A THESIS ENTITLED

THE CHITINOZOANS FROM THE LUDLOW SERIES (SILURIAN) OF THE TYPE AREA AND ADJACENT REGIONS

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This thesis is dedicated to my parents whose faith in me has meant more than they can possibly imagine.

Before the mountains were born or you brought forth the earth and the world, from everlasting to everlasting you are God. You return men back to dust, saying, "Return to dust, O sons of men." For a thousand years in your sight are like a day that has just gone by, or like a watch in the night.

PSALM 90:2-4
Stuart John Eyre Sutherland

The Chitinozoans from the Type Ludlow Series
(Silurian) and Adjacent Regions

Chitinozoans have been recovered from throughout the Ludlow Series of the type area around Ludlow and adjacent regions. Collections contain 12 genera and 42 species including 11 new species: Calpichitina (Calpichitina) granosa, Eisenackitina toddingensis, Cingulochitina gorstyensis, Belonechitina mortimerensis, Rhabdochitina wakefieldi, Ancyrochitina aymestreyensis, Ancyrochitina gogginensis, Ancyrochitina narcissus, Angochitina milleri, Gotlandochitina dinhamensis, Gotlandochitina swiftii. and 21 forms under open nomenclature. Conochitina dominates the late Wenlock and early Gorstian assemblages with Cingulochitina more common in the later Gorstian. The late Gorstian is characterised by species belonging to Belonechitina. Chitinozoan abundance and diversity decreases throughout the late Ludfordian, where Eisenackitina philipi often dominates assemblages.

A detailed biostratigraphy has permitted a greater biostratigraphical resolution than was previously possible using chitinozoans. A scheme of 12 informal chitinozoan biozones is established for the type Ludlow Series.

Chitinozoans have been used to test oceanic circulation models. Changes in chitinozoan assemblages have identified an event within the Middle Elton Formation (Gorstian Stage) and from the base of the Lower Leintwardine Formation (Ludfordian Stage). As the radiation event in the Gorstian occurs within the lithologically homogeneous Middle Elton Formation, it is concluded that chitinozoan faunas are not facies dependent. The faunal turnover in the Middle Elton Formation and the Lower Leintwardine Formation is believed to be related to changes in global climate and nutrient availability on the shelf.

A distinctive chitinozoan assemblage is recorded from the top of the Lower Bringewood Formation and includes C. (Calpichitina) granosa, A. narcissus, Fungochitina pistilliformis and significant numbers of Angochitina elongata. This assemblage is repeated at the base of the Ludfordian. These species are regarded as Lazarus taxa and interpreted as responding to specific environmental conditions on the shelf.

Due to the hermetically sealed nature of the chitinozoan vesicle and their chain forming habit, the idea that chitinozoans most likely represent the eggs of a marine metazoan is generally supported.
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INTRODUCTION

Chitinozoans are a group of organic walled, exclusively marine, microfossils that range from the Ordovician to Devonian (and possibly just into the Carboniferous). Supposed chitinozoans from the Precambrian of the Chuar Group in the Grand Canyon, Arizona (Bloeser & Schopf, 1977) have now been tentatively interpreted as algal encystment structures (Bloeser, 1985). The biological affinities of the group remain uncertain but current thinking favours a link with metazoan eggs or protistan resting cysts. The potential biostratigraphical and palaeoenvironmental usefulness of chitinozoans is considerable owing to their durability and widespread distribution during the Early Palaeozoic.

AIMS OF RESEARCH

The aims of research can be regarded as fourfold: to produce a primary data base of chitinozoans from the type Ludlow Series in the Welsh borderlands and to use this data to construct a biostratigraphical scheme; to test the usefulness of chitinozoans in modelling palaeoenvironmental change; to develop preparation techniques; to investigate the biological affinities of the group.

HISTORY OF RESEARCH

Although not credited with the discovery of chitinozoans, Eisenack was the first researcher to scientifically describe these microfossils. Eisenack (1931) reported that material taken from Baltic glacial erratics produced acritarchs, 'melanosclerites' and chitinozoans. Even with the interruption of being captured by the Red Army during the Second World War, Eisenack remained the chief chitinozan researcher for over two decades. Chitinozoans were studied in the Americas by authors such as Collinson & Schwalb (1955). Throughout the 1960's French micropalaeontologists (for example Jekhowsky, Taugourdeau and Combaz) produced many papers, chiefly on the
chitinozoans of France and North Africa. The next important work was Laufeld's 1974 study of the chitinozoans from Gotland. This featured the extensive use of the scanning electron microscope and illustrated the advantages of using this tool in the study of chitinozoans. In 1981, Paris developed and refined Eisenack's original classification scheme, producing the system that is most commonly used today. Paris (1989) has also presented a brief biostratigraphical synthesis, mostly referring to North Gondwana and Baltica forms. Work upon chitinozoans is now carried out virtually worldwide.

British chitinozoans were first recorded by Lewis (1940) from the Caradoc of North Wales and were also noted by Downie & Ford (1966) from the Manx Slate on the Isle of Man. Jenkins published a review of Chitinoza in 1970 but his work in the British Isles was chiefly concerned with Ordovician forms. Atkinson and Moy (1970) published on Upper Ordovician chitinozoans from North Wales. Lister worked upon the Ludlow chitinozoans and acritarchs from the type area for his 1968 PhD thesis. His acritarch, but not chitinozoan, findings were published in monograph form (Lister 1970). A number of M.Sc. theses have been produced at Sheffield University which deal in part or in totality with chitinozoans, for example Dean (1987) who worked on the chitinozoans and acritarchs from the Much Wenlock Limestone Formation of Harley Hill in Shropshire. Mabillard (1981) described the chitinozoans from various Llandovery and Wenlock sections in Wales and the Welsh Borderland in his PhD thesis at the University of Nottingham. Brief reviews of chitinozoans present through the Silurian of Wales and the Welsh Borderland have been presented by Aldridge et al. (1979), Dorning (1981c) and Mabillard & Aldridge (1985). Swire (1990) published data on two new species of Wenlock chitinozoans that figured in his PhD thesis. The use of chitinozoan reflectance in maturation studies has been demonstrated by Tricker et al. (1992) who utilised this technique to assess hydrocarbon source potential of the Lower Palaeozoic of Wales and the Welsh Borderlands. Pearce has used chitinozoan reflectance data in his study of illitization and organic maturity of Silurian sediments in the Southern Uplands (Pearce et al. 1991).
GEOLOGICAL SETTING

The Silurian sediments around the Shropshire town of Ludlow were described by Sir Roderick Impey Murchison (1839) in his book "The Silurian System". The Ludlow Rocks of the Ludlow area comprise around 350m of alternating siltstones and limestones, the limestones of the Much Wenlock Limestone Formation and Upper Bringewood Formation forming prominent ridges. Structurally these sediments form the Ludlow anticline, the axis of which plunges ENE below the town of Ludlow (see Text-fig 1.). In 1963, Holland et al. defined four lithostratigraphical units, termed 'Beds', within the Ludlow area. Biostratigraphical divisions, based upon characteristic benthonic macrofossil assemblages, were considered coincidental with those of the lithostratigraphy. Due to the imposed coincidence of biostratigraphical and lithological units some lithostratigraphical boundaries do not occur at points of lithological change. This has caused a certain degree of controversy (see Domning & Lawson 1982). In 1976 the Subcommission on Silurian Stratigraphy of IUGS decided to formalise the names and definitions of the internal divisions of the Silurian System. In 1980 it was announced that the base of the Ludlow Series and of the Gorstian Stage would be located at Pitch Coppice Quarry (SO 4723 7298) off the Ludlow-Wigmore Road (Holland 1980). Revisions to Ludlow stratigraphy included the replacement of 'Beds' by 'Formations' (Holland et al. 1980) and the simplification of the former fourfold chronostratigraphy to the Gorstian Stage (containing Lower, Middle and Upper Elton formations and the Lower and Upper Bringewood formations) and the younger Ludfordian Stage (containing the Lower and Upper Leintwardine formations and the Lower and Upper Whitcliffe formations) (Holland 1980). The base of the Ludfordian Stage was defined at Sunnyhill Quarry (SO 4950 7255) within the Mortimer Forest (Holland et al. 1980). The top of the Ludlow Series coincides with the base of the Pridoli defined in the Barrandian area of Czechoslovakia (Krříz 1989, p.90). This has been correlated to be coincident with the base of the Ludlow Bone Bed Member of the Downton Castle Sandstone Formation at Ludlow (Siveter et al. 1989, p.45). The most celebrated locality exposing this level is
TEXT-FIG. 1. Geological map of the eastern part of the Ludlow anticline (based on Lawson & White, 1989).
Ludford Corner in the town of Ludlow (SO 5123 7412). This locality was made famous by Murchison and taken by many to represent the base of the Devonian (for example Stamp 1920) though correlation with the Pridoli Series now places the Downton Castle Sandstone Formation in the upper Silurian. The following is a brief account of the broad characteristics of the lithological units encountered in the Ludlow Series within the Ludlow area (based upon Lawson & White 1989). The chronostratigraphy, lithostratigraphy and biostratigraphy of the Ludlow area are shown in Text-fig 2.

**Lower Elton Formation.** Soft, silty mudstones, occasionally calcareous. Pale olive green colour. Brachiopods common, for example *Atrypa reticularis* (Linnaeus) and *Aegiria grayi* (Davidson). Most of the Lower Elton Formation is covered by the earliest part of the L1 acritarch biozone in which acritarchs such as *Dateriocradus tribrachiata* (Lister) Dorning and *Neoveryhachium mayhillensis* Dorning are common (Dorning 1981b, p. 202). Acritarchs common to both the Wenlock Series and Ludlow Series include *Salopidium [Baltisphaeridium] granuliferum* (Downie), *Cymatosphaera wenlockia* Downie, *Visbysphaera dilatispinosa* Downie, Lister and *Multiplicisphaeridium variabile* (Lister) Dorning (Aldridge et al. 1979). Long ranging miospores common to the Wenlock Series and Lower, Middle and Upper Elton formations include cf. *Synorisporites verrucatus* Richardson & Lister, *Archaeozonotriletes chulus* var. *nanus* Richardson & Lister, ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova Richardson & Lister 1969. *Synorisporites downtonensis* Richardson & Lister appears in the upper part of the Lower Elton Formation and ranges through to the top of the Lower Bringewood Formation (Richardson & Lister 1969). No new ostracode species are recorded from this horizon. Only forms extending from the late Wenlock ostracode faunas are found, for example *Thlipsura' v-scripta* Jones & Holl and *Primitiopsis valida* Jones & Holl (Siveter 1978, p.66). Conodont faunas are poor in the lower Ludlow Series (Aldridge 1985, p. 75). *Ozarkodina confluens* (Branson & Mehl) is recorded throughout the Ludlow Series by Aldridge et al. (1979, p. 435) but has not been isolated from any of the lower Gorstian sections in the type area (Aldridge 1992, pers. comm.).
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<td>Flaggy calcareous silstones with shelly limestone bands</td>
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<td>Irregularly bedded, massive or thickly flaggy calcareous silstones</td>
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<td>45-105m</td>
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**Middle Elton Formation.** Soft, shaly siltstones, less calcareous than the Lower Elton Formation. Olive grey green colour. Benthonic fossils less common, fauna dominated by graptolites and orthoconic nautiloids. Bentonites common. The Middle Elton Formation falls within the L1 acritarch biozone of Doming (1981b). The ostracode faunas of the Middle and Upper Elton formations are not well known but contain two long ranging species; *Aechmina cuspidata* Jones & Holl and *Thlipsura corpulenta* Jones & Holl (Siveter 1978, p.66). These have not been recovered from the lower Gorstian sections in the type area (Siveter 1992, pers. comm.).

**Upper Elton Formation.** Regularly bedded shaly and flaggy siltstones interbedded with calcareous siltstones. Olive grey green colour. Graptolites and orthocones still present. Small brachiopods include *Shagamella minor* (Salter) and *Lingula lata* (J. de C. Sowerby). The lower part of the Upper Elton Formation is correlated with later part of the the L1 acritarch biozone in which acritarchs such as *Tylotopalla pyramidalis* (Lister) Doming and *Cymatosphaera gorstia* Doming are common (Doming 1981b, p. 202). The upper part of the Upper Elton Formation is covered by the L2 biozone in which *Cymatosphaera ledburica* Doming and *Dilatisphaera laevigata* Lister are common (Doming 1981b, p. 202). Beyrichiid ostracodes are recorded in the Upper Elton Formation and Lower Bringewood Formation along Goggin Road (Siveter *et al.* 1989, p.52).


**Upper Bringewood Formation.** 'Aymestrey Limestone' of previous classifications. Irregularly bedded and nodular limestones. Light olive grey green colour. Tabulate corals
(Favosites and Heliolites) and the brachiopod Kirkidium knightii (J. Sowerby) common. Crinoid debris common. The Upper Bringewood Formation is covered by the L2 acritarch biozone (Dorning 1981b, p. 202). The ostracodes Sleia ancon Siveter and Zorotoxotis sagena Siveter are recorded by Siveter (1980, pp.60 & 73) but are not recorded in the type area. Only a general ostracode fauna is present around the Ludlow area, including Amphitoxotis sp., Beyrichia sp., Neobeyrichia sp., Calcaribeyrichia sp., Primitiopsis sp., aechminids and podocopids (Siveter 1992, pers. comm.). Kockelella variabilis Walliser is a characteristic component of the conodont faunas. Distomodus dubius (Rhodes) and Pelekysgnathus dubius Jeppsson appear in the Upper Bringewood Formation and range to the top of the Ludlow Series (Aldridge et al. 1979, pp. 435 & 437).

Lower Leintwardine Formation. Flaggy, calcareous siltstones with shale and limestone bands. Light olive grey colour. Brachiopods common, particularly in coquinoid horizons. Species include: Sphaerirhynchia wilsoni (J. Sowerby), Isorthis orbicularis (J. de C. Sowerby), A. reticularis, Microsphaeridiorhynchus nucula (J. de C. Sowerby) and Shaleria ornatella (Davidson). The Lower and Upper Leintwardine formations are covered by the L3 acritarch biozone, the base of which is coincident with the bases of the Lower Leintwardine Formation and the Ludfordian Stage. The base of L3 is defined by the first appearance of a number of acritarchs including Cymbosphaeridium pilar (Cramer) Lister, Leoniella carminae Cramer, Multiplicisphaeridium paraguaferum (Cramer) Lister, Veryhachium leintwardinense Dorning and Leiofusa estrecha Cramer (Dorning 1981b, p. 202). Characteristic ostracode species include Neobeyrichia nutans (Kiesow) and Hemiella cf. loensis Martinsson (Siveter 1978, p.67). Various non-palaeocope ostracodes are also recorded in the upper part of the Lower Leintwardine Formation in the Mortimer Forest near Ludlow (Siveter et al. 1989, p. 55 & 59).

Upper Leintwardine Formation. Flaggy calcareous siltstones. Light olive green grey colour. This unit is distinguished by the trilobites Calymene puellaris Reed and Encrinurus stubblefieldi Tripp. Common brachiopods include A. reticularis and L. depressa. This horizon is characterised by the ostracodes Neobeyrichia lauensis
(Kiesow), *Neobeyrichia scissa* Martinsson and *Neobeyrichia confluens* Shaw (Siveter 1978, p.67). Non-palaeocene ostracodes are recorded in the Upper Leintwardine Formation exposures in the Mortimer Forest near Ludlow (Siveter et al. 1989, p.55 & 59). The miospore *Apiculiretusispora* sp. C. of Richardson & Lister appears in the Upper Leintwardine Formation and persists beyond the top of the Ludlow Series (Richardson & Lister 1969).

**Lower Whitcliffe Formation.** Thick flaggy, irregularly bedded variably calcareous siltstones. Medium grey to greenish grey colour. Molluscs increase in importance, for example, the bivalve *Fuchsella amygdalina* (J. de Sowerby) and the cephalopod *Leurocycloceras whitcliffense* Holland. The Lower and Upper Whitcliffe formations fall within the L4 acritarch biozone (Doming 1981b, p.202). The acritarchs *Visbysphaera* spp. including *V. whitcliffense* Doming are common. The characteristic ostracode of the Whitcliffe formations is *Calcaribeyrichia torosa* (Jones) (Siveter 1978, p.67). Non-palaeocene ostracodes are recorded from the Lower Whitcliffe Formation at the Deer Park Road section in the Mortimer Forest by Siveter et al. (1989, p. 59).

**Upper Whitcliffe Formation.** Flaggy calcareous siltstones. Olive green grey colour. Often more thinly bedded than the underlying formation and commonly containing coquinoid horizons. Fauna includes *Pteronitella retroflexa* (Wahlenberg), *Serpulites longissimus* J. de C. Sowerby and *Calcaribeyrichia torosa* (Jones). Upper Ludfordian conodont assemblages are dominated by *Ozarkodina excavata* (Branson & Mehl), *Ozarkodina confluens* (Branson & Mehl) and *Panderodus unicostatus* (Branson & Mehl) (Aldridge 1985, p. 75). The greatest number of miospores occurs above the Upper Whitcliffe Formation in the Downton Group.

**PALAEOGEOGRAPHY AND FACIES DEVELOPMENT**

The Ludlow sediments of Ludlow and adjacent areas are thought to have been deposited on the eastern shelf of a shallowing NE-SW trending trough, the Welsh Basin, a fault bounded structure developed on the southern side of the Iapetus Ocean. Woodcock
(1984) suggested that an analogous modern tectonic feature would be the strike slip borderland of California. After its detachment from Gondwana, the microcontinent of Eastern Avalonia (which includes modern Southern Britain) drifted, throughout the Ordovician, towards mid latitude Baltica (modern Scandinavia) and low latitude Laurentia (modern North America) (Siveter et al. 1989, p. 9). Pickering et al. (1988, p. 379) suggested that the Tornquist Ocean between Eastern Avalonia and Baltica had closed by the mid to late Caradoc and that a partial closure of the Iapetus Ocean or 'soft collision' had occurred between Eastern Avalonia and Laurentia in the latest Ashgill. Faunal evidence (for example Cocks & Fortey 1982, Vannier et al. 1989) supports the development of the Rheic Ocean between Gondwana and Avalonia by late Ordovician to early Silurian, corollary to closure of the Tornquist Ocean. Continued closure of the Iapetus Ocean throughout the late Silurian closed remaining seaways and eventually led to the development of the Caledonian structural features associated with the 'hard collision' of Pickering et al. (1988). During the Silurian the Welsh Basin is believed to have occupied sub tropical latitudes south of the equator. (Cocks & Fortey, 1982). A proposed palaeogeography of Southern Britain during the late Gorstian is shown in Text-fig. 3.

