitinozoans per 100 grams. No quantitative data are available for samples 25/43 to 25/46 as the weight of sample processed by JM is unknown.

The two specimens of *Eisenackitina* reported in sample 25/30 of unit C by Mabillard and Aldridge (1985) have not been observed, although a specimen of *Bursachitina conica* (Taugourdeau and de Jekhowsky) was recorded from this sample (Text-fig. 2; e.g. Pl. 1, figs 5–6). This study has also recovered chitinozoans from samples 25/28 (*Ancyrochitina*?, *B. conica*, *Eisenackitina causiata* Verniers; Pl. 1, figs 1–2), 25/29 (indeterminate chitinozoan, *B. conica*) and 25/32 (*Ancyrochitina* spp.). The chitinozoans from samples 25/28 to 25/35 are not diagnostic of any chitinozoan biozone (Text-fig. 2).

#### *The Margachitina margaritana Biozone*

The first *M. margaritana* were recovered from sample 25/36 (125 mm below the Wenlock Series), unit F, Purple Shales Formation, Llandovery Series (Text-fig. 2). Specimens may have prominent, cone-shaped opercula (Pl. 2, fig. 1; Pl. 3, figs 4, 7, 10). The first appearances of *Ancyrochitina ancyrea* (Eisenack), *Ancyrochitina primitiva* (Eisenack) (Pl. 3, figs 1–2), *Angochitina longicollis* Eisenack (Pl. 3, figs 3–5), *Conochitina proboscifera* Eisenack (Pl. 3, fig. 13), *Eisenackitina* sp. 1 *sensu* Mullins and Loydell (Pl. 2, figs 3–4; Pl. 3, fig. 6), *Lagenochitina* spp. and *Ramochitina nestorae* Grahn (Pl. 3, figs 8–9, 11–12), are coincident with the first occurrence of *M. margaritana* (Text-fig. 2). Chitinozoans are uncommon in the succession below sample 25/36 (Text-fig. 2) and all of these first appearances may be influenced by preservational factors.

Within the *M. margaritana* Biozone, the first *Belonechitina* sp. 1 *sensu* Mullins and Loydell (Pl. 2, fig. 6) and *Conochitina flamma* Laufeld (Pl. 2, figs 2, 5; Pl. 4, figs 2–3) occur in sample 25/37, 31 mm below the base of the Wenlock Series (Text-fig. 2).

In sample 25/38 (67 mm above the base of the Wenlock Series), *Ancyrochitina ansarviensis* Laufeld (Pl. 2, fig. 12), *Ancyrochitina digitata* sp. nov. (Pl. 2, figs 10–11, 13–14; Pl. 4, figs 8, 13), *Conochitina* cf. *claviformis sensu* Mullins and Loydell (Pl. 4, figs 6–7), *Conochitina proboscifera* with constricted bases (Pl. 6, figs 8, 14), *C. proboscifera* with wide mucrons (Pl. 6, figs 3–4, 7, 11–13) and *Pterochitina hughleyensis* sp. nov. (Pl. 4, figs 9–12, 14–15; Pl. 5, figs 1–2) first occur.

Examples of *Ancyrochitina* sp. with tubular processes were also recovered from samples 25/37 and 25/38 (Pl. 4, figs 1, 4–5). However, the processes are broken and reliable identification of the species is, therefore, not possible.

*Belonechitina* sp. 2 *sensu* Mullins and Loydell (Pl. 2, figs 7–8) and *Calpichitina densa* (Eisenack) (Pl. 5, fig. 3) were recovered from sample 25/39 (Text-fig. 2). The last *R. nestorae* and unequivocal *C. flamma* were recorded in sample 25/38 (Text-fig. 2).

The co-occurrence of *R. nestorae*, *C. flamma*, *Belonechitina* sp. 1, *Eisenackitina* sp. 1 and *C.* cf. *claviformis* with *M. margaritana* in samples 25/36, 25/37 and 25/38 indicates that the upper part of the *margaritana* Biozone is present (Text-fig. 3).

#### *The Cingulochitina bouniensis Biozone*

*C. bouniensis* Verniers occur in samples 25/40 and 25/41 (256 and 350 mm above the base of the Wenlock Series), unit G, Buildwas Formation (Text-fig. 2; Pl. 5, figs 4–6, 8–12). The first *C. bouniensis* is

coincident with the first *Belonechitina* sp. 3 (Pl. 2, fig. 9) and curved *C. proboscifera* (Pl. 7, figs 10–12; Pl. 8, figs 2, 7). The last *Belonechitina* sp. 1 *sensu* Mullins and Loydell was also found in sample 25/40 (Text-fig. 2).

*P. hughleyensis* sp. nov. and *C. bouniensis* were last recorded in sample 25/41, 350 mm above the base of the Wenlock Series (Text-fig. 2). The first specimens of *Conochitina* aff. *tuba* were observed in sample 25/42 (Text-fig. 2; Pl. 1, figs 7–12, 14; Pl. 8, figs 8–9, 14–15).

The first specimens of *Bursachitina* sp. A (Pl. 1, figs 15–16), *Bursachitina* sp. B (Pl. 1, figs 13, 17–18; Pl. 8, fig. 6) and *Conochitina praeoboscifera* Nestor (Pl. 6, figs 1–2; Pl. 8, figs 3–4, 10–11, 13) were recovered in sample 24/43 (Text-fig. 2).

### *The Salopochitina bella* Biozone

The base of this biozone is recognized by the first occurrence of *S. bella* in sample 25/44 (825 mm above the base of the Wenlock Series; Pl. 7, fig. 3), unit G, Buildwas Formation (Text-fig. 2). A questioned specimen of *Cingulochitina burdinalensis* Verniers was recovered from sample 25/44, although unequivocal *C. burdinalensis* occurs higher (sample 25/45; Pl. 7, figs 6–9). The first specimens of *Linochitina odiosa* Laufeld (Pl. 5, figs 15–17) and *Conochitina proboscifera* with no flexures on the vesicle flanks (Pl. 8, fig. 5) also occur in sample 25/44 (Text-fig. 2). The very distinctive *Eisenackitina varireticulata* Swire (Pl. 7, figs 1–2, 4–5) first occurs in sample 25/45 (Text-fig. 2).

## CORRELATION

Several studies have correlated the chitinozoan, graptolite and conodont biostratigraphical schemes (Loydell *et al.* 1998, 2003; Verniers 1999; Mullins 2000; Mullins and Loydell 2001, 2002). On the basis of these correlations, the first appearances of chitinozoans in the Hughley Brook section can be used to suggest a revision of the position of the base of the Wenlock Series within the graptolite biostratigraphical scheme to a level in the upper part of the *centrifugus* Biozone or lower part of the *murchisoni* Biozone (Text-fig. 3).

### *Sample 25/28, Llandovery Series*

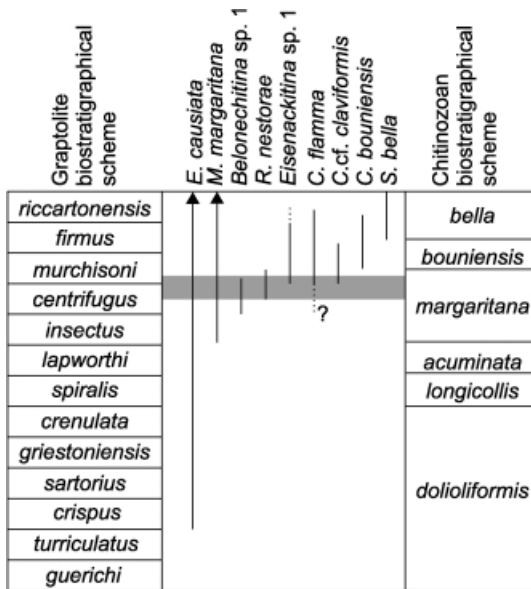
The first *E. causiata* was recovered from sample 25/28, at the base of the section studied (Text-fig. 2). The use of *E. causiata* as an upper Llandovery–Wenlock biostratigraphical marker was highlighted by Mullins and Loydell (2001); in their study of the Banwy River section (Wales), *E. causiata* appeared in strata assigned to possible *crenulata* or lower *spiralis* graptolite Biozone. It was noted, however, that there were no data for the older *griestoniensis* and unequivocal *crenulata* graptolite biozones (Mullins and Loydell 2001). In the Aizpute-41 core of Latvia, *E. causiata* first occurs in sample C97–104, at a level assigned to the *Pterospathodus eopennatus* ssp. nov. 1 conodont Biozone and *crispus* graptolite Biozone (Loydell *et al.* 2003; Text-fig. 3).

Thus, chitinozoan evidence suggests that the base of the Hughley Brook section sampled by Mabilard and Aldridge (1985) is probably no older than the *crispus* graptolite Biozone. This agrees with the graptolite evidence from the nearby Eaton Farm core, where *Monograptus griestoniensis* was recovered from c. 27 m below the top of the Purple Shales Formation (Cocks and Rickards 1969).

### *Sample 25/36, uppermost Llandovery Series*

Sample 25/36, 125 mm below the base of the Wenlock Series, contains the first *Eisenackitina* sp. 1 *sensu* Mullins and Loydell, *M. margaritana* and *R. nestorae* (Text-fig. 2).

In the Banwy River section, *Eisenackitina* sp. 1 was recovered from samples C + 6 to C + 17, with a questioned occurrence in sample C + 30 at levels assigned to the lower *murchisoni* to *firmus* and *riccartonensis* graptolite biozones respectively (Loydell and Cave 1996; Mullins and Loydell 2001). However, the stratigraphical range and occurrence of *Eisenackitina* sp. 1 elsewhere is poorly understood.



TEXT-FIG. 3. The globally known stratigraphical ranges of the biostratigraphically important taxa recovered from the uppermost Llandovery and lowermost Wenlock series of the Hughley Brook section. The correlation between the upper Llandovery and lower Wenlock graptolite and chitinozoan biostratigraphical schemes is also shown. Data from Laufeld (1974), Verniers and Rickards (1978), Verniers (1982), Swire (1990, 1993), Nestor (1993, 1994), Dufka *et al.* (1995), Loydell *et al.* (1998, 2003), Verniers (1999), Zalasiewicz and Williams (1999), Mullins (2000) and Mullins and Loydell (2001, 2002). The grey band constrains the probable position of the base of the Wenlock Series.

*Margachitina margaritana* is known to range from the *insectus* to *lundgreni* graptolite biozones (Nestor 1994; Dufka *et al.* 1995; Loydell *et al.* 1998; Verniers 1999; Mullins 2000; Mullins and Loydell 2001, 2002). In the Banwy River section, specimens with cone-shaped opercula, like those found in the Hughley Brook section, are known only from strata assigned to the *centrifugus* graptolite Biozone and higher (Mullins 2000; Mullins and Loydell 2001).

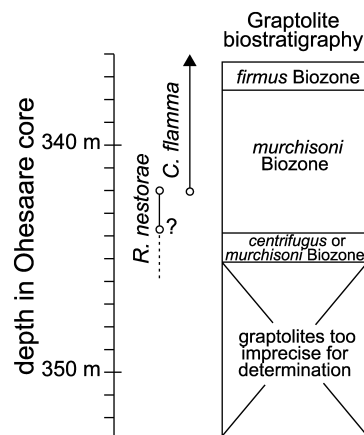
*R. nestorae* is the *nomen novum* of *Gotlandochitina magnifica* Nestor, a junior homonym of *Ramochitina magnifica* Lange according to Grahn (1995). The probable occurrence of *G. magnifica* in the Hughley Brook section was noted by Nestor (1993). *G. magnifica* is also known from the lowermost part of the Jaani Stage (referred to the lower part of the Wenlock Series) of the Ruhnu core (454–456 m, Tõlla Member), Häädemeeste core (210 m, Mustjala Member), Nagli core (612 m), Viki core (134.8–135 m, Mustjala Member) and Jaagarahu core (53.2 m) of Estonia and Latvia (Nestor 1982, 1993, 1994).