The Ludlow Series of the Welsh Borderland exhibits a generally shallowing upward sequence terminating in a transition from marine to fluviatile facies. There is evidence of occasional volcanic activity from the bentonites found in the Middle Elton Formation but this is limited and only forms a minor feature of the stratigraphy. The facies encountered in Wales and the Welsh Borderland can be divided into three parts; shelf, shelf edge and basin. The westward increase in thickness and muddy component of stratigraphic units can be regarded as being the result of the transition from the shelf towards the basin. The Ludlow Series in the west of the basin may reach thicknesses of up to 1800m; on the shelf stratigraphic units are thinner (350m in the Ludlow area). The carbonates within the Lower and Upper Bringewood formations may be used to estimate the palaeogeographical position of the shelf edge. Variations in thickness and lithological character of the succession at Aymestrey detailed by Lawson (1973) may reflect the close proximity of the shelf/basin edge (Siveter et al. 1989, p.65). Changes include thinning
of the Upper Elton Formation (possibly erosion on a ridge at the hinge - Siveter et al. 1989) and the change laterally of the Upper Bringewood Formation limestone ('Aymestry Limestone') over a few hundred meters into more argillaceous silty material (Siveter et al. 1989). Further evidence for the palaeogeographical position of the shelf edge comes from the work of Whitaker (1962) who demonstrated the existence of submarine channels trending NE-SW off the shelf. These structures were infilled during deposition of the Lower Leintwardine Formation. Towards their source they cut into the basal Leintwardine Formation (a unit not recognised in the Ludlow area) and westward into progressively older formations. These features have been compared with modern submarine canyon heads (Siveter et al. 1989, p. 63).

Calef & Hancock (1974) proposed that, following an initial deepening after the deposition of the Much Wenlock Limestone Formation, the Ludlow succession could be regarded as a regressive sequence. This is now held to be too simplistic (Lawson 1975, Doming 1981a). A deepening is recorded from the Middle Elton Formation which is characterised by graptolites, orthocones and an impoverished benthonic fauna (Lawson 1975, Lawson & White 1989). Shallower conditions prevailed at the time of deposition of the Lower Bringewood Formation which is dominated by a rich benthonic fauna. Shallowing continued into the upper Gorstian with the deposition of the Upper Bringewood Formation limestones. Lawson (1975) noted the presence of algal remains in the Upper Bringewood Formation at Aymestrey. The more argillaceous sediments of the Lower Leintwardine Formation are taken as representing a second period of deepening (Lawson, 1975). Regression occurred throughout the remainder of the Ludfordian, shallowing features such as coquinoid horizons and current laminations becoming particularly common within the Upper Whitcliffe Formation (Siveter et al. 1989, p. 37).

This model is supported by Doming (1981a) who proposed that offshore and nearshore acritarch assemblages correlate with periods of transgression and regression within the Ludlow succession. A sea level curved based on Lawson (1975) and Doming (1981a) is presented in Text-fig. 35.
The transition to Old Red Sandstone facies occurred in the Pridoli. Sands and bone bed lags developed in marine influenced mudflats. The transition is more gradual in basinal areas (Siveter et al. 1989). By the late Silurian/early Devonian (Dittonian), Wales and the Welsh borderland were dominated by fluviatile conditions.

LOCALITIES

1. Pitch Coppice Quarry (SO 4723 7298, Text-fig. 37). Sampled for the base of the Ludlow Series which is defined 22cm below a thin bentonite (Holland et al. 1963).
2. Goggin Road, Mortimer Forest (SO 4727 7184, Text-figs 6, 38-40). Sampled for the base of the Ludlow Series, the Lower, Middle and Upper Elton formations and the base of the Lower Bringewood Formation. Comparison of section logs at Pitch Coppice and Goggin Road shows that the base of the Ludlow Series should be drawn lower in the section than was proposed by White & Lawson (1978). It is now placed at SO 4724 7187 even though the thin bentonite present at Pitch Coppice is missing at Goggin Road. This placement is supported by the chitinozoans from both sections. Although no species first occurrence can be directly correlated with the base of the Ludlow Series, the character of the assemblages is very similar at Pitch Coppice and from GR1-5 on Goggin Road (Text-fig. 38). The base of the Ludlow Series proposed by Lawson & White (1978) for Goggin Road (placed at a level co-incident with GR9, Text-fig. 38) possesses a low abundance (<1/gram) of poorly preserved chitinozoans whilst those from Pitch Coppice and GR1-5 are better preserved and present in greater numbers (1-9/gram). In addition to this there are great similarities in the lithological character of both Pitch Coppice and the lower part of the section, covered by GR1-5, on Goggin Road. The large shale unit at Pitch Coppice (PC11, 2.48m below the top of the Much Wenlock Limestone Formation) is repeated on Goggin Road (2.3m below the top of the Much Wenlock Limestone Formation) and at both localities conspicuous limestones are proceeded by the soft shales of the Lower Elton Formation. The boundary was probably placed at the level of GR9 due to the presence of a thin limestone band within the Lower Elton Formation, which may have
TEXT-FIG. 4. Localities in and around the Ludlow area.
Text-fig. 5. Ludlow succession of the Ludlow area showing relative stratigraphic positions of sample localities (stratigraphy based on Siveter et al. 1989).
TEXT-FIG. 6. Geology along the Goggin Road, Mortimer Forest area of the Ludlow anticline (modified after White & Lawson (1978) and Siveter et al. 1989).
TEXT-FIG. 7. The geology of the area around Todding and lower Todding near Leintwardine (based on Whitaker 1962).

TEXT-FIG. 9. Geology along Deer Park Road, Mortimer Forest area of the Ludlow anticline (modified after White & Lawson 1978).
TEXT-FIG. 11. Localities along the Whitcliffe at Ludlow (modified from Holland et al. 1963 and Siveter et al. 1989).

been regarded as the highest limestone unit of the Much Wenlock Limestone Formation. The revised base of the Ludlow series at Goggin Road is shown on Text-figs 6 & 38.

3. Deer Park Road (SO 4845 7135, Text-figs 9, 41-42). Sampled for the Lower and Upper Bringewood formations, including the base of the Upper Bringewood Formation.

4. Sunnyhill Quarry (SO 4950 7255, Text-figs 10, 46-50). Sampled for the base of the Ludfordian (co-incident with the base of the Lower Leintwardine Formation) and central parts of the Lower Leintwardine Formation.


6. Todding (SO 4160 7530, Text-figs 7, 43-44). Sampled for the Lower Bringewood Formation. The sections at Todding are poorly exposed making a precise definition of the stratigraphical relationships between LT and T sampled horizons difficult. However both sections are placed with some certainty in the lower portions of the Lower Bringewood Formation.

7. Aymestrey (SO 4234 6548, Text-figs 8, 45). Sampled for the Upper Bringewood Formation.


All localities (except Aston Munslow) were reviewed by Siveter et al. (1989, chapter 3). The geographical relationship of all sections is shown on Text-fig 4 and a stratigraphical summary presented on Text-fig. 5.

METHODS

Collection. Each locality was logged and photographed. A sampling interval of 1-2 metres was generally used, each sample representing 5cm vertical thickness of rock. Across the boundaries between lithostratigraphical and chronostratigraphical divisions, the sampling interval was decreased to 2-10cm, with a smaller vertical thickness of sample
Uncrushed sample cleaned with detergent and wire brush

2-10mm fraction

15-20g of crushed sample washed with detergent and dried.

2mm sieve

All procedures utilising acids carried out in fume cupboard

15-20g of crushed sample washed with detergent and dried

HQ(aq) HF (aq)

2-3 washes

Polypropylene container

At least 4 water washes

Residue neutralised. Numerous water washes

Residue passed into 53 micron sieve

Residue >53 microns added to sodium polytungstate (SG 2.00)

53 micron sieve suspended in bath of water

Residue <53 microns bottled for acritarch work

Centrifuged at 2500 RPM for 10 minutes

Centrifuge tube

Undissolved mineral matter washed and weighed

Palynomorphs taken from surface of polytungstate, washed and transferred to flat dish

Palynomorphs picked with glass pipette and transferred to cover slip

Petri dish containing palynomorphs

Sodium polytungstate

Cover slip fixed to aluminium stub

taken. Where possible, winnowing features such as shell lags were avoided as fine particulate material may have been lost. Deeply weathered exposures were not sampled as organic material may have been oxidised. If the section permitted, samples of 1-2kg were taken in order to allow repeat processing.

**Sample processing.** All steps involved in the extraction and concentration of chitinozoans were recorded for each sample in a 'breakdown,' and 'post-breakdown' processing book. Processing procedure is shown in Text-fig. 13.

1. Lichens, mosses and any other plant debris were removed from each sample with a steel knife. Each piece of rock was scrubbed under running water (with a little detergent) using a wire brush to remove the outer 'skin' of each specimen.

2. The rock was crushed using hammer or fly press. The crushed sample was transferred to a 2mm mesh sieve and the fine portion removed. Any chips over 10mm were picked from the sample and re-crushed. In order to minimise contamination all equipment was washed and dried after each sample had passed through the crushing process.

3. A weak solution of detergent was added to the sample after crushing. The liquid was agitated and decanted in order to remove remaining finer portions and contaminants. This was repeated until no cloudiness was observed in the run-off water.

4. When dry, 20-25g of limestone, or 15g of shale, were transferred to polypropylene containers and labelled with a sample number.

5. Calcium carbonate was removed from each sample by the addition of concentrated hydrochloric acid in order to prevent the formation of insoluble calcium fluoride and other fluoride salts; dissolution of carbonate cements also aids the disaggregation of the rock. Each sample was covered with 45-50ml of warm water and 10ml of concentrated hydrochloric acid was introduced until effervescence ceased. After settling, the supernatant liquid was decanted and neutralised carefully with sodium carbonate before running to waste. The sample was diluted a further three times. (All the procedures involving the use of concentrated acids were carried out in a fume cupboard with the extractor on. Protective clothing, lab coat, sleeve protectors, face shield and rubber
gloves, were worn. All steps in the chemical attack of rock were recorded on a separate sheet located near the fume cupboard).

6. Silicates were removed by the addition of 45ml of 40% Hydrofluoric acid. The sample was left in acid for 24-48 hours and stirred, very gently, three times a day. After this, the acid was diluted and decanted. Hydrofluoric acid was neutralised with calcium hydroxide in preference to sodium carbonate as the reaction is more controllable and avoids the production of toxic sodium fluoride.

7. When the sample had been diluted with water four times, a solution of 5% boric acid was added. The boric acid complexes with any remaining fluorine ions and allows them to be neutralised and disposed of safely. After a further dilution, universal indicator liquid was added to the acidic residue within the polypropylene container. A dilute solution of sodium carbonate was introduced to the container until a green neutral response is gained from the indicator liquid. It is vital that only small amounts of sodium carbonate are added as saturation may cause degradation of certain palynomorphs such as spores and acritarchs. After a minimum of four further dilutions (or until a definite neutral response was gained even with agitation) the sample bottle was washed with a solution of sodium carbonate and removed from the fume cupboard.

8. Nitric acid may be used to remove pyrite or amorphous organic material but this proved unnecessary for the samples from the Ludlow area.

Chitinozoan concentration. The dissolved sample was placed in a 53μm sieve which was gently agitated within a bowl of water. The finer fraction in the bowl was retained and bottled for possible acritarch studies. The coarser portion was transferred to a 50ml measuring cylinder and sodium polytungstate, at a specific gravity of 2.00, was introduced in order to separate palynomorphs (specific gravity 1.40) from any remaining silica (specific gravity 2.65). This was left to separate for ten minutes and palynomorphs were then skimmed from the surface. After introducing additional sodium polytungstate, the remaining residue was centrifuged to extract any further organic material. After palynomorphs had been skimmed from the centrifuge tube the remaining mineral matter was washed and concentrated upon a filter paper and weighed.
Sodium polytungstate is a less toxic alternative to heavy liquids such as bromoform or zinc bromide. It is sold in powder form and is made up to the desired specific gravity (in the case of palynology 2.00) by the addition of distilled water. It is important not to use tap water as this may result in the formation of calcium polytungstate and other insoluble compounds. Chitinozoans must be thoroughly, but gently, washed with distilled water after the use of sodium polytungstate to prevent crystallisation and production of polytungstate 'pseudo-ornament.' Because of the current price of sodium polytungstate all washings were retained and the polytungstate reclaimed. The safest method of achieving this was by heating a beaker of the dilute sodium polytungstate in a water bath, taking care to ensure that the solution did not boil dry. After evaporation, the concentrated solution was filtered and the specific gravity set once more by the addition of distilled water.

**Chitinozoan picking.** After sodium polytungstate was washed from the residue, chitinozoans were picked from a petri dish filled with distilled water using the capillary action of a fine glass pipette (as suggested by Paris 1981, p. 66). The pipettes were manufactured in the laboratory by heating small lengths of 5mm diameter soda glass tubing in a bunsen flame and then drawing them out into long threads. Picking was carried out using a Wild M8 Zoom stereomicroscope with x10 eyepieces. The dish was divided into number of equal segments and, depending on abundance, all or just a number of segments were picked in order to estimate numbers of chitinozoans per gram. Individuals were deposited upon a round 21mm glass cover slip resting upon a slide labelled with the sample number and the proportion of the concentrated residue that it represents. Coverslips were dried under cover in order to prevent build up of particulate and fibrous material. Mineral salts remaining within the distilled water were sufficient to cement the chitinozoans to the glass slide; salts in tap water obscure detail by forming a crust over the specimens upon evaporation. When dry, chitinozoans could be moved around the cover slip with a fine paint brush dampened with distilled water. Any remaining residue was checked under the microscope and any unusual or particularly well preserved specimens picked and placed on a separate cover slip.
Photography. The cover slips were fixed upon 12.5mm diameter Cambridge stubs by wax or by folding tin foil, glued to the stub, onto the edges of the cover slip (as suggested by Paris 1981, p.67). Both methods were useful, and the tin foil method cleaner, but if large numbers of specimens were present on a stub the foil could obscure or damage specimens when folded. Silver dag was painted from the stub to the underside of the coverslip to ensure good electrical conductivity and minimise charging. After the dag dried the stub was gold-coated in a sputter coater for 120 seconds. Photographs were taken using a Hitachi S-520 Scanning Electron Microscope at a voltage of 20Kv. Ilford HP5 400ASA 27din black and white film was used and user initials, date, sample number and film number recorded on each frame. A data sheet recording film details, brief comments and a simple sketch was placed with each set of processed negatives. Two contact sheets were made of each film and used to prepare a species and stratigraphic index.

Slide production and logging. After S.E.M. work, coverslips were removed from aluminium stubs by heating on a hot plate if wax-cemented or by undoing the tin foil. The cover slips were inverted and fixed to a clean glass slide with Petropoxy 154 at a temperature of 135°C, curing for 10 minutes. The gold coating is sufficiently thin to allow light to pass through the slide. Any wax or silver dag remaining on the surface of the coverslip was removed with a steel blade. Counts were made using a standard palynological microscope. The percentages and numbers of chitinozoans per gram calculated are not definitive for any particular horizon as such values may show a considerable degree of variability. However, these counts allow an approximation of changing chitinozoan diversity and abundance through time to be gauged. The elucidation of the variability of chitinozoan assemblages on individual bedding planes would be of great potential use palaeoenvironmentally but is unfortunately out of the scope of this work.

Biometric studies. Individuals were measured for biometric studies. If the majority of specimens belonging to a species were crushed it became necessary to record vesicular dimensions from flattened material. Flattening causes little increase in the length of a
chitinozoan but may increase its width. To accommodate this, a correction factor suggested by Paris (1981) of 0.7 or 0.8 (depending on the degree of flattening) was applied when measuring the width of the body and neck of flattened individuals.

**Specimen location.** Specimens are located using an England Finder slide. In the code M40/SH3(ii), M40 refers to the England Finder reference, SH3 to the sample horizon and (ii) to the slide number.

**Repository.** All type material is held at the British Geological Survey, Keyworth, Nottinghamshire. A representative suit of material is held at the University of Leicester.

**MORPHOLOGY.**

The terms used to describe vesicle form are shown in Text-fig. 14. Further features are shown in Text fig. 15.

**Vesicle wall structure and composition.** Paris (1981, p. 68) recognised three layers in the chitinozoan wall: 1. periderm - the external membrane. 2. ectoderm - the inner membrane. 3. endoderm - internal structures such as a prosome. Many authors have identified a different layer composition, from single to multiple layering. The vesicles on specimens from Ludlow are often heavily fractured making detailed observation of the wall structure difficult. The suggestion of Wrona (1980a, p.133) that vesicle wall layering may be a factor of preservation could explain such diverse observations: "The nature of diagenetic transformations of organic matter may suggest that an initially multilayered wall can undergo a diagenetic homogenization, while an initially homogeneous wall can undergo diagenetic differentiation." The vesicle wall is often of variable thickness. Thinning often occurs around the oral pole and a thickening commonly forms the mucron. The vesicle wall is often perforated with circular holes, ranging from 1 to 20μm in diameter. Occasionally these perforations fail to penetrate the interior of the vesicle (see pl. 1, fig. 16 & pl. 10, fig. 6). Eisenack (1931, p. 86) interpreted these perforations as being caused by bacterial or fungal activity. The perforations appear too regular for this explanation and the suggestion of Wrona (1980a,
TEXT FIG. 14. Chitinozoan morphology for; a. Desmochitinidae, b. Conochitinidae and c. Lagenochitinidae. Figs d-k represent vesicle surface structure; d-g are classified as either textured, bald or unornamented; h-k are classified as ornamented (based on Paris 1981, pp. 68 & 70).
p.141) that the morphological distinctness and regular perforation and the smoothness of the pores is indicative of enzymal digestion is certainly plausible.

Grahn & Afzelius (1980) described the presence of pore canals and 'empty spaces' in the vesicle wall of four species of Ordovician chitinozoans. The pore canals were regarded as too small to allow the passage of pseudopodia. The 'empty spaces' if filled with gas were postulated to have acted as a flotation aid.

The chemical composition of the vesicle is not true chitin, a non-protein. It has been suggested that the original composition of the vesicle, pre-fossilisation, may have been similar to pseudochitin (Collinson & Schwalb 1955). An investigation into the chemical composition of the chitinozoan vesicle is certainly required. Unfortunately such analyses may require up to 1 g of pure material, an amount that would take a great deal of picking.