In the Ohesaare core, Estonia, *G. magnifica* was stated to occur in the Tõlla Member, between 342 and 346 m, but was illustrated as occurring only between 342 and *c.* 343.7 m, with the lower specimens being questionably assigned (Nestor 1994, p. 54, fig. 20/2). *Monograptus priodon* (Bronn) and *Retiolites geinitzianus* Barrande have been recovered at a depth of 346.22 m; these taxa occur in both the upper Llandovery and lower Wenlock series (Loydell *et al.* 1998). Graptolites recovered from between 345.11 m and 344.10 m in the Ohesaare core belong to either the *centrifugus* or *murchisoni* biozone, and unequivocal *murchisoni* Biozone occurs at a depth of 343.94–343.95 m (Loydell *et al.* 1998; see Text-fig. 4). *G. magnifica* was last recorded in the Ohesaare core below the base of the *firmus* graptolite Biozone, which was identified at 337.60 m (Nestor 1994; Loydell *et al.* 1998; Text-fig. 4).

A specimen referred to *Ramochitina* sp. 1 from sample C-7 (= middle *centrifugus* Biozone) of the Banwy River section is probably an example of *R. nestorae* (see Mullins and Loydell 2001, pl. 11, fig. 11). The specimen has no intact processes remaining, but it does possess vertically arranged scars around the basal margin that match the characteristic process arrangement of *R. nestorae*. Thus, the range of *R. nestorae* most probably corresponds with the middle *centrifugus* to lower *murchisoni* graptolite biozones (Text-fig. 3).

Grahn (1995) described *R. nestorae* from Närböringen 1, Gotland, where it occurs above the first *M. margaritana*, at a level assigned to just below the base of the Wenlock Series (*c.* 327.8–328.5 m; Grahn 1995, fig. 3). This age determination was based on a personal communication by the late Hermann Jaeger and attempts to locate the relevant graptolite material have failed (Mullins and Loydell 2001, p. 771).

TEXT-FIG. 4. Correlation of the occurrences of *Ramochitina nestorae* and *Conochitina flamma* with the graptolite biostratigraphical scheme in the Ohesaare core, Estonia. Dashed line indicates the possible occurrence of *R. nestorae* at a depth of 346 m (see text for explanation). Data from Nestor (1994) and Loydell *et al.* (1998).



In Rosendalborringen 1, Gotland, *R. nestorae* was reported from *c.* 115.5–155 m and first appears above a level assigned to the *griestoniensis* graptolite Biozone within an interval assigned to questioned *spiralis* Biozone. However, the fossil content of this core is undescribed and it is, therefore, unclear how these determinations were made (Grahn 1995, p. 58; Mullins and Loydell 2001, p. 771).

#### Sample 25/37, uppermost Llandovery Series

Sample 25/37, 31 mm below the base of the Wenlock Series, contains the first *Belonechitina* sp. 1 *sensu* Mullins and Loydell and *Conochitina flamma*.

*Belonechitina* sp. 1 was recovered from samples C-16 to C+6.5, *centrifugus*–lower *murchisoni* biozones, of the Banwy River section (Loydell and Cave 1996; Mullins and Loydell 2001; Text-fig. 3). *Belonechitina* sp. 1 may also occur in the Mehaigne area of Belgium in sample CD-1A/33, at a level below strata assigned to the *centrifugus* or *murchisoni* biozones (Verniers and Rickards 1978; Mullins and Loydell 2001).

*Conochitina flamma* is restricted to unit a and the marly south-west facies of the Högkling Formation, Wenlock Series, of Gotland (Laufeld 1974). The base of the Högkling Formation coincides with Datum 8 of the Ireviken Extinction Event, which has been correlated with the base of the Upper *Kockelella ranuliformis* conodont Biozone (Jeppsson 1979, 1997; Jeppsson and Männik 1993; Jeppsson *et al.* 1994). In the Ohesaare core, the last *Distomodus staurogathoides* (Walliser), which disappears just below the base of the Upper *K. ranuliformis* Zone, was recovered close to the boundary between the *firmus* and *riccartonensis* graptolite biozones (337–337.2 m; Loydell *et al.* 1998). The graptolite *Monograptus rickartonensis* Lapworth has also been recorded from probably the lower part of unit b of the Högkling Formation (Bassett and Cocks 1974; Jeppsson 1979; Jeppsson *et al.* 1994).

In the Banwy River section, *C. flamma* is known from sample C+13.5, in strata assigned to the upper *murchisoni* graptolite Biozone (Loydell and Cave 1996; Mullins and Loydell 2001). *C. flamma* also occurs in Formation MB4 of the Mehaigne area, Belgium, in strata assigned to the *centrifugus* or *murchisoni* or *riccartonensis* biozones (Verniers and Rickards 1978; Verniers 1982).

Those specimens assigned to *C. cf. flamma* from the Ohesaare core (at a depth of 342.2 m) by Nestor (1994, pl. 13, figs 7–8) are confirmed as this species as they possess angular basal margins and roughened bases with prominent mucrons. *C. flamma* therefore occurs from the lower part of the *murchisoni* Biozone to the *riccartonensis* Biozone in the Ohesaare core (Loydell *et al.* 1998; see also Text-figs 3–4). Specimens of *C. cf. flamma* were also reported from other Estonian cores by Nestor (1994), but no specimens were illustrated and, therefore, no further comment is possible.

Specimens lacking the characteristic ridge-like carina of *C. flamma* and having a rounded basal margin, like that of *Conochitina acuminata* Eisenack, have previously been included within this species. This has

led to some references citing *C. flamma* as occurring in the uppermost Llandovery Series (see Mullins and Loydell 2001, p. 776).

Thus *C. flamma* has a stratigraphical range that corresponds to possibly the *centrifugus* graptolite Biozone, or more probably, the lower *murchisoni* to lower *riccartonensis* graptolite biozones (Text-fig. 3).

#### *Sample 25/38 lowermost Wenlock Series*

The first sample of the Buildwas Formation, 67 mm above the base of the Wenlock Series, contains *Conochitina* cf. *claviformis sensu* Mullins and Loydell, 2001. In the Banwy River section, the first *C. cf. claviformis* were recorded in sample C + 6.5, in strata assigned to the lower *murchisoni* graptolite Biozone (Loydell and Cave 1996; Mullins and Loydell 2001). However, the distribution of *C. cf. claviformis* elsewhere is still poorly known.

#### *Sample 25/40, lower Wenlock Series*

The first occurrence of *C. bouniensis* in sample 25/40, 256 mm above the base of the Wenlock Series, suggests that this sample is most probably within the upper part of the *murchisoni* graptolite Biozone.

In the Banwy River section, the first *C. bouniensis* were recorded in sample C + 14.5, in strata assigned to the upper *murchisoni* graptolite Biozone (Loydell and Cave 1996; Mullins and Loydell 2001; Text-fig. 3). *C. bouniensis* is also known from the Builth Wells area, Wales, where it was recorded from equivocal *murchisoni* Biozone strata (Verniers 1999; Zalasiewicz and Williams 1999). In the Mehaigne area of Belgium, *C. bouniensis* occur in sample CD-20/224 of Formation MB4, which correlates with a level higher than known *centrifugus* or *murchisoni* graptolite Biozone (Verniers 1982, 1999; Verniers and Rickards 1978).

*C. bouniensis* was also recognized in sample C97–58 of the Aizpute-41 core of Latvia, at a level assigned to the upper part of the *murchisoni* graptolite Biozone, in the interval between the last occurrence of *Cyrtograptus murchisoni* (Carruthers) and the first *Monograptus firmus* (Bouček) (Loydell *et al.* 2003).

#### *Sample 25/44, lower Wenlock Series*

Sample 25/44, 825 mm above the base of the Wenlock Series, contains the first *S. bella* and this suggests that this level may be within the *firmus* graptolite Biozone. In the Banwy River section, *S. bella* first occurs in sample C + 17, in strata assigned to the *firmus* graptolite Biozone (Loydell and Cave 1996; Mullins and Loydell 2001; Text-fig. 3). *S. bella* is also known from the Builth Wells area, where specimens were recovered from sample K27 of the River Ithon section (Verniers 1999). Sample K27 contains *Monograptus* aff. *riccartonensis*, although true *M. riccartonensis* is known from the higher sample K28 (Zalasiewicz and Williams 1999). In the River Ithon East section, the youngest specimens of *S. bella* occur in sample K34c (upper *riccartonensis* Biozone) and the higher sample K35, which is unassigned to any graptolite biozone (Verniers 1999; Zalasiewicz and Williams 1999; Text-fig. 3).

*S. bella* is also known from the Lower Hill Farm borehole (Hughley, Shropshire, close to Hughley Brook), where specimens occur in the Buildwas Formation at a depth of 228.68–236.07 m (Swire 1990, 1993). Fragments of dendroids, *Monoclimacis* sp. and an indeterminate monograptid are known from this interval, but they do not allow correlation with the graptolite biostratigraphical scheme (see Bassett *et al.* 1975; Mullins and Loydell 2001). *S. bella* has also been recovered from the Woolhope Limestone of the Eastnor Park borehole, at a depth of 35.6–39.6 m (Swire 1990).



## BIOSTRATIGRAPHICAL NOTES ON OTHER TAXA

*Ancyrochitina ansarviensis*

At Hughley Brook, the first *Ancyrochitina ansarviensis* occur in sample 25/38, 67 mm above the base of the Wenlock Series (Text-fig. 2). *A. ansarviensis* is known from the upper part of unit c and the south-west marly facies of the Höglint Formation, Gotland (Laufeld 1974). The appearance of the biostratigraphically useful conodont *Ozarkodina sagitta rhenana* (Walliser) corresponds with the middle part of unit c of the Höglint Formation, and the first *A. ansarviensis* are situated above the occurrence of *M. riccartonensis* in unit b (Bassett and Cocks 1974; Jeppsson *et al.* 1994).

*A. ansarviensis* has also been recovered from a depth of 310.5 m in the Ohesaare core, Estonia, at a level just above the occurrence of *Monograptus flexilis* Elles, indicative of the *flexilis* graptolite Biozone (Nestor 1994; Loydell *et al.* 1998). Elsewhere in Estonia, Nestor (1993, 1994) recorded *A. ansarviensis* in the Ruhnu core (455–458 m, Tõlla Member, Jaani Stage), Viki core (144–149 m, Velise Formation, Adavere Stage), Pulli 2 core (34–36 m, Velise Formation, Adavere Stage), Kingissepa core (127.5 m, Paramaja Member, Jaani Stage), Kinhu core (179.7 m, Ninase Member, Jaani Stage), questionably in the Kirikuküla core (14–17 m, Velise Formation, Adavere Stage) and Jaagarahu core (45.5–59.7 m, Velise Formation to Mustjala Member, Adavere–Jaani stages). Thus, *A. ansarviensis* in Estonia has a stratigraphical range of upper Llandovery to lower Wenlock series.

Laufeld (1974) considered *A. ansarviensis* to be an excellent index fossil, as it has a short stratigraphical range on Gotland. However, with the recognition of similar forms in the upper part of the Llandovery Series in Estonia this must be questioned. Further work is required to determine if there are any discernible differences between the populations in the upper part of the Llandovery Series and the lowermost Wenlock Series.

*Linochitina odiosa*

At Hughley Brook, the first *Linochitina odiosa* were recovered from sample 25/44, 825 mm above the base of the Wenlock Series. *L. odiosa* has also been recovered from the Wenlock Series of Gotland in the Conchidium tenuistriatum Beds, the north-western part of the Slite Marl through to the Slite Siltstone and the Mulde Formation, although the latter specimens are rare and atypical (Laufeld 1974). These occurrences are stratigraphically higher than those of the Hughley Brook section. *L. odiosa* has also been recovered from the upper part of the Tõlla Beds, Jaani Stage (Wenlock Series), of the Ventspils core (depth, 767 m; Nestor 1994).

*Eisenackitina varireticulata*

The first *Eisenackitina varireticulata* at Hughley Brook occur in sample 25/45, 1017 mm above the base of the Wenlock Series. The type *E. varireticulata* were recovered from the lower part of the Buildwas Formation of the Lower Hill Farm borehole at a depth of 236.07 m, at a level coincident with the first *S. bella* (Swire 1990). Graptolites from this level do not allow to recognition of any graptolite biozone (see above). A re-examination of material from the Banwy River section, Wales (see Mullins and Loydell 2001), has identified *E. varireticulata* in sample C + 30, *riccartonensis* graptolite Biozone. The distribution of *E. varireticulata* elsewhere is still poorly known, but it may become an important and easily recognized biostratigraphical marker.

## SYSTEMATIC PALAEOLOGY

The stratigraphical distribution of the taxa described in the systematics section is shown in Text-figure 2. All figured material is deposited in the collection of the British Geological Survey, Keyworth, Nottingham, NG12 5GG, United Kingdom (prefix MPK). The measurements referred to in this section are: L, vesicle length; lb, chamber length; ln, neck length; D, maximum diameter; da, diameter of the aperture and app, appendage length. All measurements are based on flattened specimens and no conversion factor was used.

Group CHITINOZOA Eisenack, 1931  
 Order PERCULATIFERA Eisenack, 1972  
 Family DESMOCHITINIDAE Eisenack, 1931, emend. Paris, 1981  
 Subfamily DESMOCHITININAE Eisenack, 1931 emend. Paris, 1981  
 Genus BURSACHITINA Taugourdeau, 1966 restrict. Paris, 1981

*Type species. Desmochitina bursa* Taugourdeau and de Jekhowsky, 1960 (holotype lost; neotype: Taugourdeau 1967).

*Bursachitina* sp. A

Plate 1, figures 15–16

*Description.* Vesicle conical, with an indistinct rounded basal margin. The base tapers to a prominent, membraneous mucron. The flanks are gently convex and taper to the aperture. No flexure or neck is present.

*Dimensions.* L, 230  $\mu\text{m}$ ; D, 114  $\mu\text{m}$ ; da, 86  $\mu\text{m}$  (1 specimen).

*Remarks.* A specimen assigned to *Bursachitina nestorae* by Mullins and Loydell (2001, pl. 1, figs 9, 13 only) is similar to *Bursachitina* sp. A in possessing a membraneous mucron, tapering base and indistinct basal margin. It is, however, of smaller dimensions (L, 187.5  $\mu\text{m}$ ; D, 90  $\mu\text{m}$ ; da, 45  $\mu\text{m}$ ).

*Bursachitina* sp. B

Plate 1, figures 13, 17–18; Plate 8, figure 6

*Description.* Vesicle conical, with a rounded base and indistinct basal margin. No basal scar or mucron is visible on the base. The flanks are gently convex and the maximum vesicle width is situated c. 25–50 per cent above the base. No flexure or neck is present.

*Dimensions.* L, 272.5–349.1  $\mu\text{m}$ ; D, 110–115.1  $\mu\text{m}$ ; da, 67.1–75  $\mu\text{m}$  (3 specimens).

*Remarks.* *Conochitina* aff. *tuba* is similar, but differs in possessing a large, well-developed basal mucron comprising a double circular structure. *Bursachitina* sp. B is very similar to two individuals assigned to *Bursachitina nestorae* by Mullins and Loydell (2001, pl. 1, fig. 10 only), which also have smooth, rounded bases and gently convex flanks. However, these latter specimens are much smaller than *Bursachitina* sp. B (L, 143  $\mu\text{m}$ ; D, 75  $\mu\text{m}$ ).

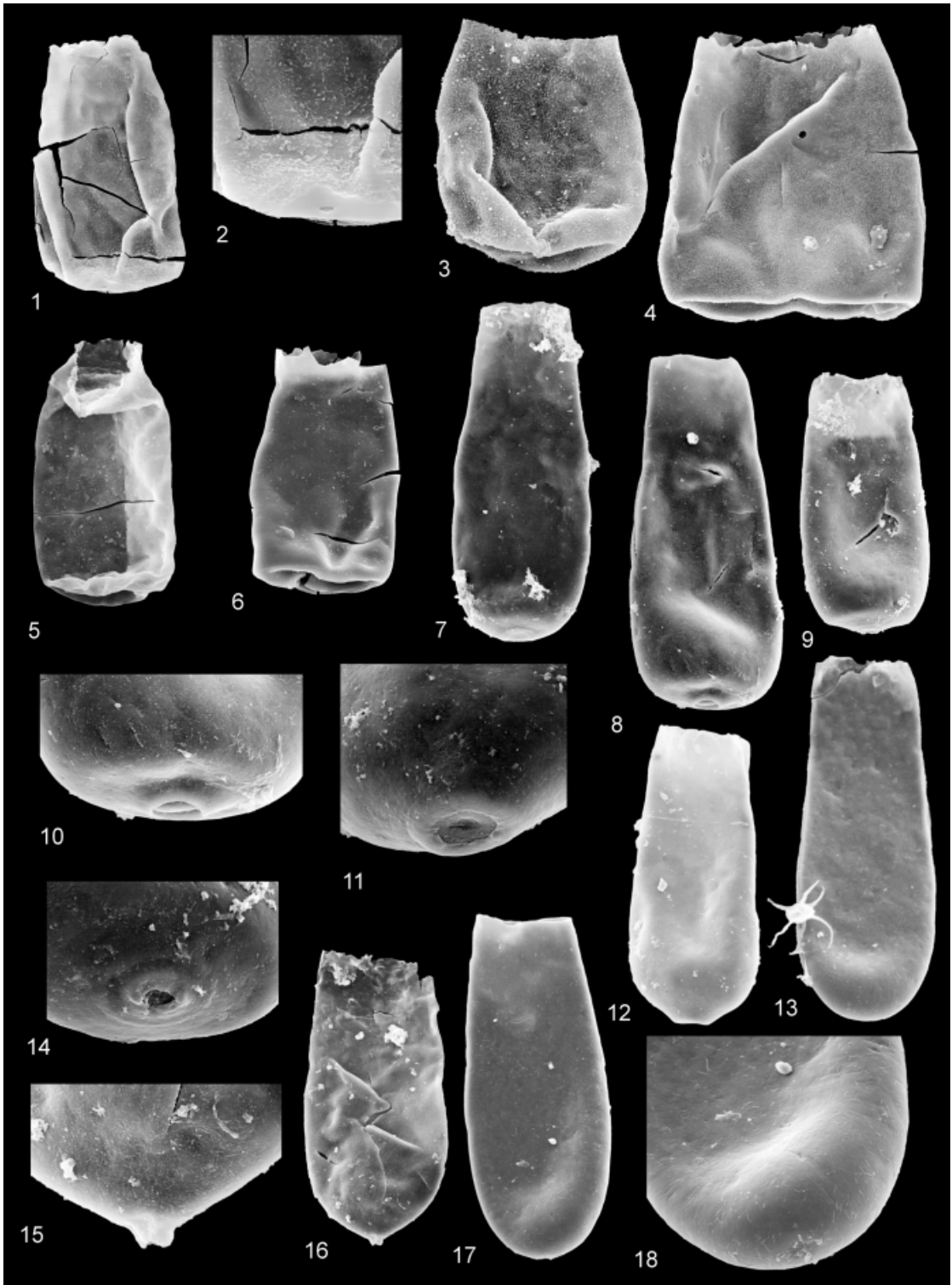
Subfamily PTEROCHITININAE Paris, 1981

Genus PTEROCHITINA Eisenack, 1955

*Type species. Bion perivelatum* Eisenack, 1937 (holotype lost, neotype: Eisenack 1955).

EXPLANATION OF PLATE 1

Figs 1–4. *Eisenackitina causiata* Verniers. 1, MPK12672; 25/28, stub HB1-1;  $\times 300$ . 2, close-up of the ornament of specimen in 1;  $\times 800$ . 3, MPK12673; 25/36, HB1-7;  $\times 300$ . 4, MPK12674; 25/38, HB1-13;  $\times 300$ .  
 Figs 5–6. *Bursachitina conica* (Taugourdeau and de Jekhowsky). 5, MPK12675; 25/37, HB1-10;  $\times 300$ . 6, MPK12676; 25/39, HB2-4;  $\times 300$ .  
 Figs 7–12, 14. *Conochitina* aff. *tuba* Eisenack. 7, MPK12677; 25/43, HB2-13;  $\times 200$ . 8, MPK12678; 25/43, HB2-13;  $\times 200$ . 9, MPK12679; 25/43, HB2-14;  $\times 200$ . 10, close-up of the mucron of specimen in 8;  $\times 400$ . 11, close-up of the mucron of specimen in 12;  $\times 600$ . 12, MPK12680; 25/43, HB2-14;  $\times 200$ . 14, close-up of the double circular mucron on the base of specimen in 9;  $\times 600$ .  
 Figs 13, 17–18. *Bursachitina* sp. B. 13, MPK12681; 25/44, HB3-1;  $\times 200$ . 17, MPK12682; 25/45, HB3-4;  $\times 200$ . 18, close-up of the base of specimen in 17;  $\times 400$ .  
 Figs 15–16. *Bursachitina* sp. A. 15, close-up of the thin, membraneous mucron of specimen in 16;  $\times 600$ . 16, MPK12683; 25/43, HB2-14;  $\times 200$ .