**Ornament.** Only the surface of the vesicle wall shows any structural differentiation. This outer layer (or layers) may become abraded by mechanical action giving the impression of a lack of ornament. In such cases detailed observation under the scanning electron microscope often reveals remnants of ornament that may have been invisible under the transmitted light microscope. The external surface may exhibit ornament composed of raised granules, filose elements such as spines or hairs or possess large appendices and branchioles. Filose elements and branchioles may exhibit preferential organisation as is found in *Gotlandochitina* or show random distribution as is the case in *Angochitina*. Concentration of granules around the aboral margin often occurs in species of *Belonechitinia* and *Eisenackitina* and certain structures may be restricted to or near the aboral margin such as the carina (or cingulum) in *Cingulochitina* and the appendices of *Ancyrochitina*. Appendices are often hollow (pl. 11, fig. 11) and may have aided flotation as suggested by Laufeld (1974, p.123) and Wrona (1980a, p.128). Appendices were not found to communicate with the interior of the vesicle. In addition to these larger scale ornamentation features, Paris (1981, p.70) identified and named various microstructural features of the test wall. These and the other forms of ornament are illustrated in Text-fig. 14d-k.
A. Vesicular dimensions; L=length of vesicle, ln=length of neck, lb=length of body, D=maximum diameter of vesicle, d=minimum diameter of vesicle, da=diameter of aperture, app=length of appendix, col=width of collarette or rim.

B. Descriptive terminology for vesicle form.
Internal structures. Internal structures include the operculum, prosome and 'opisthosome'. These are referred to as the endoderm in Paris' scheme (1981, p.72).

The operculum hermetically seals the chitinozoan from the outside environment. It is distinguished from the prosome (under Paris' scheme) by its external position such that it may come into contact with the base of the next individual in a chain and hence be functional in the formation of chains (see pl. 1, figs 13, 14 & pl. 5, figs 2, 5).

The definition of a prosome given by Paris (1981, p.72) is followed here. The position of a prosome deep within the neck of the chitinozoan differentiates it from the operculum. The prosome hermetically seals the chitinozoan, effectively plugging the neck. The prosome may be a simple disc or a more complex tubular structure. The prosome was only rarely encountered in an external position in type Ludlow material. Those recovered were poorly preserved and showed little detail (see pl. 11, fig. 8 & pl. 12, fig. 3).

The 'opisthosome' was described as a spindle shaped structure towards the aboral pole of the chitinozoan (see Combaz et al. 1967, p. 31). This feature is not recorded in any of the material recovered from Ludlow. Paris (1981, p. 72) also failed to identify the structure. Wrona (1980a, p. 142) suggested that the opisthosome is an artifact created by infolding of the vesicle or the product of mineral infill.

Organisation. In this study only forms belonging to Cingulochitina were found organised in chains. Twins of individuals were common, particularly in the Middle Elton Formation, but long chains of more than two individuals were only rarely encountered (pl. 5, fig 1, 6). More complex organisation is possible, for example in cocoons and aggregates (Kozlowski 1963, fig. 4), radial aggregates (Wrona 1980a, pl. 36, fig. 2) and as mat like structures. It is possible that all species of chitinozoan originally occurred as chains. Paris (1981, p. 74) postulated that species belonging to Angochitina, Ancyrochitina and Sphaerochitina may have originally occurred in monospecific clusters, a muscilaginous sheath reinforcing connection between individuals but disaggregating soon after release from the parent. Detailed reviews of chitinozoan organisation were given by Wrona (1980a, p.145-148) and Paris (1981, p. 73-77).
BIOLOGICAL AFFINITIES

Eisenack (1931) first speculated upon the biological affinities of the Chitinozoa and noted similarities with the protozoans of the rhizopod order Testacea. Collinson & Schwalb (1955) also favoured a protistan relationship and noted similarities with the class Rhizopoda (Sarcodina).

Kozowski (1963) suggested that chitinozoans may represent the eggs of a marine metazoan and pointed towards similarities with egg capsules of recent annelids and gastropods. Support for a metazoan origin of chitinozoans came from Jenkins (1970) who, on the basis of coincidence, stratigraphic range and vesicle composition, suggested that chitinozoans may represent a pre-sicular stage of graptolites.

The hermetically sealed nature of chitinozoan vesicles has been used to support theories that regard chitinozoans as the resting stage (cyst) of marine protists. Obut (1973) noted similarities with dinoflagellates. Paris (1981, p. 80) has noted a resemblance between the Portuguese Caradoc acritarch *Lusitanium lusitanicum* (Debbaj) and species belonging to *Eisenackitina*, with only the reduced diameter of the pylome preventing inclusion within the Chitinozoa.

Reid & John (1978) have suggested a possible relationship may exist between chitinozoans and tintinnids. To support their argument they point towards the similarity in shape, the hermetically sealed nature of chitinozoans and tintinnids, the possibility of spinose ornaments and the resistance of both groups to strong acids.

Cashman (1990, 1991) believes chitinozoans to be related to foraminifera. His theory is based upon the discovery of small structures on the surface of *Bulbochitina*, from the lower Devonian of Quebec, that he has interpreted as 'juveniles.' Cashman believes that the mucron was a dynamic feature in active chitinozoans, functioning as an opening for the emergence of pseudopodia and that pores over the surface of the chitinozoan vesicle facilitated communication between the pseudopodial cytoplasm and cytoplasm within the chitinozoan. Chitinozoans possessing a closed mucron and pores
would represent the encysted stage in Cashman's model (the state in which the majority of chitinozoans are recovered), the cycle being completed by the ejection of the mucron plug or the operculum and the release of new juveniles.

Locquin (1981) proposed that similarities exist between Chitinozoa and certain fungi and that chitinozoans represent the oldest extinct group within the Mycota, the Chitinomycetes. Unfortunately it is not possible to comment upon any specific similarities as the majority of Locquin's material is poorly illustrated. In addition, it is probable that the structures illustrated by Locquin (1981, pl. 7, figs 1-7) are framboidal pyrite spheres and not spores.

Suggestions have also been made that chitinozoans may represent an unknown group (Bockelie 1981) or possess a polyphyletic origin (Laufeld 1974).

As chitinozoans are hermetically sealed units, theories that they represent the active stage of a marine protist are untenable. The active/adult stage in the cycle proposed by Cashman (1990), in which the mucron is open, may be a preservational effect. In material from Ludlow openings on the base were only discovered on poorly preserved specimens. The overlapping nature of the holes on many chitinozoan vesicles suggests a parasitic origin and an interpretation of these structures as borings. Such structures were not pores linking the interior of the chitinozoan vesicle with the outside environment.

The sealed nature of the chitinozoan test makes theories that promote chitinozoans as a cyst or egg easier to support. The argument of Laufeld (1974, p.123) that the 'welded nature' of appendices requires the presence of external metazoan tissues has to be dropped when one considers the presence of pseudopodia in certain foraminifera. However, relationships with protist cysts are generally proposed on the basis of superficial morphological features such as vesicle shape and a definite relationship has yet to be proved.

Jaglin & Paris (1992) regard vesicles that display abnormalities, such as budding structures and multiple necks, as teratologic cases. They suggested that such 'teratologic chitinozoans' indicate a dysfunction within an 'egg laying' chitinozoan animal and do not represent vegetative reproduction, sexual dimorphism or any other normal process. Such
an assumption is contrary to theories that identify such unusual features as some part of a chitinozoan life cycle (for example Locquin, 1981 and Cashman, 1990).

The chain forming habit of chitinozoans finds its closest analogues within the Metazoa. In addition, the cocoons containing numerous monospecific clusters of chitinozoans reported by Kozlowski (1963) may be interpreted as egg sacs or egg cases. An alternative suggestion of Reid & John (1978) is that such structures may be faecal pellets, the monospecific nature of the chitinozoan clusters resulting from a bloom of a single chitinozoan species in a similar way that dinoflagellate red tides occur today.

A metazoan origin would support the graptolite/chitinozoan relationship suggested by Jenkins (1970). However, work by Paris (1981, p.79) has shown that the diversity of chitinozoans and graptolites does not show the coincidence one would expect if chitinozoans were the pre-sicular stage of graptolites: The Silurian/Devonian of the Armorican area, although rich in chitinozoans, does not show a high diversity of graptolites. Paris also noted that the only groups of organisms to exhibit a similar range to that of chitinozoans (Tremadoc to Upper Devonian, and possibly Lower Carboniferous) are the cornulites, tentaculites and certain orthoconic cephalopods. The relative diversity peaks of these organisms and chitinozoans do not match.

It is possible that the creature responsible for the production of chitinozoans was a soft bodied metazoan. In this case, physical evidence of the chitinozoan animal may have to be sought from an appropriate conservation Lagerstätten.

**TAXONOMIC / NOMENCLATURE DISCLAIMER.**

This publication is not deemed to be valid for taxonomical purposes [see article 8b in the International Code of Zoological Nomenclature (1985) edited by W.D. Ride et. al.]
SYSTEMATIC DESCRIPTIONS

Group CHITINOZOA Eisenack, 1931

Order OPERCULATIFERA Eisenack, 1972

Diagnosis. (translated from Paris 1981, p.109) Chitinozoans which are sealed with an operculum located at or near aperture such that it may be functional in formation of chains.

Remarks. Eisenack (1972, p.68) defined the Operculatifera as chitinozoans which possess a simple disk-like closing mechanism, the operculum. Paris (1981 p.109) re-defined the Operculatifera as chitinozoans which possess an operculum that may be functional in the formation of chains by adherence to the base of the next individual. Due to the difficulty in observing either an operculum or a prosome in some chitinozoans, Eisenack's classification scheme is often unworkable. A chitinozoan's potential for chain formation via the joining of an operculum of one individual to the base of another is easier to assess; if the operculum is located near the aperture it is assumed that chain formation utilising the operculum is possible. The Operculatifera effectively comprises those forms which do not possess a neck but which may show evidence of a collarette.

Family DESMOCHITINIDAE Eisenack, 1931

Diagnosis. (translated from Paris 1981, p.110) Small Operculatifera with no neck. Operculum may be simple or provided with a membranous fringe located at aperture or at base of collarette. Vesicle bald or ornamented. Carina (cingulum), mucron can be present. Chain formation common.

Subfamily DESMOCHITININAE Paris, 1981

Genera encountered. Calpichitina, Bursachitina.

Emended Diagnosis. (modified after Paris 1981, p.111) Bald or ornamented Desmochitinidae. Lenticular, spheroidal, ovoid, cylindrical or conical vesicle. Possible presence of copula or collarette. Chain formation common.
Discussion. C.(Calpichitina) granosa sp. nov., possesses granular ornament, necessitating an expansion of original diagnosis to include ornamented forms.

Genus BURSACHITINA Taugourdeau, 1966

Type species. Desmochitina bursa Taugourdeau & Jekhowsky 1960, p.1225.


Bursachitina sp. A Pl. 1, figs 1-4

Occurrence within the Ludlow area. Lowest occurrence, PC11 in the Much Wenlock Limestone Formation at Pitch Coppice, 3.5m from the base of the Ludlow Series (Text-fig. 37). Also found in the Lower Bringewood Formation around Todding (LT3, Text-fig. 43) and the Upper Bringewood Formation at Aymestrey (A2 & A5 Text-fig. 45). Highest occurrence W0 in the upper part of the Lower Leintwardine Formation along the Whitcliffe at Ludlow (Text-fig. 51). May form up to 25% of an assemblage but more commonly 2-10%. Often poorly preserved.

Description. Conical to cylindro-conical species of Bursachitina. Straight to slightly convex tapering flanks. Discrete mucron. Rounded aboral margin corresponds to maximum diameter of chitinozoan. Collarette present, flared or cylindrical. Some specimens show slight flexure at base of collarette. Unornamented vesicle may show evidence of pyrite pitting. Exact nature of mucron and base not determined due to poor preservation. Operculum not observed. No specimens found associated in chains or twins.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC13(14); PC12(3); LT3(2); A5(1); A2(1); W0(3). Length is plotted against maximum diameter of vesicle on Text-fig. 17. All measurements in μm.
TEXT-FIG. 17. Size variation for *Bursachitina* sp. A and *Bursachitina* sp. B. The measurements for each species are taken from individuals found in various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 18. Size variation of all *Calpichitina* (*Calpichitina*) species. The measurements for each species are taken from individuals found in various horizons and sections (see systematic descriptions for details).
**Discussion.** Although of similar dimensions (see Text-fig. 17) the conical vesicle form and lack of distinct flexure distinguish it from *Bursachitina* sp. B. *B.* sp. A may be confused with eroded specimens of either *Eisenackitina lagenomorpha* or *Eisenackitina toddingensis.* However, detailed observation of the vesicle surface reveals remains of ornament on eroded *Eisenackitina* species and should prevent confusion with *B.* sp. A. Although not rare, the poor preservation of this species necessitates that it be left in open nomenclature.

**Bursachitina** sp. B  
Pl. 1, figs 5, 6

*Occurrence within the Ludlow area.* Lowest occurrence in the Middle Elton Formation (GR23) on the Goggin Road section (Text-fig. 39). Only constitutes a minor proportion of assemblages; 0.1-3%. Generally restricted to the Middle Elton Formation but one possible specimen recorded from the Lower Bringewood Formation along Goggin Road (GR59 - see Text-fig. 40). Preservation variable, specimens generally flattened.

*Description.* Cylindro-conical species of *Bursachitina* with convex flanks. Flexure developed. Collarette cylindrical, non-flaring. Aboral margin broadly rounded. Base flat to slightly convex, provided with discrete mucron. Nature of mucron not observed because of poor preservation. Flexure variably developed and present just below collarette. Convex flanks and broadly rounded aboral margin give body globose appearance. Maximum diameter of vesicle developed above aboral margin. Operculum not observed. No individuals found associated in twins or chains.

*Measurements.* Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR23(5);

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<tbody>
<tr>
<td>Mean</td>
<td>135</td>
<td>73.5</td>
<td>46</td>
<td>50</td>
<td>1.9</td>
<td>1.5</td>
</tr>
<tr>
<td>Range</td>
<td>99-191</td>
<td>52-114</td>
<td>31-96</td>
<td>34-86</td>
<td>1.0-3.1</td>
<td>1.0-2.4</td>
</tr>
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</table>
GR25(5). Length is plotted against maximum diameter of vesicle on Text-fig. 17. All measurements in μm.

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<tbody>
<tr>
<td>Mean</td>
<td>180</td>
<td>93</td>
<td>61</td>
<td>62</td>
<td>2.0</td>
<td>1.5</td>
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<tr>
<td>Range</td>
<td>162-201</td>
<td>52-110</td>
<td>53-67</td>
<td>53-67</td>
<td>1.5-3.4</td>
<td>0.8-1.8</td>
</tr>
</tbody>
</table>

Discussion. Although generally larger than *B*. sp. A (Text-fig. 17) this species is most readily separated on the basis of its convex flanks. The lack of ornament separates this form from any species within Genus *Eisenackitina*. As numbers are low and preservation poor, this species is left in open nomenclature.

Genus **CALPICHITINA** Wilson & Hedlund, 1964


Subgenus **Calpichitina** *(Calpichitina)* Paris, 1981

*Type species.* As for genus.


Discussion. Original diagnosis excluded ornamented forms (Paris 1981, p.127) but is expanded here to accommodate the ornamented species *Calpichitina (Calpichitina) granosa*. Maximum diameter of the vesicle is plotted against the ratio of maximum diameter of the vesicle to diameter of the aperture for all *Calpichitina* species in Text-fig. 18.
Calpichitina (Calpichitina) granosa sp. nov. Pl. 1, figs 7, 8

Name. Latin granosus, granular, referring to the characteristic ornament of this species.

Holotype. M40/SH3(ii); pl. 1, figs. 7, 8. Lowest specimen in a chain of three. Limestone of Lower Ludfordian age; lowermost Leintwardine Formation at Sunnyhill Quarry, Mortimer Forest, Ludlow. SO 4950 7255, see Text-fig. 46.

Occurrence within the Ludlow area. First encountered from the Lower Bringewood Formation (DP15, Text-fig. 42) close to the boundary between the Lower and Upper Bringewood formations along Deer Park Road (the exact position of the base of the Upper Bringewood Formation is unclear). Common across the base of the Ludfordian at Sunnyhill Quarry. Generally a minor proportion of assemblages (0.1%) but can constitute up to 35%. Highest recovery from SH14 in the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 47). Preservation generally poor, one chain recovered.

Diagnosis. Species of C. (Calpichitina) possessing ornament of rounded granules which decrease in size and density towards the aperture. Convex flanks. Aboral margin rounded. Flat to slightly convex or concave base.

Description. Granular ornament generally concentrated on lower half of vesicle. Some specimens exhibit abrupt change in size and density of ornament below aboral margin, becoming less conspicuous on base. Largest granules 4μm in diameter, 2μm high. Operculum may show faint concentric striations in transmitted light. Only one chain of three individuals encountered (pl. 1, fig. 7) Nature of attachment not clear but possibly involves adherence of operculum or collarette of one individual to base of next individual. Given low abundance of this species it is difficult to assess if chain formation is common or rare.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). DP15(5); SH3(3); SH5(1); SH6(5). All measurements in μm.
Discussion. *C.(Calpichitina) granosa* is distinguished from other chitinozoans within the Desmochitininae by its ornament. Some confusion is possible with small individuals of *Eisenackitina*. However the absence of a mucron and the lenticular form of *C.(Calpichitina)*, where D>L, make it easily distinguishable from the conical *Eisenackitina* species where L>D. *C.(Calpichitina)* species often rest upon a glass slide with the aperture facing the observer; this makes the granular ornament of *C.(Calpichitina) granosa* difficult to observe in transmitted light. Separation of this species from others of *C.(Calpichitina)* often requires the enhanced resolution of the S.E.M.

### Calpichitina (Calpichitina) gregaria?

Paris & Kriz 1984 Pl. 1, figs 9-12


**Occurrence within the Ludlow area.** First encountered in W1 in the upper part of the Lower Leintwardine Formation, 84cm below the base of the Upper Leintwardine Formation, along the Whitcliffe at Ludlow (Text-fig. 51). Often a minor constituent of assemblages (2-7%) but forms at least 27% of the chitinozoan assemblage in W1. Last recorded in W19, 65cm below the base of the Lower Whitcliffe Formation (Text-fig. 52). Preservation poor to moderate.