MULLINS and ALDRIDGE, chitinozoans

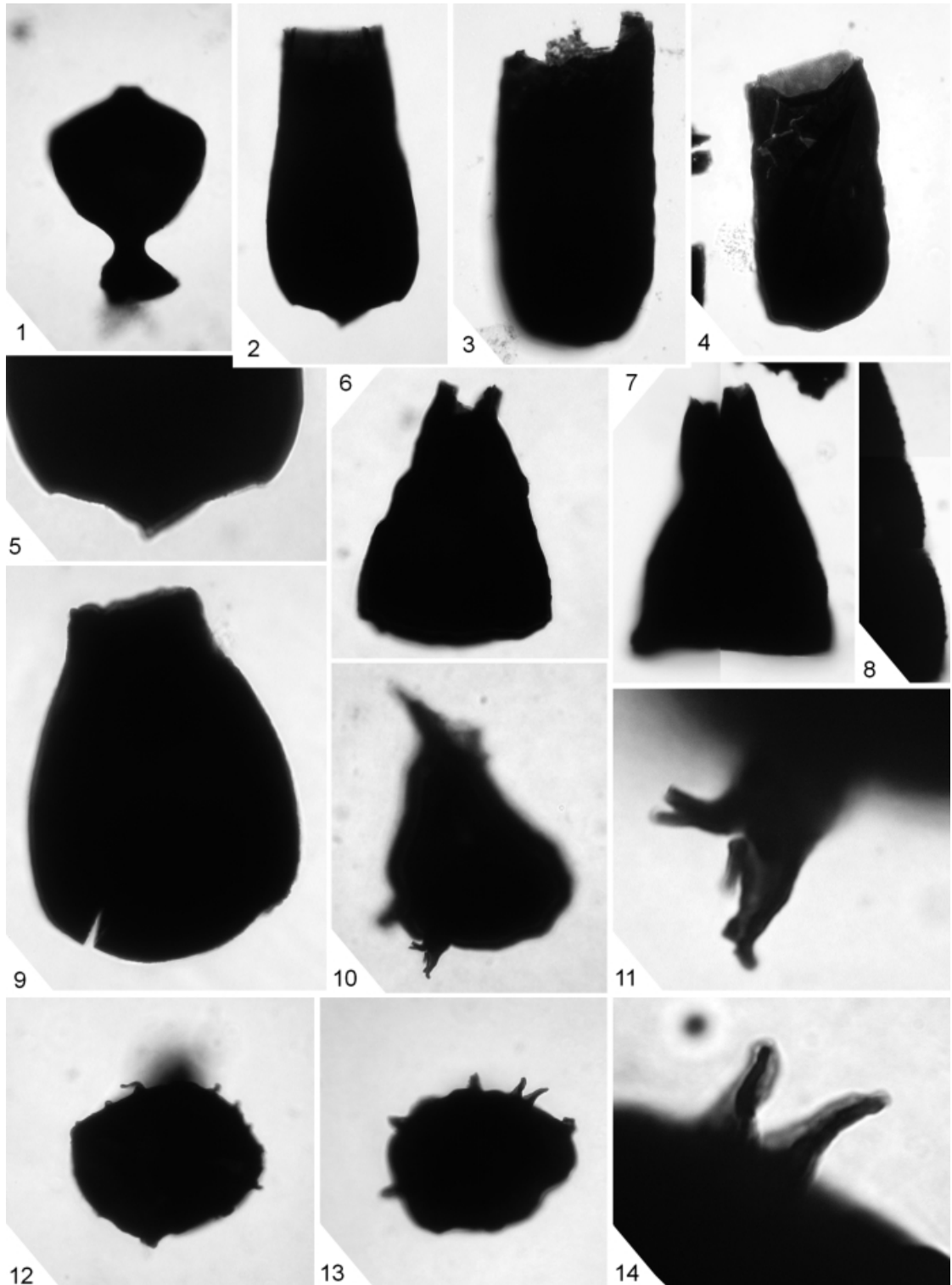
*Pterochitina hughleyensis* sp. nov. Mullins

Plate 4, figures 9–12, 14–15; Plate 5, figures 1–2

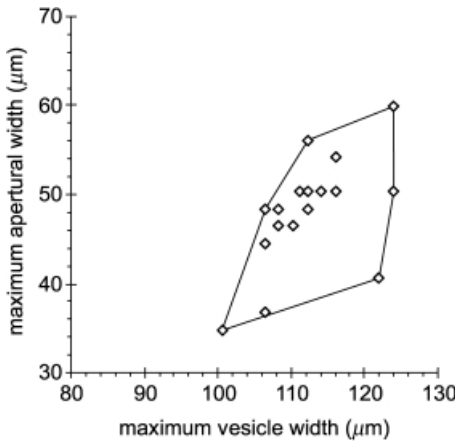
*Derivation of name.* After the village of Hughley, Shropshire.*Holotype.* MPK12714, Plate 4, figure 10, sample 25/38, lowermost Wenlock Series, Hughley Brook, Hughley, Shropshire.*Diagnosis.* In lateral view the vesicle tapers antiaperturally from a maximum diameter near the aperture to an operculum, which is usually flat, although it may rarely be cone-shaped. The vesicle is circular or elliptical in apertural view. At the point of maximum diameter a carina is present that encircles the vesicle to produce a smooth or knobby appearance in apertural view. Under transmitted light the carina appears solid and thinner-walled than the vesicle. With a scanning electron microscope the carina may show a pattern of ridges that converge towards the operculum. No peduncle or neck is present.*Dimensions.* D, 100.6–123.8  $\mu\text{m}$ ; da, 34.8–60  $\mu\text{m}$  (20 specimens; Text-fig. 5).*Remarks.* The first occurrence of *P. hughleyensis* in sample 25/38, 67 mm above the base of the Wenlock Series, raises the possibility that this taxon may be of value in recognizing the base of the Wenlock Series elsewhere. That *P. hughleyensis* has not been recognized in other sections may suggest it is of limited geographical distribution, or it may simply reflect the typical apertural compression displayed by the recovered vesicles. This gives the specimens an appearance similar to the prasinophytes *Leiosphaeridia* Eisenack and *Tasmanites* Newton when using transmitted light microscopy. The low thermal alteration of the specimens in the Hughley Brook section allow the carina and apertural opening to be observed, but with higher thermal maturation this would probably be impossible and specimens would be misidentified.The presence of a carina at the point of maximum vesicle diameter distinguishes *P. hughleyensis* from *Calpichitina densa* (Eisenack). *Margachitina banwyensis* Mullins and *M. margaritana* have vesicles that taper to a peduncle; the vesicle of *P. hughleyensis* tapers to an operculum. Specimens assigned to *Pterochitina makroptera* Eisenack by Nestor (1994) are similar to *P. hughleyensis* in possessing a carina near the aperture. However, Nestor (1994, p. 20) stated that the vesicles of her specimens were hemispherical, with a convex base, and that chain forming was unknown. The vesicles of *P. hughleyensis* taper to an operculum (i.e. they are not hemispherical) and chain forming has been observed (Pl. 4, figs 14–15; Pl. 5, fig. 1). The specimens of *P. makroptera sensu* Nestor, 1994 are

## EXPLANATION OF PLATE 2

Fig. 1. *Margachitina margaritana* (Eisenack). Specimen with a cone-shaped operculum; MPK12684; slide TS16/14, F41; 25/36;  $\times 300$ .Figs 2, 5. *Conochitina flamma* Laufeld. 2, MPK12685; slide TS17/2, B23/2; 25/37;  $\times 300$ . 5, close-up showing the sharp basal margin;  $\times 600$ .Figs 3–4. *Eisenackitina* sp. 1 *sensu* Mullins and Loydell. 3, MPK12686; slide TS16/14, M37/4; 25/36;  $\times 300$ . 4, MPK12687; slide TS21/2, Q35/2; 25/41;  $\times 300$ .Fig. 6. *Belonechitina* sp. 1 *sensu* Mullins and Loydell. MPK12688; slide TS17/2, L33; 25/37;  $\times 300$ .Figs 7–8. *Belonechitina* sp. 2 *sensu* Mullins and Loydell. 7, MPK12689; slide TS19/1, P45/3; 25/39; composite of two images;  $\times 300$ . 8, close-up of the ornament on the right flank of specimen in 7; composite of three images;  $\times 700$ .Fig. 9. *Belonechitina* sp. 3. MPK12690; slide TS20/8, S30; 25/40;  $\times 300$ .Figs 10–11, 13–14. *Ancyrochitina digitata* sp. nov. 10, MPK12691; slide TS18/2, T49; 25/38;  $\times 400$ . 11, close-up of the process of specimen in 10;  $\times 2000$ . 13, antiapertural view showing the distribution of the processes; MPK12692; slide TS38/1, R54/2; 25/46;  $\times 400$ . 14, close-up of the process of specimen in 13 displaying the central rod-like thickenings and thinner membranes;  $\times 2000$ .Fig. 12. *Ancyrochitina ansarviensis* Laufeld. Antiapertural view showing the distribution of the processes. MPK12693; slide TS34/1, V30; 25/42;  $\times 400$ .



MULLINS and ALDRIDGE, chitinozoans



TEXT-FIG. 5. Scatter plot showing the maximum vesicle width (D) and maximum apertural width (da) in specimens of *Pterochitina hughleyensis* sp. nov. All measurements were taken in apertural view from specimens in sample 25/38.

also larger (D, 200  $\mu\text{m}$ ). *Pterochitina deichaii* Taugourdeau has a thin membrane which encloses each vesicle.

Order PROSOMATIFERA Eisenack, 1972  
 Family CONOCHITINIDAE Eisenack, 1931 emend. Paris, 1981  
 Subfamily CONOCHITININAE Paris, 1981  
 Genus CONOCHITINA Eisenack, 1931 emend. Paris *et al.*, 1999

*Type species.* *Conochitina claviformis* Eisenack, 1931 (holotype lost, neotype: Eisenack 1968).

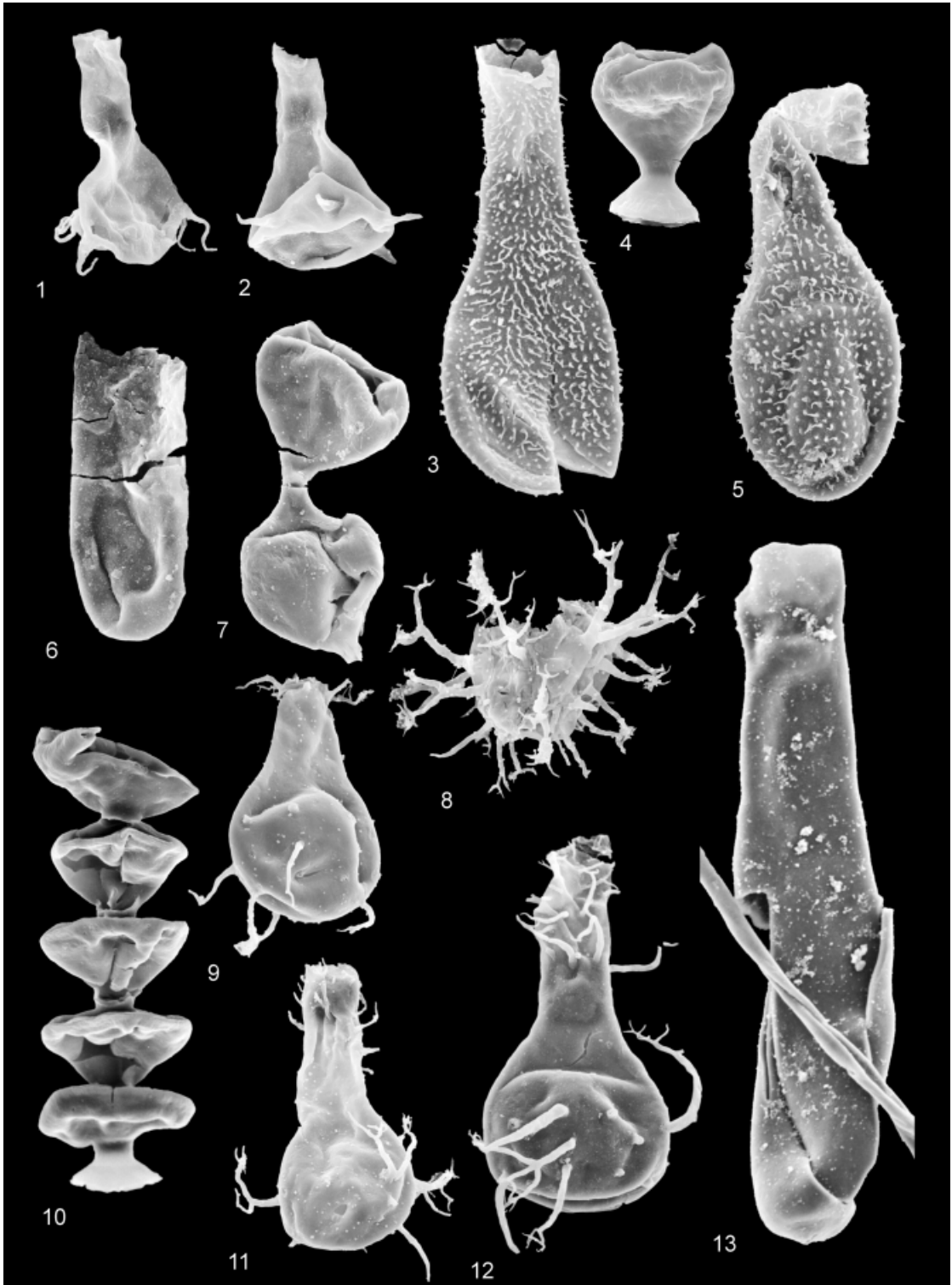
*Conochitina proboscifera* Eisenack, 1937

Plate 3, figure 13; Plate 6, figures 3–14; Plate 7, figures 10–12;  
 Plate 8, figures 1–2, 5, 7, 12

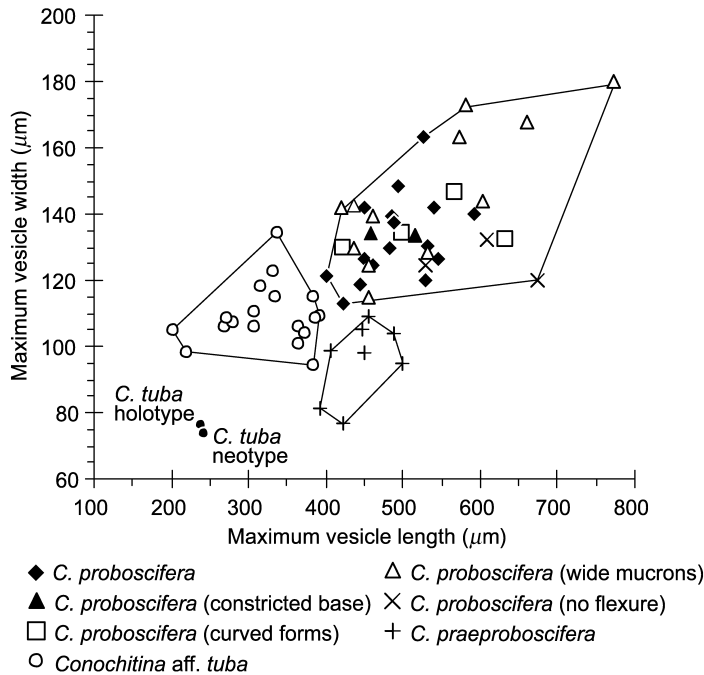
*Remarks.* Specimens of *C. proboscifera* are characteristically claviform, with a prominent, membraneous mucron and a slight flexure in the vesicle flanks (e.g. Pl. 3, fig. 13; Pl. 6, figs 5–6, 8–10; Pl. 8, fig. 1). The specimens of *C. proboscifera* from the Hughley Brook section, however, sometimes show other morphological features that may prove to be of future taxonomic importance.

EXPLANATION OF PLATE 3

- Figs 1–2. *Ancyrochitina primitiva* Eisenack. 1, MPK12694; 25/37, HB1-10;  $\times 300$ . 2, MPK12695; 25/45, HB3-3;  $\times 300$ .  
 Figs 3, 5. *Angochitina longicollis* (Eisenack). 3, MPK12696; 25/36, HB1-7;  $\times 300$ . 5, MPK12697; 25/37, HB1-11;  $\times 300$ .  
 Figs 4, 7, 10. *Margachitina margaritana* (Eisenack). 4, specimen with a prominent cone-shaped operculum; MPK12698; 25/38, HB1-13;  $\times 300$ . 7, MPK12699; 25/36, HB1-9;  $\times 300$ . 10, MPK12700; 25/37, HB1-11;  $\times 300$ .  
 Fig. 6. *Eisenackitina* sp. 1 *sensu* Mullins and Loydell; MPK12701; 25/37, HB1-11;  $\times 300$ .  
 Figs 8–9, 11–12. *Ramochitina nestorae* Grahn. 8, broken example showing the processes on the chamber; MPK12702; 25/36, HB1-9;  $\times 400$ . 9, MPK12703; 25/36, HB1-8;  $\times 300$ . 11, MPK12704; 25/36, HB1-7;  $\times 300$ . 12, MPK12705; 25/36, HB1-9;  $\times 300$ .  
 Fig. 13. *Conochitina proboscifera* Eisenack. Example with a fibre lying across the vesicle; MPK12706; 25/36, HB1-9;  $\times 200$ .



MULLINS and ALDRIDGE, chitinozoans



TEXT-FIG. 6. Scatter plot of the vesicle length (L) and maximum vesicle width (D) of the different morphotypes of *Conochitina proboscifera*, *Conochitina* aff. *tuba* and *C. praeproboscifera*. Measurements taken from specimens in samples 25/36–25/46.

A prominent constriction just above the basal margin is present in some specimens (Pl. 6, figs 8, 14) in samples 25/38–25/46, in the lowermost Wenlock Series [Text-fig. 2 as *C. proboscifera* (constricted base)]. Other specimens in samples 25/40–25/46 possess vesicles that are distinctly curved or distorted [Pl. 7, figs 10–12; Pl. 8, figs 2, 7; Text-fig. 2 as *C. proboscifera* (curved forms)]. Similar curved specimens have been described from Gotland (Laufeld 1974). Both the constricted and curved forms have the membranous mucron and the size range of typical *C. proboscifera* (Text-fig. 6).

A few examples from samples 25/44 and 25/45 lack the club-shaped, claviform vesicle and flexures of typical *C. proboscifera*, although the dimensions are comparable [Pl. 8, fig. 5; Text-fig. 2 as *C. proboscifera* (no flexure); Text-fig. 6]. *C. proboscifera* forma *gracilis* Laufeld also lacks flexures

#### EXPLANATION OF PLATE 4

Figs 1, 4–5. *Ancyrochitina* sp. 1, specimen with tubular processes; MPK12707; 25/37, HB1-12; ×300. 4, close-up of the basal margin of specimen in 5 showing the large process scars; ×500. 5, specimen with tapering flanks and lacking a distinct chamber-neck interface; MPK12708; 25/38, HB2-2; ×300.

Figs 2–3. *Conochitina flamma* Laufeld. 2, MPK12709; 25/38, HB1-14; ×300. 3, close-up of the base and mucron of specimen in 2, showing the typical sharp basal margin and roughened base; ×800.

Figs 6–7. *Conochitina* cf. *claviformis* Eisenack *sensu* Mullins and Loydell. 6, MPK12710; 25/40, HB2-8; ×200. 7, MPK12711; 25/45, HB3-4; ×300.

Figs 8, 13. *Ancyrochitina digitata* sp. nov. 8, holotype; MPK12712; 25/45, HB3-10; ×300. 13, close-up of the ornamented vesicle and processes of specimen in 8; ×600.

Figs 9–12, 14–15. *Pterochitina hughleyensis* sp. nov. 9, example with a flat operculum; MPK12713; 25/38, HB1-14; ×300. 10, holotype showing a cone-shaped operculum; MPK12714, 25/38, HB2-1; ×300. 11, MPK12715; 25/38, HB1-14; ×300. 12, chain of two vesicles; MPK12716; 25/38, HB1-14; ×300. 14, chain of two vesicles with a circular opening produced by the removal of the operculum; MPK12717; 25/38, HB2-1; ×300. 15, close-up of the carina of specimen in 14; ×800.





MULLINS and ALDRIDGE, chitinozoans

along the length of the vesicle, but is larger than the specimens recovered from Hughley Brook and has a vesicle length:width ratio of 1:9–10 (Laufeld 1974).

*C. proboscifera* with broader-based and flatter mucrons than typical were recovered from the base of the Wenlock Series in samples 25/38–25/46 [Text-fig. 2; Pl. 6, figs 3–4, 11–13; as *C. proboscifera* (wide mucrons)]. These forms are commonly split at the base (e.g. Pl. 6, fig. 7) and some specimens are larger than typical *C. proboscifera* (Text-fig. 6). A specimen assigned to *C. aff. proboscifera sensu* Nestor by Loydell *et al.* (2002, fig. 5E only) appears identical to the forms recovered from Hughley Brook. This specimen, from the Racine Dolomite (upper Sheinwoodian Stage, Wenlock Series) of Illinois, USA, suggests that *C. proboscifera* with broad mucrons may occur throughout the lower part of the Wenlock Series. *C. aff. proboscifera sensu* Nestor is differentiated from *C. proboscifera* by its considerably thinner vesicle wall (Nestor 1994, p. 36).

*Conochitina praeproboscifera* Nestor differs in possessing a thickened ridge and central indentation, not the prominent, membranous mucron of typical *C. proboscifera* (compare Pl. 8, fig. 7 with Pl. 8, fig. 10). *C. praeproboscifera* is also narrower (Text-fig. 6) and has generally straight vesicle flanks that taper to the aperture.

*Conochitina aff. tuba* Eisenack, 1932

Plate 1, figures 7–12, 14; Plate 8, figs 8–9, 14–15

*Description.* Vesicle conical, smooth, with a flat or convex base. In the centre of the base a mucron occurs. The mucron may be a thin membrane or thickened ridge surrounding a central pit. This structure is commonly surrounded by a further thickened ridge to produce a double circular structure. The basal margin is rounded to subangular and the vesicle flanks are slightly convex or straight and taper to the aperture. The maximum diameter is at, or near, the basal margin. No flexure or neck is present.

*Dimensions.* L, 205–391.3  $\mu\text{m}$ ; D, 94–134.3  $\mu\text{m}$ ; da, 49.9–105.5  $\mu\text{m}$  (18 specimens; Text-fig. 6).

*Remarks.* The vesicle width of *C. aff. tuba* is larger than the holotype and neotype of *C. tuba* from the Slite Group of Gotland (Eisenack 1931; pl. 12, fig. 8; D, 74.8  $\mu\text{m}$  and Eisenack 1962, pl. 14, fig. 13; D, 74.1  $\mu\text{m}$  respectively; Text-fig. 6). The vesicle lengths of the *C. tuba* population described by Eisenack (1962) are also generally shorter than those of *C. aff. tuba* (L, 143–284  $\mu\text{m}$  vs. L, 205–391.3  $\mu\text{m}$ ). However, the mucrons of *C. tuba* illustrated by scanning electron micrographs are identical to those of *C. aff. tuba* (compare Laufeld 1974, fig. 36A with Pl. 1, fig. 14). The basal structures of *C. aff. tuba* are also similar to

EXPLANATION OF PLATE 5

Figs 1–2. *Pterochitina hughleyensis* sp. nov. 1, a chain of three vesicles in near-lateral view showing the antiapertural taper from the carina; MPK12718; 25/38, HB2-1;  $\times 300$ . 2, example in near-lateral view showing the antiapertural taper of the vesicle from the carina and a cone-shaped operculum; MPK12719; 25/38, HB2-2;  $\times 300$ .