**Description.** *C.(Calpichitina)* species without ornament but exhibiting scaly folds of vesicle. Aperture provided with thin rim upon which may be developed a small collarette. Flanks convex. Aboral margin rounded. Base convex. Scales on vesicle distributed randomly over surface of chitinozoan, may occur on the simple disk-like operculum. Scales can reach height of 1.5 - 2µm. Where present, collarette is thin, often

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<td>57-85</td>
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</table>

Mean da 13 individuals; mean D/da, 13 individuals; mean col, 8 individuals.
ripped, and of similar height to vesicle scales. No chains or any organisation between individuals observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). W1(8); W19(1). All measurements in μm, compared with the mean values from Paris & Kriz (1984, p.159) for 40 specimens of *C. (Calpichitina) gregaria*

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<td>34-42</td>
<td>1.4-2.8</td>
<td>1.6-2.0</td>
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Mean col; 4 individuals

**Discussion.** One of the main diagnostic features of *C.(Calpichitina) gregaria* is its ability to form large colonies (Paris 1984, p. 159; pl. 1, figs 8,11,13). Due to the lack of characteristic juxtaposition and the poor preservation of material, the specimens encountered at Ludlow are not directly assigned to *C.(Calpichitina) gregaria*. *C.(Calpichitina) gregarial* is distinguished from *C.(Calpichitina) sp. aff. hemsiensis* by its vesicle scales and from *C.(Calpichitina) granosa* by the lack of granular ornament.

**Calpichitina (Calpichitina) sp. aff. hemsiensis** (Laufeld, 1974) Pl.1, figs 13-19 aff. 1974  *Desmochitina hemsiensis* Laufeld, p.78, figs 40A-C.

**Occurrence within the Ludlow area.** Lowest occurrence SH17 in the Upper Bringewood Formation, 40cm below the base of the Ludfordian at Sunnyhill Quarry (Text-fig.46). Where encountered, commonly forms 2-3% of assemblages (36% in SH3). Last specimen recorded from W18, 75cm below the base of the Lower Whitcliffe Formation as exposed along the Whitcliffe at Ludlow (Text-fig. 52). Preservation variable.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). SH2(1); SH5(3); SH16(1); W1(2); W18(1). All measurements in μm, Lauf’74 are a range of values for *C.(Calpichitina) hemsiensis* from Laufeld (1974, p.78).

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<td>62-79</td>
<td>23-41</td>
<td>1.1-3.4</td>
<td>1.3-2.8</td>
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Col; 6 individuals

Discussion. The short rapidly widening collar observed by Laufeld (1974, p 78) on *C. (Calpichitina) hemsiensis* is not found on specimens from Ludlow. *C. (Calpichitina) hemsiensis* is reported from the Hemse and Eke beds on Gotland (Laufeld 1974, p.78). The thickened rim around the aperture distinguishes *C.(Calpichitina)* sp. aff. *hemsiensis* from other *C.(Calpichitina)* species in this study. Confusion is possible with specimens of *C.(Calpichitina) gregaria* but vesicle folds and the remains of a collarette on specimens of *C.(Calpichitina) gregaria* enable separation.
Subfamily EISENACKITININAE Paris, 1981

*Genera encountered. Eisenackitina.*


**Genus EISENACKITINA** Jansonius, 1964

*Type species. Eisenackitina* Jansonius, 1964


*Discussion.* The majority of *Eisenackitina* species found in the type Ludlow possess an ornament of randomly distributed granules, commonly concentrated around the aboral margin, similar to those recorded from Gotland (Laufeld 1974, p.80).

**Eisenackitina intermedia** (Eisenack, 1955) Pl. 1, figs 16-18 & Pl. 2, figs 1-7

1955 *Conochitina intermedia* Eisenack, p. 161-162, pl. 3, fig. 8.

1964 *Conochitina intermedia* Eisenack; Eisenack, p. 317-318, pl. 26, figs 14, *non* fig.15.

1968 *Conochitina intermedia* Eisenack; Eisenack, p. 161, pl. 25, figs 26-27.

1974 *Conochitina intermedia* Eisenack; Laufeld, p. 63, figs 26a-e.

1982 *Conochitina intermedia* Eisenack; De Bock, p. 852, pl. 1, figs 9-11.

*Holotype.* Geologisch-Palaontologisches Institut der Universität Tübingen, pl. 3, fig. 8, präparat 51 Nr. 7.

*Occurrence within the Ludlow area.* Numerous specimens from Gorstian and Ludfordian strata in the Ludlow area. Lowest recovery from GR30 in the the Middle Elton Formation (Text-fig. 39). Only becomes important in the upper Gorstian and Ludfordian where it commonly forms 10-30% of assemblages. Highest occurrence W45
TEXT-FIG. 19. Size variation of *Belonechitina lauensis* and *Eisenackitina intermedia*. The measurements for each species are taken from individuals found in various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 20. Size variation of *Eisenackitina lagenomorpha* and *Eisenackitina lagenomorpha?*. The measurements for each species are taken from individuals found in various horizons and sections (see systematic descriptions).
in the Upper Whitcliffe Formation along the Whitcliffe at Ludlow (Text-fig. 55).

Preservation variable.

**Diagnosis** (after Eisenack 1955, p. 161). Conical vesicle form. Flanks parallel or taper towards the aperture. Operculum sits at base of variably developed, variably flaring, thin collarette. Aboral margin rounded to sub-rounded. Base flat to slightly convex; supports discrete basal scar. Granular ornament covers most of vesicle apart from central portion of base. Granules commonly 1.5\(\mu\)m in diameter, 0.5-1\(\mu\)m high on aboral margin; decrease in size and concentration towards aperture and central portion of base.

**Description.** Collarette may flare slightly. Faint, concentric striations sometimes visible around variably developed basal scar. No individuals found associated in twins or chains.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR38(1); GR45(2); GR48(1); GR51(2); LT3(1); LT5(1); SH2(3); SH3(4); SH3(4); SH15(4); SH16(1); SH17(1); SH22(10); SH24(3); SH30(1). Vesicular dimensions are compared with those of *Belonechitinia lauensis* in Text-fig. 19. Values of holotype are for *Conochitina intermedia* from Eisenack (1955, p.161). All measurements in \(\mu\)m.

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<tr>
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<td>63</td>
<td>38</td>
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<td>2.0</td>
</tr>
<tr>
<td>Range</td>
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<td>41-88</td>
<td>23-57</td>
<td>23-62</td>
<td>1.5-3.0</td>
</tr>
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**Discussion.** The oral position of the operculum is inconsistent with an assignment of this species to *Conochitina* or any species of the Conochitinidae. The conical vesicle form and ornament place it within *Eisenackitina*. *E. intermedia* is distinguished most readily from *E. lagenomorpha*, *E. philipi* and *E. toddingensis* on the basis of its straight flanks and, in the case of *E. philipi*, lack of distinctive basal differentiation. The larger
forms of \textit{E. intermedia} are distinguished from \textit{B. lauensis} by their straight flanks and lack of a neck. In general \textit{E. intermedia} possesses a lower L/D ratio than \textit{B. lauensis} (see Text-fig 19).

\textit{Global occurrence.} Laufeld (1974, p. 65) recorded \textit{E. intermedia} from the Burgsvik, Harma and Sundre Beds on Gotland (upper Ludfordian). Nestor (1990, p. 81) reported this species from the Kuressaare Formation (Ludfordian) and Pridoli strata of Estonia, but the specimen illustrated (pl. 15, fig. 11) resembles \textit{B. lauensis} or possibly \textit{E. lagenomorpha} rather than the straight-flanked \textit{E. intermedia}. De Bock (1982, p. 856) noted the presence of \textit{E. intermedia} in the upper Ludlow sequence of the South-eastern Montagne Noire of France.

\textbf{Eisenackitina lagenomorpha} (Eisenack, 1931) Pl.2, figs 8-14.

1931 \textit{Conochitina lagenomorpha} Eisenack, p. 85, pl. 1, fig. 12-13.

1955 \textit{Conochitina lagenomorpha} Eisenack; Eisenack, p. 160-161, pl. 1, figs 1-2.

1964 \textit{Conochitina lagenomorpha} Eisenack; Eisenack, p. 318, pl. 26, fig. 16.

1968 \textit{Conochitina lagenomorpha} Eisenack; Eisenack, p. 164, pl. 25, fig. 28-33.

1970 \textit{Conochitina lagenomorpha} Eisenack; Eisenack, p. 306, figs 1p-q.

1974 \textit{Eisenackitina lagenomorpha} (Eisenack); Laufeld, p. 80, figs 44a-f.

1982 \textit{Eisenackitina lagenomorpha} (Eisenack); De Bock, p. 852, pl. 1, fig. 6-8.

\textit{Holotype.} Holotype lost during the second world war.

\textit{Neotype.} Geologisch-Paläontologisches Institut der Universität Tübingen, 1955, pl. 1, fig. 1, präparat Gotl. 48 Nr. 7.

\textit{Occurrence within the Ludlow area.} Lowest recovery LT3 in the Lower Bringewood Formation in the Todding area (Text-fig. 43). Only becomes important across the base of the Ludfordian where it commonly constitutes 20-40\% of assemblages. Highest recovery SH40 in the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 50). Well preserved material found across the base of the Ludfordian at Sunnyhill Quarry.
Diagnosis (after Laufeld 1974, p. 80). Cylindro-conical vesicle. Flanks gently curved to sygmoideal. Flexure variably developed. Base flat to slightly convex, provided with low, wide and concentrically striated mucron surrounded by wide furrow. Aboral margin rounded. Ornament consists of rounded, irregularly shaped granules; preferential concentration and maximum size (4μm long, approximately 1-1.5μm high) on aboral margin. Ornament disappears towards aperture and central portion of base.

Description. Curvature of flanks and overall length of *E. lagenomorpha* very variable (see Text-fig. 20). Flexure may be developed so as to give impression of neck. Degree to which ornament decreases in size and density also variable. Some specimens exhibit concentric striations on surface of vesicle, parallel to aperture. Operculum situated at base of large, variably fringed, often flaring collarette which makes detailed observation of operculum structure difficult.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). SH2(4); SH3(8); SH4(5); SH6(6); SH15(2); SH16(2); SH17(2); SH18(4); SH24(8); SH26(2). Length is plotted against maximum diameter of vesicle on Text-fig. 20. All measurements in μm, compared with those for the holotype of *Conochitina lagenomorpha* from Eisenack (1931, p.85).

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<td>47-108</td>
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<td>28-59</td>
<td>1.3-2.7</td>
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Discussion. Because of its great variability, *E. lagenomorpha* is easily confused with other *Eisenackitina* species. Many transitional forms exist, especially with *E. intermedia*. The two species are most readily separated on the basis of the curvature of the flanks: *E. lagenomorpha* exhibits a curvature whereas the flanks of *E. intermedia* are straight. In contrast to specimens described by Laufeld (1974, p. 82), some British
specimens show a distinct flexure. *E. lagenomorpha* is distinguished from *E. toddingensis* sp. nov. by the rectangular / box-like body and, where preserved, the distinctive ring-like mucron of the latter. *E. lagenomorpha?* has a squat appearance with a lower L/D ratio, although it can be seen that the two fields overlap (Text-fig. 20).

**Global occurrence.** Eisenack has reported this species from the *Beyrichia* Limestone (Eisenack 1955, p.161) and the Öved-Ramsåsa Group in Scania, Sweden (Eisenack 1964, p. 318). Nestor (1990, p. 81, 83) recorded *E. lagenomorpha* from the Paadla Formation (approximately upper Gorstian / lower Ludfordian) and noted its importance at the base of the Kuressaare Stage (Ludfordian) in Estonia; a similar increase in the significance of this species is noted at the base of the Ludfordian in the type area. *E. lagenomorpha* was also recorded from the Kaugatuma Formation (Pridoli) in the same publication. A similar range was noted by Laufeld (1974, p. 82) for Gotland, *E. lagenomorpha* appearing towards the top of the Hemse Marl and ranging through the Eke and Sundre beds (a range from upper Gorstian to upper Ludfordian). De Bock (1982, p. 856) reported this species from upper Ludlow sediments in the South-eastern Montagne Noire region of France and suggested a correlation may be possible with the Eke beds of Gotland, approximately equivalent to the Lower and Upper Leintwardine formations in the type Ludlow area.

**Eisenackitina lagenomorpha?** (Eisenack, 1931) Pl. 2, figs 15, 16 & Pl. 3 figs 1, 2

**Occurrence within the Ludlow area.** Lowest occurrence SH21, 4.2m below the base of the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 46). Common throughout the Lower Leintwardine Formation (Ludfordian) at Sunnyhill Quarry. Commonly 10-30% of assemblages, 48% of assemblage of SH28. Highest occurrence W0 in the upper Lower Leintwardine Formation along the Whitcliffe at Ludlow (Text-fig. 51). Preservation variable.

**Description.** Small, cylindro-conical species of *Eisenackitina* with pronounced curvature to flanks, wide flat base and characteristic squat appearance (low L/D ratio). Simple circular operculum sits at base of thin, slightly flaring collarette. Irregularly
granular ornament shows preferential concentration on rounded to sub-rounded aboral margin; ornament size and concentration decreases towards aperture and central portion of base. If point of maximum convexity is located close to aboral margin a pronounced sygmooidal curvature may be developed. Granular ornament reaches a size of 1μm in diameter, 1μm high. No individuals were observed in twins or chains.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). SH1(6); SH2(6); SH3(5); SH4(3); SH5(2); SH6(2); SH15(7); SH16(10); SH22(4); SH26(3); SH30(2).Length is plotted against maximum diameter of vesicle on Text-fig. 20. All measurements in μm.

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<td>17-51</td>
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**Discussion.** It is possible that *E. lagenomorpha?* represents a small morphotype of *E. lagenomorpha* or an entirely separate species. Morphological features and biometrics have failed to adequately solve this problem which is why it has been designated *lagenomorpha?* rather than 'sp. aff' or 'cf.' Specimens referred to *E. lagenomorpha?* are generally smaller than *E. lagenomorpha*; their low L/D ratio giving them a characteristically squat appearance.

**Eisenackitina philipi** Laufeld, 1974        Pl. 3, figs 3-9

1974 *Eisenackitina philipi* Laufeld; p. 83, figs 46a-f.

1882 *Eisenackitina philipi* Laufeld; De Bock, p. 853, pl. 1, figs 1-5.

**Holotype.** Dept. Historical Geology and Palaeontology, University of Lund, fig. 46B, LO 4637 T.

**Occurrence within the Ludlow area.** Lowest occurrence from W20 in the Upper Leintwardine Formation, 46cm below the base of the Lower Whitcliffe Formation along
TEXT-FIG. 21. Size variation of *Eisenackitina philipi* from various sections. (see systematic descriptions for details).

TEXT-FIG. 22. Size variation of *Eisenackitina toddingensis* from various sections (see systematic descriptions for details).
TEXT-FIG. 23. Size variation of *Cingulochitina* sp. aff. *cingulata* from various sections and horizons (see systematic descriptions for details).

TEXT-FIG. 24. Size variation of *Cingulochitina convexa*, *Cingulochitina gorstynensis* and *Cingulochitina* sp. A. Individuals taken from various horizons and sections (see systematic descriptions for details).
the Whitcliffe at Ludlow, (Text-fig. 52). This species is important in assemblages from the Lower Whitcliffe Formation, often constituting over 50% of all recovered specimens (97% in W29). Highest recorded occurrence from W45 in the Upper Whitcliffe Formation (Text-fig. 55). Preservation of material within the Lower Whitcliffe Formation is very variable but generally poor.

**Diagnosis** (after Laufeld 1974, p.83). Cylindro-conical vesicle. Flanks curved, broadly rounded flexure and shoulder. Collarette may flare slightly. Base convex, provided with protruding central portion. Vesicle covered by granules which show slight concentration around rounded aboral margin. Maximum diameter of vesicle located at or just above aboral margin.

**Description.** Protruding central portion of base may reach height of 6|μm and occupy over half of basal area. This structure may exhibit concentric striations and be surrounded by a low depression. Centre of base may exhibit hole (5-20|μm in diameter); this does not communicate with interior of vesicle. Maximum size of granular ornament (5|μm) at aboral margin. Granule size does not decrease significantly in size or concentration towards the aperture. Body often globose in appearance. On many specimens oral diameter is narrow giving high mean D/da ratio of around 2.0. No individuals found associated in twins or chains.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). W28(19); W29(1); W31(5); W32(4); W34(8); W41(8). Length is plotted against maximum diameter of vesicle on Text-fig. 21. All measurements in |μm. Holotype values taken from Laufeld (1974, p.83).

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<td>30-59</td>
<td>1.2-2.4</td>
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</table>

36
Discussion. Specimens of *E. philipi* encountered in this study, like those described from Gotland by Laufeld (1974, p.83), show great variability in overall vesicle form. Degree of curvature of flanks and presence or absence of shoulder are the most variable features. However, the large central portion of the base easily distinguishes *E. philipi* from other Eisenackitina species in the type Ludlow.

Global occurrence. Laufeld (1974, p.83) reported this species from the uppermost Hemse Marl through the Eke Beds and into the lower part of the Burgsvik Beds of Gotland (approximately equivalent to uppermost Gorstian to mid Ludfordian). In Estonia it is found in the Paadla Formation and the lowermost Kuressaare Formation, approximately upper Gorstian to lower Ludfordian (Nestor 1990, p. 81, 83). De Bock (1982, p. 856) noted the presence of *E. philipi* in the upper Ludlow sediments of the South-eastern Montagne Noire region of France and suggested a correlation may be possible with the Eke beds of Gotland, approximately equivalent to the Lower and Upper Leintwardine formations in the type Ludlow area.

**Eisenackitina toddingensis** sp. nov. Pl. 3, figs 10-13 & Pl. 4 figs 1, 2

Name 'toddingensis' after the village of Todding, Shropshire.

Holotype. K34-1/DP24(i); pl. 3, fig. 10. Limestone of high Lower Bringewood Formation (Gorstian); Deer Park road, Mortimer Forest, Ludlow. SO 4845 7135 (Text-fig. 42).

Occurrence within the Ludlow area. Lowest occurrence GR31 in the Middle Elton Formation along Goggin Road (Text-fig. 39). Common from top of Upper Elton Formation and throughout the Lower Bringewood Formation commonly forming 20-30% of assemblages. Highest occurrence DP25 close to the Lower Bringewood Formation / Upper Bringewood Formation boundary on Deer Park Road (the base of the Upper Bringewood Formation is unclear, see Text-fig. 42). Preservation variable.

Diagnosis. Cylindro-conical vesicle. Flanks slightly convex to straight. Slight shoulder. Aboral margin rounded. Small, ring like, mucron occupies central portion of
base. Ornament of low rounded granules sparsely distributed over vesicle surface. Base free of ornament.