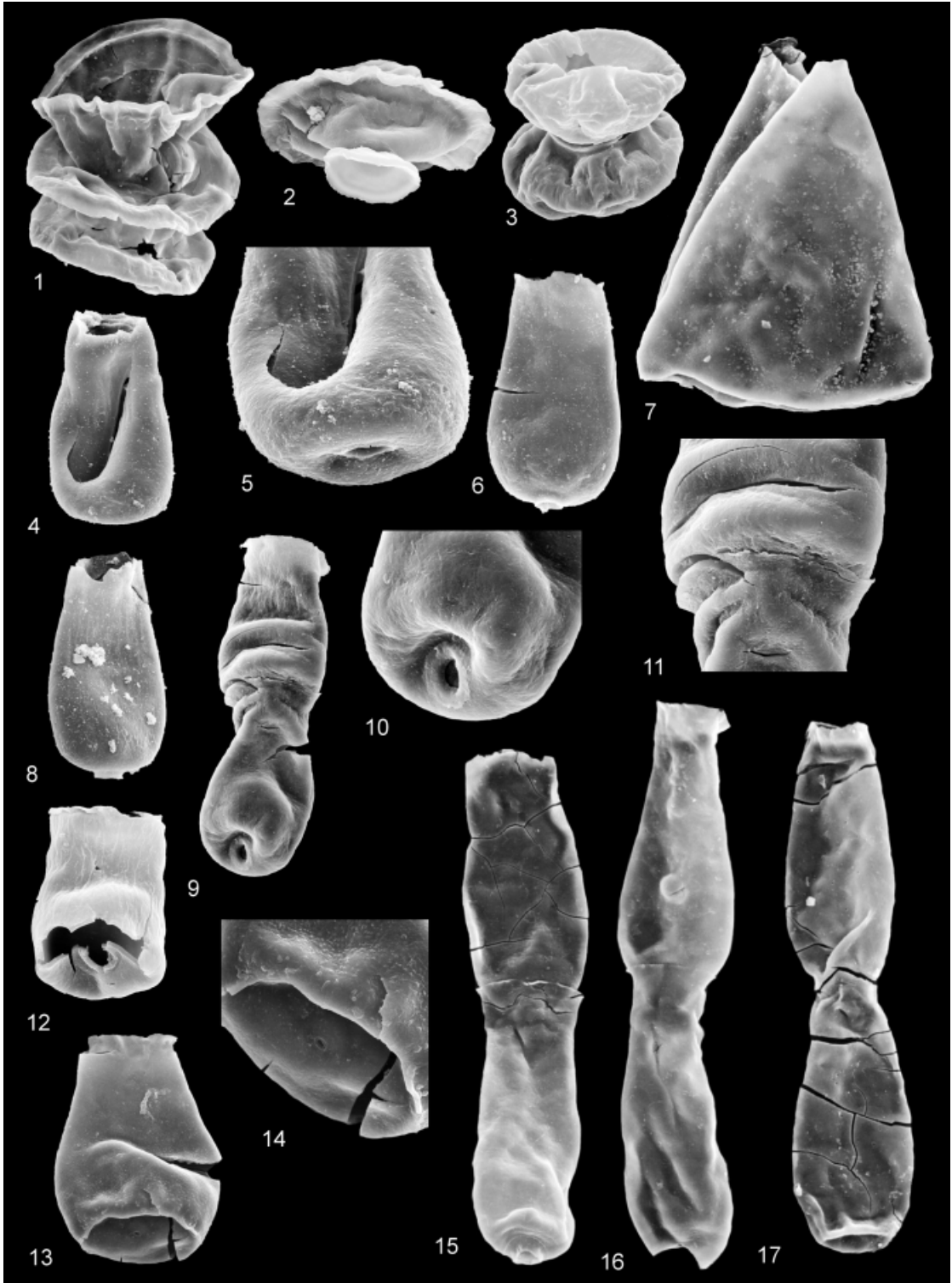
Fig. 3. *Calpichitina densa* (Eisenack); MPK12720; 25/39, HB2-5;  $\times 300$ .

Figs 4–6, 8–12. *Cingulochitina bountiensis* Verniers. 4, MPK12721; 25/40, HB2-7;  $\times 300$ . 5, close-up of the base and mucron of specimen in 4;  $\times 600$ . 6, MPK12722; 25/40, HB2-8;  $\times 300$ . 8, note the striate ornament on the upper half of the vesicle; MPK12723; 25/40, HB2-8;  $\times 300$ . 9, chain of two vesicles, with the upper vesicle displaying a striate vesicle ornament; MPK12724; 25/40, HB2-9;  $\times 300$ . 10, close-up of the mucron of specimen in 9;  $\times 600$ . 11, close-up of the vesicle of specimen in 9;  $\times 600$ . 12, example with a striate vesicle ornament; MPK12725; 25/40, HB2-11;  $\times 300$ .

Fig. 7. *Belonechitina* sp. 1 *sensu* Mullins and Loydell. MPK12726; 25/39, HB2-5;  $\times 300$ .

Figs 13–14. *Cingulochitina burdinalensis* Verniers. 13, MPK12727; 25/46, HB3-6;  $\times 300$ . 14, close-up of the carina and button-like mucron of specimen in 13.

Figs 15–17. *Linochitina odiosa* Laufeld. 15, chain of two vesicles; MPK12728; 25/45, HB3-10;  $\times 300$ . 16, chain of two vesicles; MPK12729; 25/44, HB3-2,  $\times 300$ . 17, chain of two vesicles; MPK12730; 25/44, HB3-2;  $\times 300$ .



MULLINS and ALDRIDGE, chitinozoans

those of *Bursachitina nestorae* Mullins and Loydell. *B. nestorae* differs in having conico-ovoid vesicles that are generally smaller (L, 128–264.1  $\mu\text{m}$ ; D, 76–138  $\mu\text{m}$ ; da, 40.8–82  $\mu\text{m}$ ).

Subfamily BELONECHITININAE Paris, 1981

Genus BELONECHITINA Jansonius, 1964 emend. Paris *et al.*, 1999

*Type species. Conochitina micracantha* subsp. *robusta* Eisenack, 1959.

*Belonechitina* sp. 1

Plate 2, figure 6; Plate 5, figure 7

- ?p 1981 *Eisenackitina* sp. A Verniers, pl. 2, fig. 18 (only).  
 ?p 1982 *Eisenackitina* sp. A Verniers, pl. 5, fig. 89A–B (only).  
 2001 *Belonechitina* sp. 1 Mullins and Loydell, p. 760, pl. 5, figs 13–14.

*Description.* Vesicle cylindrico-conical, smooth, with an angular basal margin. The maximum vesicle width is situated at the basal margin. The base is flat. The flanks are generally straight and taper to the aperture, although some specimens show a distinct flexure and the development of a short neck.

*Dimensions.* L, 113–154.8  $\mu\text{m}$ ; D, 69.7–101.4  $\mu\text{m}$ ; da, 22.1–43.3  $\mu\text{m}$ ; lb, 89 per cent of the vesicle length where distinct (3 specimens).

*Remarks.* The specimens recovered from the Hughley Brook section appear identical to those assigned to *Belonechitina* sp. 1 by Mullins and Loydell (2001). However, the button-like mucron has not been observed due to the compaction and folding of the vesicles at Hughley Brook (see Pl. 5, fig. 7). In the Banwy River section, *Belonechitina* sp. 1 occurs in samples C-16 to C+6.5, *centrifugus* to lower *murchisoni* biozones (Mullins and Loydell 2001).

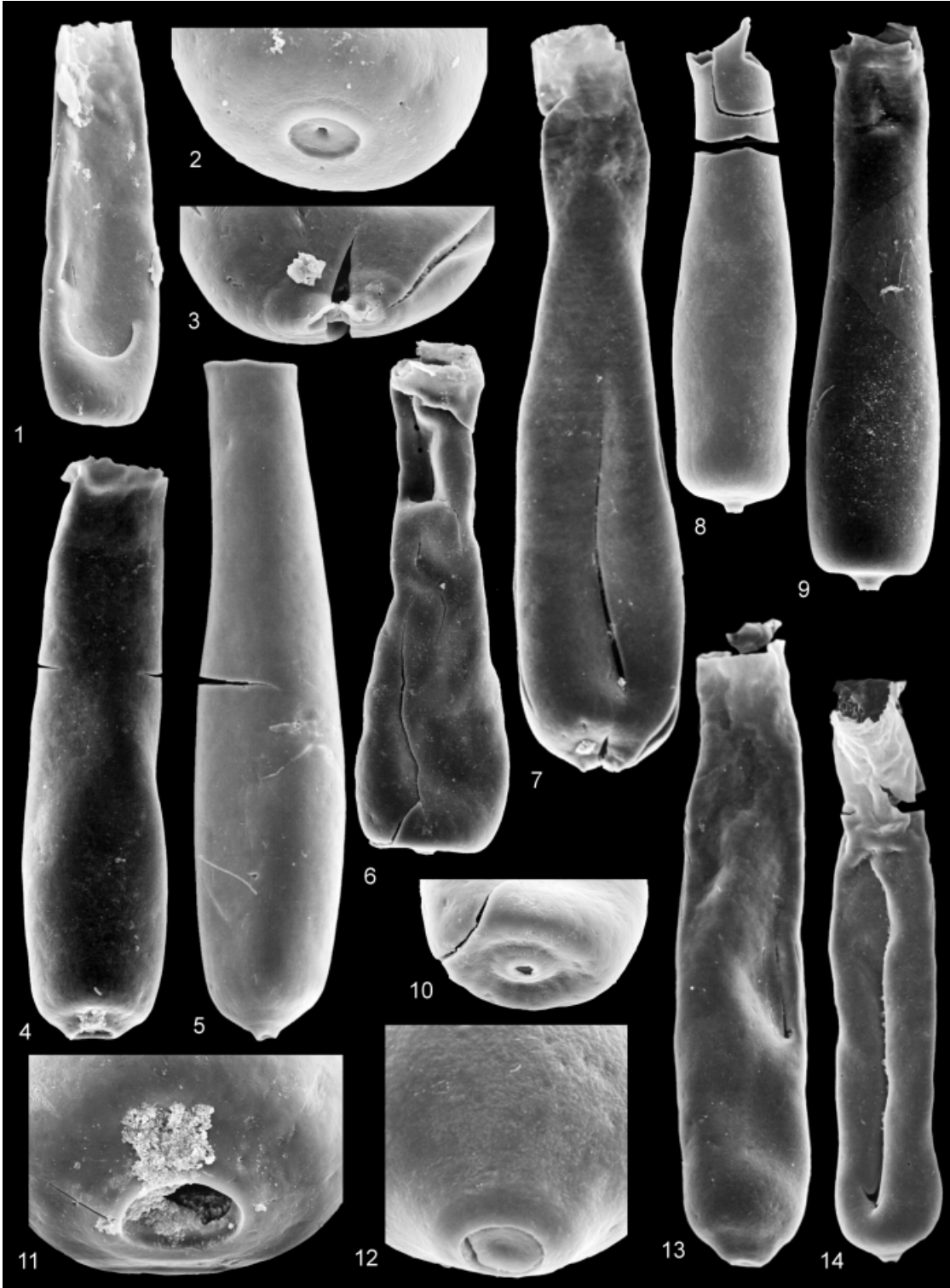
A specimen assigned to *Eisenackitina* sp. A by Verniers (1981, 1982) was questionably included in synonymy with *Belonechitina* sp. 1 by Mullins and Loydell (2001). This individual occurs in Verniers's sample CD-1A/33 of Formation MB 4A in the Mehaigne area, Belgium, at a level below certain *centrifugus* or *murchisoni* Biozone (Verniers and Rickards 1978). Further, this specimen of *Eisenackitina* sp. A is the paratype of *Eisenackitina anulifera* Verniers 1999.

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EXPLANATION OF PLATE 6

Figs 1–2. *Conochitina praeroboscifera* Nestor. 1, example with a flat base, thickened rim and central indentation; MPK12731; 25/44, HB3-1;  $\times 200$ . 2, close-up of the indented mucron of specimen in 1;  $\times 600$ .

Figs 3–14. *Conochitina proboscifera* Eisenack. 3, close-up of the wide mucron of specimen in 7;  $\times 300$ . 4, specimen with a broad-based, mound-like mucron which is open to the vesicle interior; MPK12732; 25/39, HB2-4;  $\times 200$ . 5, typical example with gentle flexures; MPK12733; 25/38, HB2-1;  $\times 200$ . 6, specimen with distinctly tapering flanks; MPK12734; 25/42, HB2-12;  $\times 200$ . 7, example with a broad-based, flat mucron; MPK12735; 25/44, HB3-2;  $\times 150$ . 8, specimen with a prominent constriction just above the basal margin; MPK12736; 25/39, HB2-5;  $\times 150$ . 9, typical specimen with a circular, membranous mucron; MPK12737; 25/42, HB2-12;  $\times 150$ . 10, close-up of the mucron of specimen in 6;  $\times 300$ . 11, close-up of the open, wide mucron of specimen in 4;  $\times 600$ . 12, close-up of the broad-based, mound-like mucron of specimen in 13;  $\times 600$ . 13, MPK12738; 25/45, HB3-5;  $\times 200$ . 14, example with a constriction just above the basal margin; MPK12739; 25/46, HB3-6;  $\times 200$ .



MULLINS and ALDRIDGE, *Conochitina*

*Belonechitina* sp. 2

Plate 2, figures 7–8

- p 1981 *Eisenackitina* sp. A Verniers, pl. 2, fig. 19 (only).  
 p 1982 *Eisenackitina* sp. A Verniers, pl. 5, fig. 90 (only).  
 2001 *Belonechitina* sp. 2 Mullins and Loydell, p. 762, pl. 5, figs 8–9.

*Description.* Vesicle cylindrico-conical, ornamented, with a flat base and a maximum vesicle diameter at the basal margin. The basal margin is very distinct and angular. The straight flanks of the vesicle taper distinctly to the aperture and a flexure is present c. 73–86 per cent along the length of the vesicle from the basal margin.

*Dimensions.* L, 144.4  $\mu\text{m}$ ; D, 109.1  $\mu\text{m}$ ; da, 31  $\mu\text{m}$  (1 specimen).

*Remarks.* This form appears to be nearly identical to the specimens from the Banwy River section referred to *Belonechitina* sp. 2 by Mullins and Loydell (2001). The single specimen recovered from the Hughley Brook section was observed under transmitted light microscopy and hence it has not been possible to compare the basal structures directly with the example from sample C + 12.25 (*murchisoni* Biozone) of the Banwy River section described by Mullins and Loydell (2001, p. 762, pl. 5, figs 8–9). However, the specimen recovered here has comparable dimensions to that from the Banwy River section (L, 180.8  $\mu\text{m}$ ; D, 104  $\mu\text{m}$ , da, 52  $\mu\text{m}$ ; Mullins and Loydell 2001). The single example of *Eisenackitina* sp. A Verniers (1981, pl. 2, fig. 19; 1982, pl. 5, fig. 90) considered synonymous with *Belonechitina* sp. 2 by Mullins and Loydell (2001) is also of comparable size (L, 188.1  $\mu\text{m}$ ; D, 120  $\mu\text{m}$ ; da, 52  $\mu\text{m}$ ). This specimen occurs in Verniers's sample CD-1A/33 of Formation MB 4A in the Mehaigne area, Belgium, at a level below unequivocal *centrifugus* or *murchisoni* Biozone (Verniers and Rickards 1978; Verniers 1999). *Belonechitina* sp. 2 may prove to be a reliable indicator of the lower part of the Wenlock Series, although it occurs in very low numbers; at present only three specimens are known.

*Belonechitina* sp. 3

Plate 2, figure 9

*Description.* The vesicle is cylindrico-conical, with a distinctly rounded base and basal margin. The vesicle may be ornamented. The flanks are convex and taper to a flexure situated 77 to 93 per cent of the vesicle length from the basal margin. A short neck is present.

*Dimensions.* L, 135.5–174.2  $\mu\text{m}$ ; D, 92.9–143.2  $\mu\text{m}$ ; da, 34.1–65.8  $\mu\text{m}$  (2 specimens).

*Remarks.* The rounded base and convex vesicle flanks distinguish this taxon from *Belonechitina* sp. 1 and *Belonechitina* sp. 2, which both have flat bases and straight flanks.

## EXPLANATION OF PLATE 7

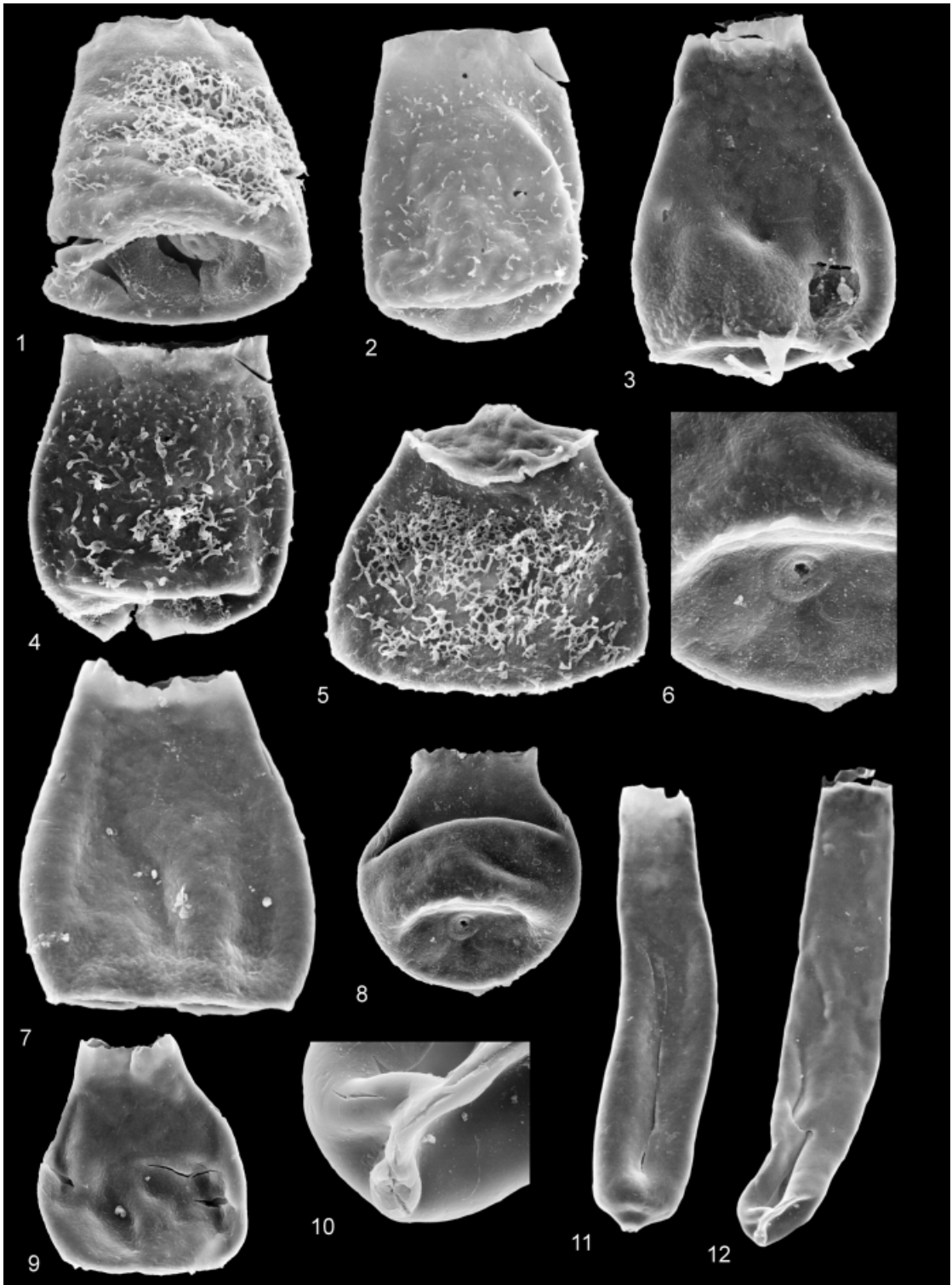
Figs 1–2, 4–5. *Eisenackitina varireticulata* Swire. 1, example showing a well-developed, interlocking, mesh-like ornament and button-like mucron; MPK12740; 25/45, HB3-4;  $\times 300$ . 2, specimen with reduced ornamentation; MPK12741; 25/45, HB3-3;  $\times 300$ . 4, example showing a poorly developed mesh-like ornament; MPK12742; 25/45, HB3-3;  $\times 300$ . 5, example with a well-developed mesh-like ornament, with an operculum in the oral opening; MPK12743; 25/45, HB3-3;  $\times 300$ .

Fig. 3. *Salopochitina bella* Swire. MPK12744; 25/44, HB3-1;  $\times 300$ .

Figs 6–8. *Cingulochitina burdinalensis* Verniers. 6, close-up of the button-like mucron of specimen in 8;  $\times 600$ . 7, MPK12745; 25/45, HB3-4;  $\times 300$ . 8, MPK12746; 25/46, HB3-6;  $\times 300$ .

Fig. 9. *Cingulochitina burdinalensis?* Verniers. MPK12747; 25/44, HB3-1;  $\times 300$ .

Figs 10–12. *Conochitina proboscifera* Eisenack. 10, close-up of the mucron of specimen in 12;  $\times 600$ . 11, example with a gently curved vesicle; MPK12748; 25/44, HB3-1;  $\times 150$ . 12, specimen with a distorted vesicle near the basal margin; MPK12749; 25/45, HB3-4;  $\times 150$ .



MULLINS and ALDRIDGE, chitinozoans

Family LAGENOCHITINIDAE Eisenack, 1931 emend. Paris, 1981

Subfamily ANCYROCHITININAE Paris, 1981

Genus ANCYROCHITINA Eisenack, 1955

*Type species.* *Conochitina ancycra* Eisenack, 1931.

*Ancyrochitina digitata* sp. nov. Mullins

Plate 2, figures 10–11, 13–14; Plate 4, figures 8, 13

1994 *Ancyrochitina* aff. *convexa* Nestor; Nestor, p. 63, pl. 2, fig. 6.

*Derivation of name.* From digitate, referring to the finger-like branching of the processes.

*Holotype.* MPK12712, Plate 4, figures 8, 13, sample 25/45, lower part of the Wenlock Series, Hughley Brook, Hughley, Shropshire.

*Diagnosis.* Vesicle covered with a dense ornament of irregularly shaped low mounds and short ridges between 0.5–5.5  $\mu\text{m}$  in length. The chamber is generally rounded, although it may be flattened antiaperturally. A gentle flexure occurs at the chamber–neck contact and the neck may, or may not, flare aperturally. The aperture appears generally smooth, without crenulations or processes. At the basal margin up to eight processes occur. The processes may be simple, although they are more commonly broad-based, wide along their length and orientated vertically. The broad-based processes (6–25  $\mu\text{m}$ ) appear to comprise two thickened rod-like structures (which make up the two branches), around and between which a thinner membrane can occur. The rod-like structures may possess digitate branching of the first order. Minor processes may be developed along the neck, although they are never distinct.