Description. Flanks and shoulder often give body rectangular outline. Collarette often straight but may flare slightly. Mucron consists of ring of material, 14μm in diameter, 4μm wide and approximately 1μm high. Base flat, slightly convex or highly concave. High degrees of basal concavity probably due to preservational effects. Granules show slight increase in size and concentration on aboral margin where they can reach 1-1.5μm in diameter. Concentration of ornament varies greatly between individuals. No individuals found associated in twins or chains.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR36(3); GR48(5); GR49(1); GR52(7); DPR3(3); DP4(1); LT1(5); LT2(11); LT3(7); LT5(6); LT6(8). Vesicle length is plotted against maximum vesicle diameter on Text-fig. 22. All measurements in μm.

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Discussion. Dimensions of *E. toddingensis* are very similar to *E. intermedia* and *E. lagenomorpha* and separation of these species via biometric studies is not possible. However, in well preserved material, the cylindro-conical vesicle form of *E. toddingensis* separates it from the more purely conical *E. intermedia*. *E. lagenomorpha* shows a greater flank curvature and lacks the rectangular body outline of *E. toddingensis*. If well preserved, the ring-like mucron may be used as a distinguishing feature.
Subfamily PTEROCHITININAE Paris, 1981


Genus **CINGULOCHITINA** Paris, 1981

*Type species. Desmochitina cingulata* Eisenack, 1937.


*Discussion.* Shoulder and flexure may be present. Base may be flat to highly convex. Base may support a mucron. Flaring collarette observed on some species. Chain formation common.

**Cingulochitina** sp. aff. *cingulata* (Eisenack, 1937) Pl. 4. figs 3-6

aff. 1937  *Desmochitina cingulata* Eisenack, p. 220, pl. 15, figs 6-7.

aff. 1974  *Linochitina cingulata* (Eisenack); Laufeld, p.97, figs 57a-e.

aff. 1982  *Cingulochitina cingulata* (Eisenack); Verniers, p.20, pl. 6, fig. 122; pl.7, figs 148, 157-169.

*Occurrence within the Ludlow area.* Common from across the base of the Ludfordian at Sunnyhill Quarry (Text-fig. 46). Lowest occurrence in the Lower Bringewood Formation, DP15, close to the boundary between the Lower and Upper Bringewood formations on Deer Park Road (Text-fig. 42). Forms 2-10% of assemblages. Highest recovery SH9, 50 cm above the base of the Ludfordian at Sunnyhill Quarry (Text-fig. 46). Well preserved, three dimensional material has been isolated.

*Description.* Cylindro-conical vesicle. Base flat. No mucron or basal scar. Simple operculum sits at base of well-developed flaring collarette. Constriction developed just above carina. Carina wide, thin and structurally undifferentiated. Maximum diameter of

39
vesicle located just above constriction. Flanks commonly convex but can be straight. Base sometimes exhibits faint concentric striations. No individuals observed in twins or chains. Carina shows range in width from 6.6 - 8.5μm.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). SH2(5); SH3(1); SH15(4); SH16(7). Vesicle length is plotted against maximum vesicle diameter on Text-fig. 23. All measurements in μm.

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**Discussion.** The well-developed thin carina separates *C. sp. aff. cingulata* from any other *Cingulochitina* species encountered within this study. It is possible that *C. cingulata* (reported from the Wenlock of Gotland by Laufeld, 1974) represents an ancestral form of the species that is found in the Ludlow area but is separated from that species by its lack of a basal scar.

*Cingulochitina convexa* (Laufeld, 1974) Pl.4, figs 7-12


1982 *Cingulochitina convexa* (Laufeld ); De Bock, p. 852, pl.1, fig. 23-24.

1982 *Cingulochitina convexa* (Laufeld ); Verniers, p. 22. pl.6, fig. 126, 127a, b.

**Holotype.** Dept. Historical Geology and Palaeontology, University of Lund, fig. 58D, LO 4655 T.

**Occurrence within the Ludlow area** Restricted to the Middle Elton Formation (Gorstian). Lowest occurrence GR21 (Text-fig. 39). Constitutes a variable proportion of assemblages from 10-57% Highest recovery GR33 (Text-fig. 39). Generally well preserved.
**Diagnosis.** (after Laufeld 1974, p.97) Cylindro-conical to cylindro-ovoid *Cingulochitina* species with highly convex flanks and convex base. Carina short, 1.2-2.00\(\mu\)m wide. Shoulder and flexure broadly rounded. Vesicle widens into a long thin collarette towards aperture. Maximum width of vesicle occurs some distance above carina.

**Description.** Base often shows concentric striations. Possibility of faint basal scar. No twins or chains of individuals were found.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR21(1); GR22(6); GR23(12); GR24(4); GR25(10); GR31(3). Vesicle length is plotted against maximum vesicle diameter on Text-fig 24. All measurements in \(\mu\)m; holotype values taken from Laufeld (1974, p.98).

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**Discussion.** *C. convexa* is distinguished from *C. sp. aff. cingulata* on the basis of its shorter carina and highly convex base. Although of similar dimensions *C. sp. A* is readily separated from *C. convexa* by its straight to only slightly convex flanks. *C. gorstiensis* is generally shorter, and possesses a base that is flat or only slightly convex.

**Global occurrence.** Laufeld noted this species in unit c of the Hemse Beds (Gorstian) through to the Eke beds (lower Ludfordian) on Gotland. De Bock (1982, p.856) noted it from the upper Ludlow sequence of the South-eastern Montagne Noire of France. Verniers (1982, p. 22) reported this species in formation MB9 (early to middle Ludlow) of his informal lithostratigraphic scheme in the Mehaigne area of the Brabant Massif, Belgium.
Cingulochitina gorstyensis sp. nov. Pl.4, figs 13-15 & Pl. 5, figs 1-7

Name. 'gorstyensis' after the village of Gorsty near Ludlow.

1981 Cingulochitina sp. aff. serrata. (Taugourdeau & Jekhowsky); Paris, p. 170, pl. 21, figs 12, 13, 16.

Holotype. K38/GR31(i); highest individual in a chain of three, pl. 5, figs 1-3. Siltstone of Gorstian age. Middle Elton Formation along Goggin Road, Mortimer Forest, Ludlow. SO 4748 7160 (Text-fig. 39).

Occurrence within the Ludlow area. Lowest occurrence GR19 in the Middle Elton Formation along Goggin Road (Text-fig. 39). Numerous individuals and chains of individuals recovered from the Middle Elton Formation where it normally forms 10-30% of assemblages and sometimes up to 80% (GR26). Occasional specimens from the Lower Bringewood Formation (Gorstian age) at Lower Todding. Highest recovery LT4 in the Lower Bringewood Formation at Lower Todding (Text-fig. 43). Well preserved material is common.

Diagnosis. Short, cylindro-conical species of Cingulochitina with convex flanks and flaring collarette. Aboral margin angular and supports short carina commonly 2μm wide. Vesicle widens rapidly above carina towards its maximum diameter. Base flat to slightly convex, free of any structures. Disk-like operculum seals wide aperture, edges of operculum curving orally and aborally fitting flush with edge of vesicle (see pl. 5, fig. 2, 5).

Description. Degree of flank curvature and flare of collarette vary greatly. Faint, concentric striations, running parallel to aperture sometimes present. Spacing of lineations irregular. Chains and twins common. Collarette attaches itself to base of next individual, covering most of basal area. Carina plays no part in attachment of individuals.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR22(7); GR23(25); GR24(12); GR25(6). Length is plotted against maximum vesicle diameter on
Text-fig. 24. All measurements in µm, compared with mean values from 50 specimens of *Cingulochitina* sp. aff. *serrata* from Paris (1981, p. 171).

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<td>120</td>
<td>65</td>
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<td>46</td>
<td>1.8</td>
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Discussion. Although the length of *C*. sp. aff. *serrata* described by Paris (1981, p. 171) exceeds that of *C. gorstyensis*, the similarity of the carina and overall vesicle form suggest that they are the same species. Paris (1981, p. 171) suggests that *C*. sp. aff. *serrata* (named *C. gorstyensis* here) could be the ancestral form of *C. serrata* (Taugourdeau & Jekhowsky 1960). *C. gorstyensis* is distinguished from *C. convexa* by its flat base and from *C*. sp. A by its shorter vesicle length and greater flank curvature.

Global occurrence. Paris (1981, p. 171) reported this species from the Formation de Sazes, Synclinal de Buçaco, Portugal (basal Ludlow) and the Formation du Val, Heuzé, Amorican Massif (Pridoli).

*Cingulochitina* sp. A Pl. 5, fig. 8-13

Occurrence within the Ludlow area. Restricted to the Middle Elton Formation. Lowest occurrence GR23 along Goggin Road (Text-fig. 39). Only forms a minor portion of assemblages (less than 3%) Highest recovery GR31 (Text-fig. 39). Moderately well preserved.

Description. Conical vesicle. Flanks straight, tapering towards the aperture; possibility of slight convexity just above carina. Shoulder and flexure lacking. No basal differentiation. Base slightly convex. Variably developed carina, 1.5µm - 3µm wide. Maximum diameter of vesicle located at or just above carina. Collarette flares
slightly. Twins of individuals encountered, collarette adhering to base of next individual. Carina plays no part in attachment.

**Measurements.** Measurements have been taken from 6 specimens from GR23. Vesicle length is plotted against maximum vesicle diameter on Text-fig. 24. All measurements in μm.

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**Discussion.** This species shows greatest affinities with *C. convexa.* with which it shares similar vesicular dimensions (see Text-fig. 24) but is separated by its basal convexity and flank curvature. It is easily distinguished from *C. gorstiensis* by its straight flanks and larger size and from *C. sp. aff. cingulata* by its smaller carina. Until additional material is recovered this species is left in open nomenclature.

Order PROSOMATIFERA Eisenack, 1931

**Diagnosis** (translated from Paris 1981, p. 109-110). Chitinozoans sealed by a prosome located within the neck, such that it is non functional in chain formation.

**Remarks.** Eisenack (1972 p. 68) defined the Prosomatifera as chitinozoans which are closed by a prosome. Redefinition of the group by Paris (1981, p. 109) was based upon the position of the sealing mechanism rather than its structural complexity. Thus in the scheme of Paris, Prosomatifera are those forms with a neck sealed by a simple disk or by a more complex annulated structure, both of which are referred to as a prosome.

Family CONOCHITINIDAE Eisenack, 1931

Discussion. Under Eisenack's (1972, p. 68) scheme, forms belonging to Family Conochitinidae would be included within the Operculatifera because of their relatively simple sealing structure, described by Eisenack as an operculum. Under the scheme of Paris (1981 p. 109-110) the sealing structure's position in the middle or at the base of a neck places such forms in the Prosomatifera and identifies the sealing structure as a prosome.

Subfamily BELONECHITININAE Paris, 1981


Genus BELONECHITINA Jansonius, 1964

Type species. Conochitina micracantha robusta Eisenack, 1959


Discussion. Jansonius (1964, p. 906) included forms with ornament restricted to the aboral margin within Conochitina. Such forms are included here within Belonechitina leaving Conochitina restricted to completely unornamented forms.

Belonechitina latifrons (Eisenack, 1964) Pl. 6 figs 8-13

1964 Conochitina latifrons Eisenack, p. 316, pl. 26, fig. 11.
1974 Conochitina latifrons Eisenack; Laufeld, p. 65, figs 27a-e.
1990 Conochitina latifrons Eisenack; Nestor, p. 81, pl. 15, fig. 7.

Holotype. Geologisch-Palaontologisches Institut der Universität Tübingen, pl. 26, fig. 11, präparat Gotl. 48 Nr. 7.

Occurrence within the Ludlow area. Restricted to the upper Gorstian. When recovered it forms only 0.7-3.6% of assemblages. Lowest recovery GR48 in the upper
TEXT-FIG. 25. Size variation of *Belonechitina latifrons*, *Belonechitina lauensis* and *Belonechitina mortimerensis*. Individuals taken from various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 26. Size variation for four species of *Conochitina*. Individuals taken from various horizons and sections (see systematic descriptions for details).
Upper Elton Formation along Goggin Road (Text-fig. 40). Also recovered from the Lower Bringewood Formation on the same section, the Lower Bringewood Formation on Deer Park Road (Text-fig. 42) and from the Lower Bringewood Formation in the Todding area. (Text-fig. 43, 44). Highest recovery along Deer Park Road from DP22 (Text-fig. 42) in the Lower Bringewood Formation, close to the boundary with Upper Bringewood Formation.


*Description.* Constriction near aboral margin variably developed. Possibility of slight flexure 2/3 along length of vesicle from aboral margin. Neck often cylindrical. Ornament shows greatest concentration and size (1-1.5μm in diameter) around aboral margin becoming less prominent towards the aperture. Wide mucron (up to 60μm in diameter) often stands proud of base (6μm in some cases). Central portion of mucron commonly shows evidence of concentric striations, picked out by very fine rugose structure.

*Measurements.* Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR49(1); GR59(3); GR66(1); DP20(1); T7(1);. Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig. 25. All measurements in μm, compared with holotype from Eisenack (1964, p. 316).

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Discussion. This species is moved to the Belonechitinae on the basis of its conspicuous granular ornament. Although it would appear that the type Ludlow specimens are more slender than those reported by Eisenack (1964, p. 316), the low numbers of individuals encountered from the type Ludlow precludes reliable comparisons with other populations. Constriction of the vesicle near the aboral margin is the characteristic feature of this species. It is further separated from *B. mortimerensis* sp. nov. by the lack of a distinct shoulder or flexure. *B. lauensis* is separated from *B. latifrons* on the basis of its large size and aboral constriction. Eroded specimens of *B. latifrons* may be mistaken for *C. pachycephala* which also possess a constriction near the aboral margin. In such circumstances, detailed observation of the vesicle using the scanning electron microscope should reveal evidence of ornament, even on eroded specimens.

Global Occurrence. Laufeld 1974 (p. 66) reported this species from the upper Klinteberg Marl through to the Hemse Marl of Gotland, a range approximately equivalent to strata from the Lower Elton Formation to at least the Lower Bringewood Formation. Nestor (1990, p. 81) noted the presence of this species in the mid Ludlow of Estonia.

**Belonechitina lauensis** (Laufeld, 1974) Pl. 6 figs 1-7

1974 *Conochitina lauensis* Laufeld, p. 66, fig 28a-c.

1990 *Conochitina lauensis* Laufeld; Nestor, p.81, pl. 15, fig. 9.

*Holotype.* Dept. Historical Geology and Palaeontology, University of Lund, fig. 28A, LO 4635 T.

*Occurrence within the Ludlow area.* Lowest recovery GR30, Middle Elton Formation along Goggin Road (Text-fig. 39). Numerous specimens from the Middle Elton Formation to the Lower Leintwardine Formation. Forms a common component of assemblages in strata of Gorstian age. Forms a varying proportion of Gorstian assemblages (0.9 to 50%). Less common in strata of Ludfordian age where it very rarely makes up 10% of assemblages. Highest occurrence W20, Upper Leintwardine
Formation, 44cm below the base of the Lower Whitcliffe Formation along the Whitcliffe at Ludlow (Text-fig. 52). Preservation variable.


**Description.** Degree of flank curvature varies from straight to concave. In some cases initial convexity observed around aboral margin. Ornament of irregularly shaped granules covers entire vesicle except central portion of base. Granules show maximum concentration and size (1.3μm in diameter) on aboral margin. Occasional specimens from Lower Leintwardine Formation show the development of small cones (commonly 1μm in length) on the aboral margin. Mucron wide and low (around 32μm in diameter) often situated in depression at centre of base. Mucron may show evidence of concentric striations. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR47(5); GR49(4); GR51(3); LT3(3); LT5(2); LT6(3); LT11(2); DP10(1); DP11(2); DP20(1); SH20(1); SH25(1). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig. 19 and Text-fig. 25. All measurements in μm, compared with the holotype figured by Laufeld (1974 p. 66).

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<td>Range</td>
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<td>34-62</td>
<td>36-75</td>
<td>1.8-2.8</td>
<td>1.2-2.1</td>
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</table>

**Discussion.** This species was formerly included within Genus *Conochitina* by Laufeld (1974, p.66). Under the taxonomic scheme of Paris (1981, p.108) ornamented Conochitinidae are moved to the Genus *Belonechitina* within the Belonechitininae. The specimens from the type Ludlow area are generally larger than those from Gotland. The
holotype figured by Laufeld (1974, p. 66, fig. 28) does not show a high degree of flank concavity, with one side of the vesicle virtually straight; this was also found to be the case for many specimens from Ludlow. The concavity of the flanks and the small size of *B. lauensis* separates it from other *Belonechitina* species. *B. latifrons*, as encountered within the Ludlow area, may also exhibit a slight concavity of the flanks but is much larger than *B. lauensis* and possesses a constriction orally of the aboral margin. *Eisenackitina intermedia* resembles this form but is separated on the basis of its 'external' operculum and smaller size.

**Global Occurrence.** In Gotland this species ranges from the Hemse Beds to the lower middle Eke Beds, a range very similar to that in the type Ludlow (Laufeld 1974, p. 67). The species is reported from the mid Ludlow of Estonia, approximately equivalent to the Lower Bringewood and Upper Leintwardine formations (Nestor 1990, p.81).

**Belonechitina mortimerensis** sp. nov. Pl. 6, fig. 14 & Pl. 7, figs 1-8

Name ‗mortimerensis‘ refers to Mortimer Forest near Ludlow.

**Holotype.** T41/DP10(ii); pl.7, figs 5, 6. Calcareous siltstone of Gorstian age from the Lower Bringewood Formation on Deer Park Road, Mortimer Forest, Ludlow, SO 4852 7122, see Text-fig. 41.

**Occurrence within the Ludlow area.** Lowest recovery DPR3, Lower Bringewood Formation along Deer Park Road (Text-fig.41). This species forms a common component of assemblages from the Lower Bringewood Formation along Deer Park Road. Forms 2-15% of populations. Occasional specimens recovered from the Upper Bringewood Formation at Aymestrey (Text-fig. 45). Highest recovery from SH16, Upper Bringewood Formation, 20cm below the base of the Ludfordian at Sunnyhill Quarry (Text-fig. 46).

**Diagnosis.** Cylindro-conical vesicle. Shoulder and flexure variably developed but always present. Flanks below shoulder convex. Base flat to convex. Aboral margin

**Description.** Great variation in length and vesicle form. A constriction may be developed at base of neck. Neck may flare slightly, take on cylindrical form or exhibit a bulge at some point along its length. Wide mucron (commonly 45µm in diameter) may stand 12µm proud of base. Possibility of variably developed depression (3-16µm in diameter) in centre of mucron. This does not communicate with interior of vesicle. Granular ornament commonly shows maximum concentration and development (1-1.5µm in diameter) around aboral margin. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). DP10(3); DP11(1); DP22(2); DP20(1); DP24(9); A5(4); A7(5); SH20(4). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig 25. All measurements in µm.

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<td>2.4-3.9</td>
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</tr>
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</table>

**Discussion.** *B. mortimerensis* shows greatest affinities with *B. latifrons* but lacks the aboral constriction of that species. *B. mortimerensis* is separated from *B. lauensis* by its higher degree of mucron development and larger size.

Subfamily CONOCHITININAE Paris, 1981

*Genera encountered.* Conochitina Eisenack, 1931, Rhabdochitina Eisenack, 1931.

Discussion. Members of this subfamily are structurally simple, so the effects of preservation, especially the flattening of individuals, often makes identification to specific level difficult. Observation under the scanning electron microscope is often essential when dealing with such specimens.

Genus CONOCHITINA Eisenack, 1931

Type species. Conochitina claviformis Eisenack, 1931


Discussion. As argued by Paris (1981, p. 177), Conochitina should be restricted to unornamented forms. Ornamented Conochitinidae otherwise resembling Conochitina should be included within the Belonechitininae. Conical ornamented species with an external operculum, originally included within Conochitina are included within the Eisenackitininae. Following Paris (1981, p. 178), conical unornamented species with an external to near external operculum are included within the Genus Bursachitina of the Desmochitininae.

Conochitina edjelensis elongata? Taugourdeau, 1963  Pl. 7, figs 9-14, Pl. 8, figs 1, 2

? 1963 Conochitina edjelensis elongata Taugourdeau, p. 138, pl. 3, fig. 59-66

? 1967 Conochitina edjelensis elongata Taugourdeau; Cramer, p. 87-88, pl. 2, fig 48-59, non 50.

Occurrence within the Ludlow area. Common across the base of the Ludlow Series at Pitch Coppice and Goggin Road. Lowest recovery PC13, 3.5m from the base of the Ludlow Series at Pitch Coppice. Constitutes a variable proportion of assemblages; 5-69%. Occasional specimens recovered from the Middle Elton Formation on Goggin
Road (GR23-GR25, Text-fig. 39). Highest recovery in the Upper Elton Formation 2.4m from the base of the Lower Bringewood Formation (GR42, Text-fig. 40).

**Description.** Cylindrical chitinozoan with characteristic rectangular outline. Flanks straight. Shoulder and flexure absent. Base flat. Small centrally located mucron. Flanks parallel or taper slightly towards the aperture. Aboral margin rounded. Mucron often faint, sometimes surrounded by low, concentrically striate depression. Mucron commonly 10μm in diameter. Vesicle surface unornamented, or may show faint rugose ornament at higher magnifications. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC11(2); PC13(17); GR1(2); GR2(6); GR3(1); GR5(5); GR23(4); GR25(1). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig 26. All measurements in μm, compared with the mean of 43 specimens of *C. edjelensis elongata* in Taugourdeau 1963, p. 133.

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**Discussion.** The rectangular outline of this species distinguishes it from any other within the type Ludlow area. *C. pachycephala* is often found associated with this species but is separated by its larger size and higher L/D ratio. Although of similar size (Text-fig. 26) the absence of shoulder or flexure distinguishes *C. edjelensis elongata* from *Conochitina* sp. A. *C. cf. proboscisfera forma truncata* has a distinctive mucron and *C. sp. aff. elegans* possesses concave flanks. Although the overall cylindrical form of this species is similar to that of *Rhab dochitina wakefieldi* sp. nov., the latter is much larger.

*C. edjelensis elongata* and the form described here both share a distinctive rectangular outline and vesicular dimensions. However, as *C. edjelensis elongata* is
regarded as a Saharan "middle to late" Llandovery species by Taugourdeau (1963, p. 138) and Combaz et al. (1967, p. 79) the form described here is not directly assigned to *C. edjelensis elongata*. The query placed after the specific name does not infer that poor preservation or low numbers prevent identification. In this case it indicates that a definite assignment is uncertain given the absence of this species through the majority of the Wenlock.

**Conochitina** sp. aff. *elegans* Eisenack, 1931 Pl. 8, figs 3-8

aff. 1931 *Conochitina elegans* Eisenack, p. 87, pl. 2 fig. 4.


**Occurrence within the Ludlow area.** Lowest recovery PC10 at Pitch Coppice, 2.6m below the top of the Wenlock Series (Text-fig. 37). Also recorded from across the Wenlock/Ludlow boundary on Goggin Road (Text-fig.38). Never forms more than 8% of an assemblage. Highest occurrence GR9, Lower Elton Formation on Goggin Road (Text-fig. 38). Preservation variable.

**Description.** Conical vesicle, flanks concave. Maximum diameter of vesicle located at or just above aboral margin. Base flat, mucron low and poorly developed. Oral portion of vesicle, including collarette, flares. Vesicle unornamented but may show faint rugose structure at high magnifications. Faint concentric striations observed on base of some specimens. Centre of mucron slightly concave; may exhibit small hole in centre, not possible to see if this communicates with interior of vesicle. Diameter of mucron varies from 11 - 17.5μm but always low-lying and inconspicuous. Aboral margin sometimes angular. Possible slight constriction of vesicle above aboral margin. Fringing observed on collarette of some specimens. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC10(1); GR9(3). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig. 26. All measurements in μm, compared with 12 specimens of *C. cf. elegans* from Paris (1981, p. 181).
Discussion. As only rare, generally poorly preserved, material has been recovered this species is left in open nomenclature. C. elegans is an upper Ordovician species (Eisenack 1959, p. 3). Unlike C. elegans, which possesses straight flanks with an accentuated curvature just above the aboral margin, the form encountered here shows a progressive curvature along the flanks. In this feature it shows similarities with C. cf. elegans described by Paris from the Arenig/Llanvirn sediments of the Synclinal de Domfront, NW France (1981, p. 181) but C. sp. aff. elegans of this study is shorter. Laufeld (1974, p. 60) reported specimens he called C. sp. aff. elegans from Gotland and Pitch Coppice. Unfortunately the Gotland form, which ranges from the upper Sheinwoodian to upper Gorstian on Gotland, was not illustrated and no vesicular dimensions were presented making direct comparisons difficult. The concave flanks of C. sp. aff. elegans distinguish it from other Conochitina species within this study. The slight shoulder and convexity of its body flanks separates Conochitina sp. A from C. sp. aff. elegans.

**Conochitina pachycephala** Eisenack, 1964

Pl. 8, figs 9-15 & Pl. 9, figs 1-3.

1964 *Conochitina pachycephala* Eisenack, p. 315, pl. 26, fig. 6.

1974 *Conochitina pachycephala* Eisenack; Laufeld, p. 69, figs 31a-e.

1981 *Conochitina pachycephala* Eisenack; Paris, p.182, pl. 19, figs 15-17.

1990 *Conochitina pachycephala* Eisenack; Nestor, p. 81, pl. 15, fig. 1.

**Holotype.** Geologisch-Paläontologisches Institut der Universität Tübingen, pl. 26, fig. 6, präparat Gotl. 10 Nr. 6.
TEXT-FIG. 27. Size variation of *Conochitina pachycephala* and *Rhabdochitina wakefieldi*. Individuals taken from various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 28. Size variation of *Ancyrochitina ancyrea, Ancyrochitina aymestreyensis* and *Ancyrochitina gogginensis*. Individual taken from various horizons and sections (see systematic descriptions for details).
Occurrence within the Ludlow area. Common from across the base of the Ludlow Series at Pitch Coppice and Goggin Road. Constitutes a variable proportion of assemblages, 13-86%. First identified in PC12, 3m below the top of the Wenlock Series at Pitch Coppice (Text-fig. 37). Highest recovery 20m above the base of the Lower Bringewood Formation along Goggin Road (GR68, Text-fig. 40).


Description. Maximum diameter of vesicle located at, or just below, mid length. Vesicle unornamented but may show faint rugose structure at higher magnifications. Concentric striation on mucron reported by Laufeld (1974, p.69) not observed on Ludlow material. Hole in centre of mucron not found to communicate with interior of vesicle. Diameter and height of mucron variable but can reach 20μm in diameter and stand 9.4μm proud of base. Constriction above aboral margin often very slight. Straight, unflared collarette may show slight fringing. Prosome not observed.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC1(2); PC2(2); PC4(3); PC6(11); PC7(3); PC10(1); GR2(4); GR3(2); GR9(2). Length is plotted against ratio of length and maximum diameter of vesicle on Text-fig 27. All measurements in μm, compared with the holotype figured by Eisenack (1964, p.315).

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<td>64-114</td>
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<td>40-93</td>
<td>3.1-6.1</td>
<td>0.8-2.0</td>
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</table>

Discussion. The large size and, when sufficiently developed, the vesicular constriction above the aboral margin distinguish this from other Conochitina species. Other than this feature, the higher L/D ratio separate it from C. edjelensis elongata? and
Conochitina sp. A. Although the mucron of C. pachycephala can be quite large, it lacks the robust qualities of that found on C. cf. proboscifera forma truncata. C. pachycephala is chiefly distinguished from Rhabdochitina wakefieldi sp. nov. by the basis of its clavate rather than cylindrical vesicle form.

Global Occurrence. Domning (1981c, p. 206) noted the presence of this species from the Coalbrookdale Formation (Wenlock Series, Sheinwoodian Stage) to the Lower Elton Formation (Ludlow Series, Gorstian Stage) in Shropshire. However, as this was not illustrated it is not possible to make a direct comparison with those figured here. A similar range from the Slite Beds to the lowermost part of the Hemse marl of Gotland has been reported by Laufeld (1974, p. 70). Paris (1981, p. 183) reported this species from the Wenlock and basal Ludlow sediments of the Synclinal de Buçaco, Portugal. In Estonia, it has only been recorded in the Wenlock (Nestor 1990, p. 81).

Conochitina cf. proboscifera forma truncata Laufeld, 1974 Pl.9, figs 4-9

Occurrence within the Ludlow area. Rare specimens from across the base of the Ludlow Series at Pitch Coppice (Text-fig. 37). Lowest recovery PC8, 50cm below the top of the Wenlock Series. Common in the Middle Elton Formation on Goggin Road, particularly between GR19 & 21 (Text-fig. 39) where it may form up to 80% of an assemblage. Highest occurrence GR48 in the Upper Elton Formation along Goggin Road (Text-fig. 40).

Description. Claviform vesicle. Flanks convex. Base flat to slightly convex. Prominent mucron. Aboral margin broadly rounded. Shoulder and flexure present but variably developed. Maximum diameter of vesicle located above aboral margin or at some point along flanks. Large mucron (up to 42μm in diameter standing 10-13.5μm proud of base) located centrally on base. Centre of mucron exhibits small depression which does not communicate with interior of vesicle. Concentric striations observed on mucron of some specimens. Vesicle unornamented but rugose texture observed around
aboral margin of some specimens. Where preserved, thin collarette may flare slightly.

Prosome not observed.

*Measurements.* Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC8(3); GR23(6); GR24(4); GR25(4); GR36(1). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig 26. All measurements in μm, compared with the range of values from an unspecified number of specimens in Laufeld (1974, p. 72).

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<td>48.68</td>
<td>2.5-3.9</td>
<td>1.3-1.6</td>
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*Discussion.* Overall vesicle form and vesicular dimensions of the species described here fit the limited description given by Laufeld (1974, p. 72). However, although a number of specimens have been recovered, no well preserved populations have been encountered. Because of this, and due to the fact that *C. proboscifera* is regarded as a Wenlock form (see Laufeld 1974, p.72), the species encountered in the Ludlow is not directly associated with *C. proboscifera*. Because of the possibility of a shoulder *C. cf. proboscifera forma truncata* may be confused with *Conochitina* sp. A, but is separated by its distinctive mucron and larger size. *C. pachycephala* possesses a mucron but this is only moderately developed when compared to that of *C. cf. proboscifera forma truncata*. In addition, *C. pachycephala* generally exhibits a higher L/D ratio. C. sp. aff. *elegans* possesses convex flanks lacking on *C. cf. proboscifera forma truncata*.

*Conochitina* sp. A  Pl. 9, figs 10-13

*Occurrence within the Ludlow area.* Only rarely encountered. Lowest recovery, PC12, 3m below the top of the Wenlock Series at Pitch Coppice. Also recovered from the Lower Elton Formation on Goggin Road. Highest recovery from GR9 in the Lower
Elton Formation (Text-fig. 39). Where it occurs, this species constitutes less than 5% of assemblages in the Wenlock of Pitch Coppice and 8-16% of the assemblages in the Lower Elton Formation of Goggin Road. Generally poorly preserved.

**Description.** Claviform vesicle. Flanks below variably developed shoulder and flexure are convex. Neck cylindrical. Maximum diameter of vesicle located at or just above angular aboral margin. Convexity of lower portion of flanks variable. Majority of individuals possess cylindrical neck; flare in oral portion of vesicle observed on some specimens. Test unornamented but may show faint rugose structure at high magnifications. Base damaged on all specimens but impression of flat base with discrete mucron gained from some (pl. 9, fig. 11). Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR8(2); GR9(3). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig 26. All measurements in μm.

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</table>

**Discussion.** *C. cf. proboscifera forma truncata* may also possess a flexure and shoulder. However, *C. sp. A.* is smaller and does not exhibit a prominent mucron. *C. pachycephala* is larger (higher L/D ratio) and, has a less prominent flexure than that seen in this species. *Conochitina* sp. A. lacks the rectangular, cylindrical vesicle form of *C. edjelensis elongata*? and the concave flanks of *C. sp. aff. elegans.*
Genus **RHABDOCHITINA** Eisenack, 1931

*Type species.* **Rhabdochitina magna** Eisenack, 1931


*Discussion.* Very few features separate *Rhabdochitina* from *Conochitina*. The latter may also be cylindrical with a very poorly differentiated neck (see *C. edjelensis elongata*?). The only convincing feature that separates the two forms is the overall length of the vesicle. Size alone is not a desirable feature upon which to separate genera, but the genus will be retained as these very large cylindrical forms are very distinctive within chitinozoan residues.

**Rhabdochitina wakefieldi** sp. nov. Pl. 9. figs 14-16 & Pl. 10, figs 1-4

*Name.* 'wakefieldi' after micropalaeontologist and colleague Dr. Matthew Wakefield who aided in the collection of material that yielded this species

*Holotype.* M32-3/LT11(i); pl. 9, fig 14-16. Limestone of Gorstian age from the Lower Bringewood Formation in the Todding area. SO 4100 7520, see Text-fig. 43.

*Occurrence within the Ludlow area.* Lowest occurrence PC13, 3.5m below the top of the Wenlock Series at Pitch Coppice (Text-fig. 37). Also encountered in the the Upper Elton Formation and the Lower Bringewood Formation on Goggin Road. (Text-fig. 40). Rare component of assemblages, where present constituting 3-5% of populations but occasionally 8% (GR63, Lower Bringewood Formation on Goggin Road, Text-fig. 40) and 21% (LT11, Lower Bringewood Formation, Lower Todding area, Text-fig. 43). Quite common in the Lower Bringewood Formation around Todding. Highest occurrence LT11 (Text-fig. 43).


*Description.* Cylindrical collarette may exhibit slight widening towards aperture. Discrete mucron commonly 10.5μm in diameter, often surrounded by wide circular
depression. Most of vesicle smooth, rugose structure may be present on aboral margin of some specimens. Vesicle often shows evidence of parasite boring. Prosome not observed.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC2(3); PC6(1); PC8(1); PC9(1); GR48(1); GR63(4); LT11(11). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig. 27. All measurements in μm.

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Discussion. Although *R. wakefieldi* exhibits similar dimensions to *C. pachycephala* (Text-fig. 27) it is separated by its cylindrical vesicle form. *C. edjelensis elongata* shows greatest affinities with this species, but the large difference in vesicular dimensions separates the two.

Family LAGENOCITINIDAE Eisenack, 1931


Subfamily ANCYROCHITININAE Paris, 1981


Genus ANCYROCHITINA Eisenack, 1955

Type species. Conochitina ancyrea Eisenack 1931

Diagnosis (After Eisenack 1955, p. 163). Ancyrochitininae with simple, branched or ramified appendices.

Remarks. It is difficult to differentiate Ancyrochitina species on the basis of vesicular dimensions (Text-fig. 28), so ornament form and style are important. Unfortunately the appendices are often broken, making specimens of the genus among the most difficult to determine to specific level in poor to moderately preserved material. The tubular prosome of this genus was not easily observed in the type Ludlow material. Prosomes present in an emergent position were poorly preserved and revealed no detailed structure (pl. 11, fig 8 & pl. 12, fig. 3).

Ancyrochitina ancyrea (Eisenack, 1931) Pl.10, figs 7-13

1931 Conochitina ancyrea Eisenack, p. 88-89, pl. 2, figs 8-11; pl. 4, fig. 4.
1955 Ancyrochitina ancyrea (Eisenack); Eisenack, p. 163-164, pl. 2, figs 7-9.
1974 Ancyrochitina ancyrea (Eisenack); Laufeld, p. 38, figs 4a-b; figs 5a-f.
1981 Ancyrochitina ancyrea (Eisenack); Paris, p. 274. pl. 20, figs 9, 11; pl. 21, figs 10, 19.
1982 Ancyrochitina groupe ancyrea (Eisenack); De Bock, p. 851, pl. 3, figs 14-17.

Holotype. Lost during second world war.

Neotype. Geologisch-Paläontologisches Institut der Universität Tübingen, 1955, pl. 2, fig. 7, Präparat 53 Nr. 1.

Occurrence in the Ludlow area. Lowest recovery from GR45 in the Upper Elton Formation along Goggin Road (Text-fig. 40). Common across the boundary between the Upper Elton Formation and Lower Bringewood Formation on Goggin Road, commonly comprising 20-60% of assemblages. Highest recovery W19, 64cm below the top of the Upper Leintwardine Formation along the Whitcliffe at Ludlow (see Text-fig. 52).