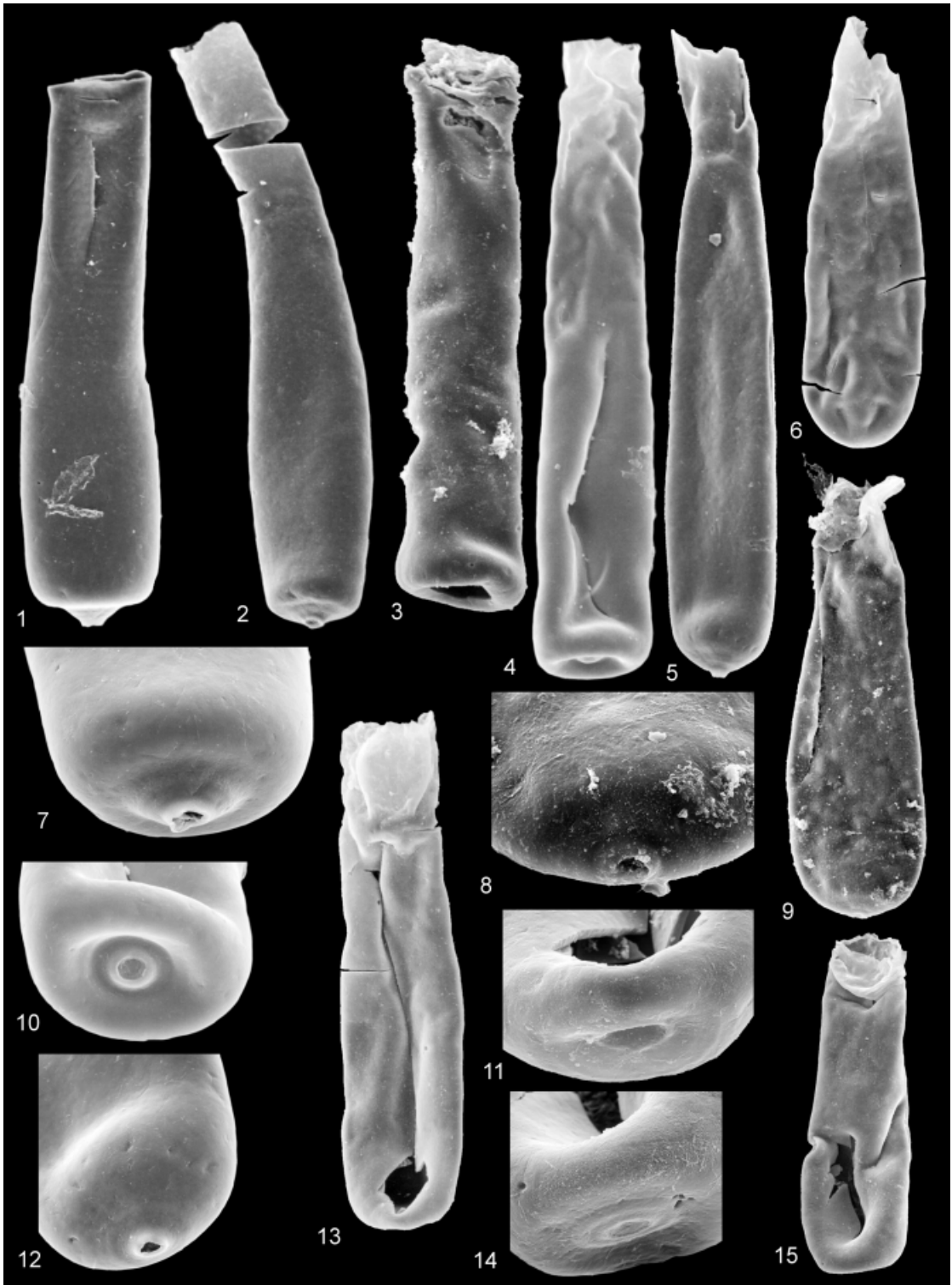
*Dimensions.* L, 87–183  $\mu\text{m}$ ; lb, 56–100  $\mu\text{m}$ ; ln 31–83  $\mu\text{m}$ ; D, 66–93  $\mu\text{m}$ ; da, 27–57  $\mu\text{m}$ ; app, 7–21  $\mu\text{m}$  (6 specimens).

*Remarks.* The processes have a characteristic divaginate and digitate structure (Pl. 2, figs 11, 14; Pl. 4, fig. 13). The specimen illustrated as *A.* aff. *convexa* by Nestor (1994, pl. 2, fig. 5) has a tuberculate vesicle ornament and shows the same broad-based divaginate and digitate processes as *A. digitata* and is, therefore, included in synonymy. The processes of the type material of *A. convexa* are more complicated than those of *A. digitata*. In *A. convexa* there are 6–8 processes, each containing 2–5 appendages, which may be simple, branched up to 3–4 times, or have small cross-bars or membranes joining the appendages (Nestor 1980, p. 142, pl. 1, figs 1–2).

#### EXPLANATION OF PLATE 8

Figs 1–2, 5, 7, 12. *Conochitina proboscifera* Eisenack. 1, typical example showing gentle flexures on the vesicle flanks and a prominent, membranous mucron; MPK12750; 25/44, HB3-2;  $\times 150$ . 2, specimen with a gently curved vesicle; MPK12751; 25/45, HB3-5;  $\times 150$ . 5, example lacking flexures on the vesicle flanks; MPK12752; 25/44, HB3-2;  $\times 150$ . 7, close-up of the mucron of specimen in 1;  $\times 300$ . 12, close-up of the mucron of specimen in 5;  $\times 300$ .  
 Figs 3–4, 10–11, 13. *Conochitina praeproboscifera* Nestor. 3, MPK12753; 25/43, HB2-14;  $\times 200$ . 4, MPK12754; 25/45, HB3-3;  $\times 200$ ; 10, close-up of the mucron of specimen in 4 showing the thickened ridge and central indentation typical of this species;  $\times 300$ . 11, close-up of the mucron of specimen in 13 showing a circular ridge and a central depression;  $\times 600$ . 13, MPK12755; 25/43, HB2-14;  $\times 200$ .  
 Fig. 6. *Bursachitina* sp. B. 6, MPK12756; 25/38, HB2-2;  $\times 200$ .  
 Figs 8–9, 14–15. *Conochitina* aff. *tuba*. 8, close-up of the mucron of specimen in 9;  $\times 600$ . 9, MPK12757; 25/43, HB2-13;  $\times 200$ . 14, close-up of the mucron of specimen in 15 displaying a central, double circular ring structure;  $\times 600$ . 15, MPK12758; 25/43, HB2-13;  $\times 200$ .





MULLINS and ALDRIDGE, *Bursachitina*, *Conochitina*

Specimens of *A. digitata* have been recovered from the Rumba Formation (Adavere Stage, Llandoverly Series) of the Varbla core (154.5 m), Ikla core (307–309.5 m), Häädemeeste core (230.8 m), Pulli 2 core (59.7 m) and Viki core (186–190 m) of Estonia (Nestor 1994). *A. digitata*, therefore, occurs from the upper part of the Aeronian Stage, Llandoverly Series to the lowermost part of the Sheinwoodian Stage, Wenlock Series.

## DISCUSSION

The base of the Wenlock Series was defined at the base of their 'unit G' by Bassett *et al.* (1975), 150 mm above an impersistent 80-mm-thick siltstone band in the section on the north bank of Hughley Brook, c. 200 m south-east of Leasows Farm. However, the base of the Wenlock Series is not well constrained palaeontologically. No faunal or floral marker was identified at this level, and the boundary horizon was not shown to be coincident with the base of any biozone. The definition was ratified by the International (IUGS) Commission on Stratigraphy in 1980 and reported by Holland (1980) and Martinsson *et al.* (1981), who stated that the base of the Wenlock Series corresponded to the base of the *Cyrtograptus centrifugus* graptolite Biozone. However, the macrofossils in the stratotype section do not include graptolites (Bassett *et al.* 1975; Loydell 1993) and this correlation is based on regionally distributed graptolite data. In particular, the occurrence of *Pristiograptus watneyae* Rickards in the Buildwas Formation of Ticklerton brick pit, at a horizon 18.3 m above the base of the Wenlock Series, was noted by Bassett *et al.* (1975) as evidence for the *centrifugus* Biozone. This species had previously been recorded by Rickards (1967) from the *centrifugus* Biozone of the Howgill Fells, Yorkshire.

It cannot, therefore, be demonstrated directly that the correlation of the base of the Wenlock Series with the base of the *centrifugus* Biozone is accurate. Moreover, error bands on this correlation cannot be easily determined. The uncertainties are clearly considerable, as graptolite macrofossils have not been reported from several metres below or above the boundary in the type area, and biostratigraphically diagnostic species are even further removed.

The micropalaeontological study of the stratotype section by Mabillard and Aldridge (1985) identified a number of appearances and disappearances of microfossils that bracketed the boundary. Again, however, no biostratigraphical marker at the boundary horizon was found. These authors considered that the best guide to the boundary was the base of the *Pterospiriferus amorphognathoides* conodont Biozone, which was recognized 0.65 m below the base of the Wenlock Series in the Hughley Brook section. They further constrained the boundary by identifying that it lay within the *P. amorphognathoides* Biozone, at a level between the base of acritarch zone 5 of Hill (1974) and the disappearance of *P. amorphognathoides* Walliser. These two levels are separated by approximately 0.4 m in the Hughley Brook section. At the Domas locality, less than 4 km to the north-east, the same interval is represented by 0.9 m of strata (Mabillard and Aldridge 1985); the different thicknesses in the two sections may reflect greater condensation of the sedimentary sequence at Hughley Brook or, more probably, minor faulting in the stratotype section.

The lack of precision in the biostratigraphical recognition of the boundary is magnified away from the type area. Mabillard and Aldridge (1985) noted that the conodont *P. amorphognathoides* ranges through just 0.95 m of strata at Hughley Brook; at Domas the range is at least 2 m; in Marloes Bay, Pembrokeshire, it is at least 40 m (Mabillard and Aldridge 1983); and in the Ringerike District, Oslo Region, Norway, it is 30 m (Worsley *et al.* 1983). It is impossible to identify the boundary level with any accuracy in such areas, where the sedimentary thicknesses are much greater than at Wenlock Edge.

The conodonts recovered from Hughley Brook indicate that the base of the Wenlock Series lies close to, or is coincident with, Datum 2 of the Ireviken Event (Aldridge *et al.* 1993; Jeppsson 1997). In the Aizpute-41 core, Latvia, Datum 2 of the Ireviken Event has been recognized in strata near the base of the *murchisoni* graptolite Biozone (Loydell *et al.* 2003). Furthermore, the analysis of magmatic sanidine has been used to correlate bentonite beds in the Viki, Ohesaare and Aizpute-41 cores of Estonia and Latvia (Männik *et al.* 2002). These correlations, in addition to a re-interpretation of the biostratigraphical importance of coniform conodonts of the genus *Panderodus*, were used to suggest that the base of the Wenlock Series occurs high in the *murchisoni* Biozone, although it was noted that more work was needed

to confirm this (Männik *et al.* 2002). This correlation of the base of the Wenlock Series with a level above the base of the *centrifugus* graptolite Biozone partly agrees with the chitinozoan data from the Hughley Brook section. However, the chitinozoans suggest that the base of the Wenlock Series correlates with a level in the upper part of the *centrifugus* Biozone or the lower part of the *murchisoni* Biozone.

The recognition that *Plectochitina hughleyensis* sp. nov. first occurs in sample 25/38, 67 mm above the base of the Wenlock Series, may enable the Llandovery–Wenlock boundary to be accurately recognized elsewhere. Further, the identification of the *bouniensis* and *bella* chitinozoan biozones 256 mm and 825 mm above the base of the Wenlock Series, suggests that these levels correlate with the upper part of the *murchisoni* Biozone and *firmus* graptolite Biozone respectively. The recognition of probable *firmus* Biozone just 825 mm above the base of the Wenlock Series suggests that the *riccartonensis* graptolite Biozone perhaps occurs much lower than currently recognized and most probably within the Buildwas Formation.

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