Description. Appendices generally wide-based, tapering towards bifurcating tip. Branching usually only occurs once although tips of some found to bifurcate to second order very slightly. Appendices circular in cross section, usually positioned perpendicular to aboral-oral axis of chitinozoan. Fine rugose texture observed on surface of vesicle. Small spines may occur on neck, but not common. Body flanks often convex, occasionally straight. In specimens with extremely convex base body may appear spheroidal. Neck may flare towards the aperture. Body constitutes 1/3-1/2 of the vesicle length. Prosome 30-40\(\mu\)m in length.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR47(12); GR48(3); GR49(7); GR51(2); GR59(2); GR60(3); DP25(1); A7(2); SH21(4); SH38(1); W19(3). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig. 28. All measurements in \(\mu\)m, compared with the holotype (Eisenack 1931, p. 88).

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<td>35-97</td>
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Discussion. As A. ancyrea exhibits similar vesicular dimensions to many other species of Ancyrochitina (see Text-fig. 28) a separation based primarily on the style and branching pattern of appendices and neck ornament is used. The simple branching pattern of A. ancyrea distinguishes it from species such as A. gogginensis and A. narcissus. Problems may occur where broken appendices give the impression of simple branching. A. ancyrea may be separated from A. aymestreyensis by the lack of
conspicuous neck ornament. A cf. *primitiva* does not exhibit any branching and the appendices commonly show a high degree of curvature.

*Global occurrence.* This species is reported from the Ordovician to Devonian but, following Laufeld (1974, p. 39), a restriction of this species to forms with simply branching appendices excludes those outside the Silurian. On Gotland Laufeld (1974) reported this species from the Lower Visby Beds to the top of the Hemse Beds (a range of Llandovery Series, Telychian stage to the Ludlow Series, lower Ludfordian Stage). Dorning (1981c, p.206), recorded it from the Telychian to upper Ludfordian of Shropshire and Paris (1981, p. 274) reported *A. ancyrea* from the Formation de Sazes (upper Wenlock, Ludlow and Pridoli?) of Portugal. De Bock reported forms he attributed to *Ancyrochitina* group *ancyrea* in the Upper Silurian to Devonian contact strata of the South-Eastern Montagne Noire, France.

*Ancyrochitina ansarviensis?* Laufeld, 1974 Pl. 10, fig 14, 15

*Ancyrochitina ansarviensis* Laufeld 1974, p. 39, figs 6a-b.

*Occurrence in the Ludlow area.* 1 specimen from SH3, 10cm above the base of the Ludfordian at Sunnyhill Quarry (O36-1/S3H3(ii), Text-fig. 46).


*Measurements.* Measurements made on only one specimen from the Lower Leintwardine Formation (SH3) at Sunnyhill Quarry. All measurements in μm, compared with the holotype of *A. ansarviensis* (Laufeld, 1974, p. 41).
Discussion. With only one specimen recovered it is very difficult to directly assign this specimen to *A. ansarviensis* or a new species. There is a high degree of similarity to *A. ansarviensis* reported from the Höggliq Beds (Wenlock, Sheinwoodian) of Gotland by Laufeld (1974, p. 41). However, the holotype figured by Laufeld exhibits less ornament and possesses larger appendices.

**Ancyrochitina aymestreyensis** sp. nov. Pl. 11, figs 1-5

*Name.* 'aymestreyensis' meaning from the village of Aymestrey in Shropshire.

*Holotype.* O35-1/A5(i); pl. 11, fig. 4. Limestone of Gorstian age, Upper Bringewood Formation at Crown Cliffe Quarry, Aymestrey. SO 4248 6547, see Text-fig. 45.

*Occurrence in the Ludlow area.* Lowest recovery in the Upper Elton Formation on Goggin Road (GR48, Text-fig. 40). Additional specimens also recovered from the Lower Bringewood Formation along Goggin Road (Text-fig. 40) and the Lower Bringewood Formation exposure along Deer Park Road (Text-fig. 41). Highest recovery A4, 2m from the top of the Upper Bringewood Formation at Aymestrey (Text-fig. 45).


*Description.* Body 1/3-1/2 of vesicle length. Simple appendices broad based, circular in cross section. Appendice length variable, branching either at tip or close to base of appendices. Long neck spines (up to 20µm in length) located in proximal, central.

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Values of app for the holotype are a range of values for specimens which include the holotype.
or distal position on neck, relative to aperture. Neck spines branch simply at the tip. Fine rugose texture observed on surface of vesicle. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). A4(1); A5(9). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig. 28 and against the ratio of length to neck length on Text-fig. 31. All measurements in µm.

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</table>

Values of app; 7 individuals only

**Discussion.** It is difficult to separate this species from *A. ancyrea* on the basis of vesicular dimensions (see Text-fig. 28). Like *A. ancyrea* it possesses simply branching appendices but may be distinguished by the conspicuous neck ornament and the elongate appearance of *A. aymestreyensis*. *A. sp. B* shares a similar vesicle form but is generally larger (Text-fig. 31) and lacks conspicuous neck ornament.

**Ancyrochitina gogginensis** sp. nov. Pl. 11, figs 6-12 & Pl. 12, figs 1-4

*Name.* 'gogginensis' after Goggin road

*Holotype.* J36/GR23(ii); pl. 11. figs 10-12. Siltstone of Gorstian age; Middle Elton Formation exposure along Goggin Road, Mortimer Forest, Ludlow. SO 4746 7170 (Text-fig. 39).

*Paratype.* G45-4/PC9(ii); pl. 12, fig. 2. Limestone of Wenlock age; Much Wenlock Limestone Formation exposure at Pitch Coppice Quarry, Ludlow-Wigmore Road, SO 4723 7298 (see Text-fig. 37).

*Occurrence in the Ludlow area.* Lowest recovery PC12, 3m below the top of the Wenlock Series at Pitch Coppice Quarry (Text-fig. 37). Recovered sporadically
TEXT-FIG. 29. Size variation of *Ancyrochitina gogginensis* and *Ancyrochitina narcissus*. Individuals taken from various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 30. Size variation of *Ancyrochitina cf. pachyderma* and *Ancyrochitina cf. primitiva*. Individuals taken from various horizons and sections (see systematic descriptions for details).
throughout the Gorstian. Highest recovery from the Lower Leintwardine Formation, SH4, 22cm above the base of Ludfordian Stage at Sunnyhill Quarry (Text-fig. 46). Forms a variable proportion of assemblages; present in high numbers in the Middle Elton Formation, constituting 32% of the assemblage in GR23 (Text-fig. 39). Preservation moderate to good

**Diagnosis.** Vesicle conical. Neck cylindrical, often encircled by long, simply branching, variably positioned, neck spines. Base convex. Rounded aboral margin supports 6-8 broad based, hollow appendices. Appendices branch 2-4 times. Shoulder variably developed.

**Description.** Body flanks straight to slightly convex. Branching of appendices occurs either at the tip or closer to the base of appendices. Appendices hollow. Neck spines may reach 20μm in length especially in Wenlock populations (see paratype). Above neck spines neck provided with small, randomly distributed spines (3-14μm long, usually 1μm in diameter) which show greatest development in populations from the Middle Elton Formation. Neck may flare towards aperture. Aperture may be finely fringed. Rugose texture observed on vesicle of some specimens. Body forms 1/2-1/3 of vesicle length. Prosome 20-30μm in length.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC6(2); PC7(1); PC8(2); PC9(4); PC10(1); PC11(1); PC12(5); GR23(11); GR25(3). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig. 28 & 29. All measurements in μm.

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Values of app; 26 individuals only.
Discussion. Variation in spine development in material from the Much Wenlock Limestone Formation and the Middle Elton Formation is not regarded as sufficiently significant to merit separation, as transitional forms are found in both populations. Confusion is possible with *A. narcissus* sp. nov. which also exhibits a conspicuous neck ornament and broad based branching appendices. Separation is made on the basis of the petalloid neck ornament and the concave base of *A. narcissus*. *A. gogginensis* exhibits many similarities with *Ancyrochitina gutnica* described by Laufeld (1974, p.45) from the Slite Beds to mid Kliteberg Beds (Wenlock) of Gotland. It differs in the lack of neck spines that decrease in size towards the aperture that are apparent on *A. gutnica*. It is possible that *A. gutnica* represents an ancestral form of *A. gogginensis*.

*Ancyrochitina narcissus* sp. nov. Pl. 12, figs 5-13 & Pl. 13, figs 1, 2.

Name. 'narcissus' referring to the daffodil-like appearance of the oral-most portion of the vesicle.

*Holotype*. L35/SH3(ii); pl. 12, figs 5-8. Limestone of early Ludfordian age, lower part of the Lower Leintwardine Formation at Sunnyhill Quarry, Mortimer Forest, Ludlow, SO 4950 7255. (see Text-fig. 46).

*Occurrence in the Ludlow area*. Lowest recovery DP6, Lower Bringewood Formation along Deer Park Road (Text-fig. 41). Also recovered from the Lower Bringewood Formation along Deer Park Road (DP15, Text-fig. 42). Not encountered again until the top of the Upper Bringewood Formation at Sunnyhill Quarry. Last encountered from SH4, 22cm above the base of the Lower Leintwardine Formation at Sunnyhill Quarry. (Text-fig. 46).

*Diagnosis*. Conical body. Neck cylindrical to subcylindrical and circled by conspicuous petalloid neck ornament, positioned perpendicular to vesicle surface. Petalloid neck ornament broad based, taper rapidly to a point. Towards aperture neck provided with small, randomly distributed spines. Flexure broadly rounded, shoulder lacking. Aboral margin rounded and provided with 8-10 ramified, broad-based
appendices. Appendices branch 2-4 times, initial bifurcation taking place in oral-aboral plane. Base concave. Vesicle surface exhibits granular texture.

Description. Appendices branch most commonly close to their base but branching at the tip also observed. Body flanks commonly straight but may be slightly concave or convex. Petalloid neck ornament may reach lengths of 20-35μm, less than 0.3μm thick; often convex in aboral direction, may be perforated. These structures may be rolled upon themselves and point in an aboral direction. Neck spines 8-9μm long, approximately 1μm in diameter; often showing preferential curvature towards oral pole. Most of neck spines circular in cross section, occasionally with flattened bases elongated in oral-aboral direction. Granular ornament shows no preferential concentration or development. Granule size 0.8-1.0μm in diameter. Body occupies 1/2-1/3 of vesicle length. Prosome not observed.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). DP15(1); SH2(3); SH3(7); SH15(2). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig. 29. All measurements in μm.

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Values of app; 10 individuals only.

Discussion. The petalloid neck ornament is the distinguishing feature of this species. Other species (for example the Wenlock forms of A. gogginensis and G. swifti) may exhibit prominent neck spines but these, while sometimes flattened, are never developed into the thin structures seen on A. narcissus.
Ancyrochitina cf. pachyderma Laufeld, 1974

Pl. 13, figs 3-7, 9

cf. 1974 Ancyrochitina pachyderma Laufeld, p.45, figs 10a-f.

Occurrence in the Ludlow area. Lowest recovery PC13, 3.5m below the base of the Ludlow Series at Pitch Coppice Quarry (Text-fig. 37). Common throughout the Wenlock exposure at Pitch Coppice (forming 12-21% of assemblages). Highest recovery PC2, 10cm above the base of the Ludlow Series at Pitch Coppice. Preservation moderate to poor.

Description. Body conical. Neck cylindrical. Aboral margin broadly rounded, provided with about 6 flattened, wide-based appendices of triangular outline. Base flat to slightly convex. Flexure present but variably developed. Shoulder not present. Appendices commonly flattened in oral/aboral direction. Distal terminations of appendices may bifurcate; more commonly pointed. Short spines observed on neck of some specimens (commonly 4μm long). Vesicle smooth or slightly granular to rugose. Body occupies upto half of vesicle length. Prosome up to 30μm in length, often not observed.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC6(2); PC2(1); PC7(3); PC12(1); PC13(2). Length is plotted against the ratio of length to maximum diameter of vesicle on Text-fig. 30. All measurements in μm, compared with the holotype of A. pachyderma Laufeld (1974, p. 45).

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Values of app; 8 individuals only.

Discussion. The poor preservation of this species makes a direct affiliation with the Gotland species difficult. Ancyrochitina pachyderma was reported by Laufeld (1974, p.
45) from the Llandovery and lower Wenlock of Gotland. The simple yet characteristic appendices of A. cf. *pachyderma* distinguish it from all other *Ancyrochitina* species. A. cf. *primitiva* also possess simple unbranched appendices but these lack the characteristic flattened character of those on A. cf. *pachyderma*.

**Ancyrochitina cf. primitiva** Eisenack, 1964

Pl. 13, figs 8, 10, 11

cf. 1964 *Ancyrochitina primitiva* Eisenack, p. 323-324, pl. 27, figs 1-6, 8-14; pl.28, figs 1-5.

cf. 1974 *Ancyrochitina primitiva* Eisenack; Laufeld, p. 47, figs 12a-f, figs 13a-d.

**Occurrence in the Ludlow area.** Lowest recovery from GR45 in the Upper Elton Formation along Goggin Road (Text-fig. 40). Encountered sporadically through the Upper Elton Formation but never forms an important proportion of assemblages (1-6%). Occasional specimens from the Lower Bringewood Formation along Deer Park Road (see Text-fig. 41). Dubious specimens from the Upper Bringewood Formation at Sunnyhill Quarry (SH21, Text-fig. 46). Preservation poor.

**Description.** Conical to spheroidal body. Cylindrical neck. Broadly rounded aboral margin supports 8 simple unbranched appendices. Appendices broad based, taper towards tip. Appendices hollow, circular in cross-section. Shoulder lacking, flexure broadly rounded. Appendices developed perpendicular to oral-aboral axis of vesicle, distal portion curved either orally or aborally, or entire structure exhibits marked curvature in an aboral direction. Vesicle may show slight rugose texture. Evidence of neck spines found on some specimens. Body comprises about 1/2 of vesicle length. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR51(3); GR52(1); DP23(2). Length is plotted against ratio of length to maximum diameter of vesicle on Text-fig. 30. All measurements in μm, compared with the holotype of A. *primitiva* (Eisenack 1964, p. 323).
Discussion. As this species is only rarely encountered and poorly preserved a straightforward association with *A. primitiva* from Gotland is not possible. Laufeld (1974, p.40) reported *A. primitiva* from the Lower Visby Beds to the Hemse Beds on Gotland (Llandovery, Telychian, to mid Ludlow). It is possible that recovery of additional material will allow a direct affiliation. *A. cf. pachyderma* also possesses simple appendices but is separated on the basis of appendice cross section, which is circular in *A. cf. primitiva* but flattened in an oral-aboral direction in *A. cf. pachyderma*.

**Ancyrochitina sp.A** Pl. 13, figs 12-17 & Pl. 14, figs 1-3.

*Occurrence in the Ludlow area.* Lowest recovery PC12, 3m below the top of the Wenlock Series at Pitch Coppice Quarry (Text-fig. 37). Encountered across the base of the Ludlow Series at Pitch Coppice Quarry and Goggin Road (Text-fig. 38). Also found in the Lower Bringewood Formation in the Todding area (Text-fig. 43). Highest recovery in the Lower Leintwardine Formation 60cm above the base of the Ludfordian at Sunnyhill Quarry (SH8, Text-fig. 46). Where present only forms a minor component of assemblages. Preservation poor.

*Description.* Body conical, Neck cylindrical to sub-cylindrical. Variably developed shoulder. Rounded aboral margin supports 8-10 appendices of indeterminable character. Base flat to slightly concave or convex. Vesicle covered with randomly distributed granular to spinose ornament. Ornament often patchily developed. Spines vary in length from 1.5-8.5μm, granules commonly 1-1.5μm in diameter. Either spinose or granular ornament shows preferential development. Some specimens possess

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<td>19-81</td>
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Values of app; 4 individuals only.
remnants of neck ornament. Appendices hollow. Flanks of body generally straight but may exhibit slight convexity or concavity. Neck may flare slightly towards aperture. Body occupies 1/2-1/3 of vesicle length. Prosome upto 20μm in length.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). PC1(1); PC3(1); PC6(3); LT2(1); LT3(1); LT5(3); SH8(1). All measurements in μm.

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<td>1.4-2.3</td>
<td>19</td>
<td>54-81</td>
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</table>

Values of app; 2 individuals only.

**Discussion.** As no well preserved material was recovered this species is left in open nomenclature. Despite the poor quality of recovered material the spinose to granular ornament easily distinguishes it from any other species of *Ancyrochitina* within the Ludlow area.

*Ancyrochitina* sp. B Pl. 14, figs 4-7

**Occurrence in the Ludlow area.** One dubious specimen from GR9 in the Lower Elton Formation on Goggin Road (Text-fig. 38). Rare specimens from the Middle Elton Formation (Text-fig. 39). One poorly preserved specimen from DPR3 in the Lower Bringewood Formation on Deer Park Road (Text-fig. 41). The majority of specimens were recovered from the Lower Bringewood Formation in the Todding area (Text-fig. 43). Forms a minor proportion of assemblages except in LT11 where it constitutes 24% of the chitinozoan population. Preservation poor.

TEXT-FIG. 31. Size variation of *Ancyrochitina aymestreyensis* and *Ancyrochitina sp. B*. Individuals taken from various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 32. Size variation of *Angochitina* sp. aff. *echinata*, *Angochitina elongata* and *Angochitina milleri*. Individuals taken from various horizons and sections (see systematic descriptions for details).
with both narrow or broad bases observed. Appendices branch simply, either close to their base or at the tip. Body occupies 1/3 of vesicle length. One prosome observed, 15μm in length.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR23(1); GR24(1); LT5(2); LT11(3); DPR3(1) Length is plotted against the ratio of length to neck length on Text-fig. 31. All measurements in μm.

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>D</th>
<th>lb</th>
<th>dh</th>
<th>L/D</th>
<th>app</th>
<th>ln</th>
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<tr>
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<td>57</td>
<td>65</td>
<td>30</td>
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<td>19</td>
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<td>147-267</td>
<td>39-66</td>
<td>46-77</td>
<td>25-39</td>
<td>2.3-6.9</td>
<td>15-23</td>
<td>77-220</td>
<td>1.2-1.9</td>
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</tbody>
</table>

Values of app 4 individuals only.

**Discussion.** As this species was only rarely encountered and poorly to moderately preserved it is left in open nomenclature. The long neck separates it from most other *Ancyrochitina* species within the Ludlow area. *A. aymestreyensis* is also elongate in appearance but possesses conspicuous neck ornament lacking on *A. sp. B*.


Genus ANGOCHITINA Eisenack, 1931

Type species. Angochitina echinata Eisenack, 1931


Discussion. Forms with ornament arranged in longitudinal rows are included within Gotlandochitina Laufeld (1974, p.83).

Angochitina sp. aff. echinata Eisenack, 1931 Pl. 14, figs 8-12.

aff. 1931 Angochitina echinata Eisenack, p.82, pl.1, figs 6-7.

aff. 1974 Angochitina echinata Eisenack; Laufeld, p.53, figs 16a-f; figs 17a-c.

Occurrence in the Ludlow area. Lowest occurrence GR30, Middle Elton Formation on Goggin Road (Text-fig. 39) Where recovered it commonly forms 2-3% of populations. Importance increases in the lower Lower Leintwardine Formation at Sunnyhill Quarry where it comprises 5-13% of assemblages. After SH9 (75cm above the base of the Lower Leintwardine Formation, Text-fig. 46) it only occurs sporadically. Highest recovery SH36 in the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 49).

Description. Species of Angochitina with spheroidal body. Flexure broadly rounded. Aboral margin rounded. Flanks convex. Neck cylindrical. Ornament of spines and longer filose elements. Shoulder often inconspicuous. Density and style of ornament variable. Spinose ornament (3.2µm long, 0.5 - 0.6µm in diameter) common on Gorstian forms, longer filose elements (8-14µm long, around 1µm in diameter) predominate in Ludfordian. Elements in Ludfordian specimens may be bi or tri-podal. Neck of Gorstian forms often shorter than in Ludfordian. Body 2/3 of vesicle length in Gorstian, more commonly 1/2 of vesicle length in Ludfordian. As a transition exists between long and short necked specimens there is no need to create two separate morphotypes. Prosome not observed.
Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR30(2); LT1(2); LT2(3); LT11(1); SH1(2); SH30(1). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig. 32. All measurements in µm, compared with the neotype A. echinata (Eisenack 1964, p. 319).

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>D</th>
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<tr>
<td>Neotype</td>
<td>152</td>
<td>62</td>
<td>34</td>
<td>-</td>
<td>-</td>
<td>2.4</td>
<td>-</td>
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<tr>
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<td>36</td>
<td>69</td>
<td>86</td>
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<tr>
<td>Range</td>
<td>116-181</td>
<td>62-82</td>
<td>29-50</td>
<td>41-85</td>
<td>43-102</td>
<td>1.7-2.5</td>
<td>1.5-3.1</td>
</tr>
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</table>

Discussion. In Gotland A. echinata exhibits a range from the middle of the Hemse Beds to the top of the Eke Beds (range approximately equivalent to Upper Elton to Lower Whitcliffe Formation) with an atypical form, A. cf. echinata ranging from the Harma Beds to the lower part of the Sundre Beds (approximately equivalent to the Upper Whitcliffe Formation, Laufeld (1974, p.53). The Ludlow species exhibits a similar range to A. echinata but differences in the ornament of the vesicle preclude a direct association. The Ludlow form does not show the same concentration of ornamentation as those illustrated by either Eisenack, 1964 (p. 319, pl. 29, fig 9-13) or Laufeld, 1974 (p. 53, fig 16, A-F). A sp. aff. echinata is distinguished from other Angochitina species by its spheroidal body. The ovoid body and characteristic ornament of A. milleri separate it from A. sp. aff. echinata. The more granular character of ornament and higher degree of body sphericity separates Sphaerochitina. cf. lycoperdoides. from A. sp. aff. echinata.

Angochitina elongata Eisenack, 1931 Pl. 14, figs 13-15 & Pl. 15, figs 1-5

1931 Angochitina elongata Eisenack, p. 82, pl. 1, figs 8-9.
1964 Angochitina elongata Eisenack; Eisenack, p. 319, pl. 30, fig. 2.
1974 Angochitina elongata Eisenack; Laufeld, p. 53, figs 18a-d.

Holotype. Lost during second world war.
Neotype. Geologisch-Paläontologisches Institut der Universität Tübingen, 1964, pl. 2, fig. 7, präparat 51 Nr. 1.

Occurrence in the Ludlow area. Lowest occurrence GR30 in the Middle Elton Formation (Text-fig. 39). Only a minor constituent of Gorstian assemblages (2-10%) with one notable exception in the Lower Bringewood Formation on Deer Park Road (DP15, Text-fig. 42) where this species makes up 60% of assemblage. A. elongata forms a more important part of assemblages in the lower part of the Lower Leintwardine Formation, constituting between 20-40%. Highest recovery SH36 in the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 49). Preservation variable.

Diagnosis. (translated after Eisenack, 1931) Body cylindrical-ovoid with straight to slightly convex flanks, shoulder and flexure present but variably developed. Neck cylindrical. Collarette flares.

Description. Specimens from Middle Elton Formation and Lower Bringewood Formation commonly possess dense ornament of spines and fine filose elements (1.5\(\mu\)m long). In Upper Bringewood and Lower Leintwardine formations body more elongate, ornament less dense, composed of more robust filose elements (6\(\mu\)m long). Some specimens exhibit crude organisation of ornament reminiscent of that found in Gotlandochitina. Shoulder and flexure often developed to greater degree in later forms. Body occupies 1/2-2/3 of vesicle length. Prosome 30-40\(\mu\)m in length.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR36(2); GR48(1); GR50(1); DP6(2); DP15(7); LT1(2); LT2(1); LT11(2); SH2(4); SH8(3); SH9(1); SH15(3); SH16(4); SH24(3). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig 32. Measurements of the neotype are for A. elongata (Eisenack 1964, p. 319). All measurements in \(\mu\)m.
Discussion. The great variation of this species was also noted by Laufeld (1974, p. 53) for specimens of *A. elongata* on Gotland. He reported that populations from the NW outcrops of the Hemse Marl are more akin to the neotype figured by Eisenack in 1964 (p. 319, pl. 30, fig 2.). Populations from the SE of the Hemse Marl outcrop and Eke Beds are more akin to the holotype (lost during World War II) figured by Eisenack in 1931 (p. 82, pl. 1, fig. 8). A similar variation exists between younger and older populations in the Ludlow area; the broad outline of the holotype in Eisenack's 1931 paper resembles that of the later populations of the type Ludlow area, the neotype in his 1964 paper resembling the older forms in the type Ludlow. As a broad morphological transition exists between the two it is not necessary to separate them. As Laufeld (1974, p. 53) states for the populations on Gotland, "there are transitions between them, and so there is no reason for distinguishing them as separate species." At a generic level, this species may become confused with *Gotlandochitina* due to the occasional presence of spines arranged in longitudinal rows, and in particular with *Gotlandochitina* sp. A which shares similar vesicular dimensions with *A. elongata*. Despite this, *A. elongata* encountered here is retained in *Angochitina* as the majority of spines are distributed in a random manner unlike that found on *G*. sp. A where the ornament exhibits definite longitudinal organisation. In addition to this the filose elements of *A. elongata* are smaller, less robust and are present in greater concentrations. *A. elongata* is separated from *A*. sp. aff. *echinata* by its longer, ovoid-cylindrical body and higher L/D ratio. *A. milleri* sp. nov. possess a very characteristic ornament lacking on *A. elongata*.

Global occurrence. Laufeld (1974, p. 56) reported this species as ranging from the uppermost part of the Klinteberg Marl to the *Rhizophylum* Limestone of the Eke Beds of
Gotland (a range approximately equivalent to Lower Elton to lower Lower Whitcliffe Formation). Nestor (1990, p. 81) noted this species from the Paadla Formation in Estonia (approximately upper Gorstian, lower Ludfordian).

**Angochitina milleri** sp. nov. Pl. 15, figs 6-12

_Name 'milleri' after fellow Silurian micropalaeontologist Giles Miller who aided the collection of material that yielded this species._

_Holotype._ R29/SH26. Calcareous siltstone of lower Ludfordian age, Lower Leintwardine Formation at Sunnyhill Quarry, Mortimer Forest, Ludlow. SO 4950 7255, see Text-fig. 48.

_Occurrence in the Ludlow area._ Lowest occurrence SH25, 8m above the base of the Ludfordian at Sunnyhill Quarry (Text-fig. 47). When it is encountered it constitutes 1.2-4.1% of the total chitinozoan assemblage except for SH29 where it represents 30% of the total assemblage. Highest recovery SH31 (Lower Leintwardine Formation), 5m above SH25 (Text-fig. 48). Variable preservation, generally flattened.


_Description._ Filose elements reach lengths of 12µm, 1µm in diameter, may be bipodal. Tops of spines tend to tangle giving impression of linked mesh structure. Ornament development often patchy, may occur in roughly aligned longitudinal rows. Body occupies varied proportion of vesicle length, but generally 1/2-2/3.

_Measurements._ Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). SH25(1); SH26(6); SH29(6); SH31(5). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig 32. All measurements in µm.
Discussion. At generic level, roughly arranged 'clumps' of ornament may cause confusion with *Gotlandochitina*. Closer observation of the ornament reveals that filose elements are arranged in a random fashion, showing that the correct assignment is to *Angochitina*. With its elongate, ovoid body this species very closely resembles *A. elongata*. The two species are separated on the basis of the characteristic ornament of *A. milleri*. The spherical body of *A. sp. aff. echinata* separates it from *A. milleri*.

**Genus FUNGOCHITINA** Taugourdeau, 1966

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


*Discussion.* *Fungochitina* is distinguished from *Sphaerochitina* and *Angochitina* by its conical body, sharper aboral margin and flat to only slightly convex base.

**Fungochitina** cf. *pistilliformis* (Eisenack, 1931) Pl. 16, fig. 1.

cf. 1931 *Conochitina pistilliformis* Eisenack, p.88, pl. 2, figs 6-7; pl. 4, figs 2-3.

*Occurrence in the Ludlow area.* Mostly restricted to the lowest 60cm of the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 46) where it commonly constitutes 0.3-3.5% of assemblages (9% in SH7). Lowest occurrence DP15, close to the boundary between the Lower and Upper Bringewood Formations along Deer Park.
TEXT-FIG. 33. Size variation of *Gotlandochitina swifti*, *Gotlandochitina sp. aff. villosa*, *Gotlandochitina dinhamensis*, *Gotlandochitina sp. A* and *Gotlandochitina villosa*. Individuals taken from various horizons and sections (see systematic descriptions for details).

TEXT-FIG. 34. Size variation for *Fungochitina cf. pistilliformis* and *Sphaerochitina cf. lycoperooides*. Individuals taken from various horizons and sections (see systematic descriptions for details).
Road (Text-fig. 42). Highest recovery from SH26, 9m above the base of the Ludfordian (Text-fig. 48). Preservation moderate.

**Description.** Conical body. Sharp aboral margin. Base flat to slightly convex. Flexure prominent, no shoulder. Neck sub-cylindrical, widens rapidly from a point midway along neck towards aperture. Ornament of small randomly distributed spines. Spines around 1µm in length. Prosome 40µm in length.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). DP15(1); SH3(2); SH6(1); SH7(1); SH8(1). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig 34. All measurements in µm, compared with *Conochitina pistilliformis* from Eisenack (1931, p. 88).

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<tr>
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<td>66-97</td>
<td>31-52</td>
<td>1.2-1.6</td>
<td>1.3-1.6</td>
</tr>
</tbody>
</table>

**Discussion.** It is difficult to determine if the rare specimens recovered from the type Ludlow are typical of *F. pistilliformis* or represent the extreme forms of a variable population. It is for this reason, and because *F. pistilliformis* is generally encountered in the Pridoli, that I have not directly assigned these specimens to *F. pistilliformis*. The holotype of *F. pistilliformis* was extracted from Baltic glacial erratics by Eisenack (1931, p.88). Nestor (1990, p. 81, 83 pl 15, fig 21.) reported *F. pistilliformis* from the Kaugatuma Regional Stage (Pridoli) of Estonia. It is separated from species within *Sphaerocritina* and *Angochitina* by its sharp aboral margin and 'mushroom-like' vesicle form. Damaged specimens of *Ancyrochitina* may resemble this species but are distinguished by the presence of appendice scars.
Genus **GOTLANDOCHITINA** Laufeld, 1974

*Type species.* *Gotlandochitina martinssoni* Laufeld, 1974

*Diagnosis.* (after Laufeld 1974, p.83) Angochitininae with ornament arranged in longitudinal rows.

**Gotlandochitina dinhamensis** sp. nov. Pl. 17, figs 1-6

Name. 'dinhamensis' after the Dinham Bridge which spans the River Teme along the Whitcliffe section.

*Holotype.* O30/W25; pl. 17, figs 2, 3. Calcareous siltstone of Ludfordian age, Lower Whitcliffe Formation from the Whitcliffe exposure along the River Teme, Ludlow. SO 5071 7428.

*Occurrence in the Ludlow area.* Lowest occurrence W25, immediately above the base of the Lower Whitcliffe Formation (Text-fig. 52) where it forms 28% of the assemblage. It is found again at W26 (30cm above W25 in the same section), where it forms 47% of the chitinozoan assemblage. The species is not recovered again till W45 (Text-fig. 55), 2.4m above the base of the Upper Whitcliffe Formation, where it forms 9% of the chitinozoan assemblage. This species is last encountered at W45. Most specimens flattened.

*Diagnosis.* Conical body. Short cylindrical neck. Spines arranged in variably developed longitudinal rows. Aboral margin angular, base flat to slightly convex. Body flanks straight to slightly convex. Flexure developed, shoulder lacking.

*Description.* Body occupies approximately 1/2 of vesicle length. Neck may flare towards the aperture. Spines may exhibit simple branching. Maximum spine development on base and aboral margin (9μm in length, 1.8μm in diameter). Spines on neck commonly shorter (maximum length of 4-5μm) and finer (approximately 0.9μm in diameter). Vesicle between spines is smooth. Prosome not observed.

*Measurements.* Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). W25(3);
W26(5). Length is plotted against ratio of length to maximum diameter of the vesicle on Text-fig. 33. All measurements in \( \mu m \).

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<td>27</td>
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<td>27.66</td>
<td>39.73</td>
<td>1.1-1.9</td>
<td>1.5-3.5</td>
</tr>
</tbody>
</table>

A correction factor of 0.8 has been applied to \( D \) and \( da \) for the holotype.

Discussion The conical body of this species distinguishes it from other Gotlandochitina species around Ludlow. It is possible that this species represents poorly preserved individuals of \( G. \) villosa. However, although generally poorly preserved, specimens have been isolated which clearly exhibit a flat base. In addition, \( G. \) dinhamensis possesses a shorter neck than \( G. \) villosa. Confusion is possible with Fungochitina, which also has a conical body. The two are separated by the greater development and arrangement of ornament on \( G. \) dinhamensis sp. nov. and the more 'mushroom-like' vesicle form of Fungochitina.

Gotlandochitina swifti sp. nov. Pl. 16. figs 2-12

Name. 'swifti' after fellow micropalaeontologist at Leicester University, Andrew Swift who aided in the collection of material that yielded this species.

Holotype. P39/DP6(i); pl. 16, fig. 2-4. Limestone of early Gorstian age; Lower Bringewood Formation on Deer Park Road, Mortimer Forest, Ludlow. SO 4845 7135 (Text-fig. 41).

Occurrence in the Ludlow area. Lowest occurrence GR62 in the Lower Bringewood Formation on Goggin Road (Text-fig. 40). Also recovered from the Lower Bringewood Formation on Deer Park Road (Text-fig. 41) and from the Upper Bringewood Formation at Aymestrey (Text-fig. 45). Latest occurrence A7, 8m below the base of the Lower Leintwardine Formation in the main quarry, Beechenback Wood.
Aymestrey. Where present, this species only forms a minor constituent of assemblages, between 2-9%. Well preserved, three dimensional material has been recovered from the Deer Park Road section.

**Diagnosis.** Body spheroidal, neck cylindrical to subcylindrical. Flexure evident, shoulder lacking. Aboral margin rounded, base convex. Aboral margin provided with up to 8 hollow, ramified appendices. Large branchioles, resembling appendices, arranged in longitudinal rows above appendices. Cylindrical neck provided with large ramified spines. Neck flares towards aperture.

**Description.** Body occupies 1/2-2/3 of vesicle length. Appendices and branchioles in more aboral positions commonly point in aboral direction, branchioles closer to oral pole point orally. Bases of appendices and first set of branchioles may merge. Appendices and branchioles may reach lengths of 40μm. Neck spines (commonly 35-40μm long) often positioned at bulge midway along neck. Vesicle surface may be covered by fine rugose texture. Prosome not observed.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). GR62(2); DP6(5); A8(1). Length is plotted against the ratio of length to maximum diameter of vesicle on Text-fig. 33. All measurements in μm.

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<tr>
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**Discussion.** This species shows greatest similarity with *A. narcissus*. Both possess complex neck ornament and ramified appendices but the spheroidal body and presence of longitudinally arranged branchioles on *G. swifti* separates the two species. Differences also exist in the nature of the neck ornament which is circular in cross section in *G. swifti* and flattened in *A. narcissus*. 
Gotlandochitina villosa Laufeld, 1974

1974 *Gotlandochitina villosa* Laufeld, p.95, figs 56a-e.

**Holotype.** Dept. Historical Geology and Palaeontology, University of Lund, fig. 56A, LO 4587 T.

**Occurrence in the Ludlow area.** First recovered from W1, 84cm from the top of the Lower Leintwardine Formation, along the Whitcliffe at Ludlow (Text-fig. 51). Where it is encountered, this species constitutes from 4% (W21) - 35 % (W25) of assemblages. Accessible exposure of the lowest Lower Whitcliffe Formation ends after only 50cm at W26. The species is not recovered again till W45 (Text-fig. 55), 2.4m above the base of the Upper Whitcliffe Formation, where it forms 63% of the chitinozoan assemblage. This species is last encountered at W45. Well preserved, three dimensional material recovered.


**Description.** Body occupies 1/3-1/2 of vesicle length. In agreement with Laufeld (1974, p.97) spines are hollow. Some spines develop from common base. Maximum spine length 13μm. Surface of vesicle between spines exhibits fine rugose texture. Neck may flare towards aperture. Prosome not easily observed, possibly 25-30μm in length.

**Measurements.** Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). W25(8); W26(3). Length is plotted against the ratio of length to maximum diameter of vesicle on Text-fig. 33. All measurements in μm. Measurements of the holotype are from Laufeld (1974, p.96-97).
Discussion. The holotype figured by Laufeld (1974, p. 96, figs 56a-b) does not exhibit the same density of spinose ornament found on specimens from Ludlow. This, however, is not such a significant difference as to warrant separation from the Gotland species. *G. sp. aff. villosa* is similar but shows a less ordered arrangement of spines, possesses a more oval body and a higher L/D ratio (see Text-fig. 33) It is possible that *G. sp. aff. villosa* is an ancestral form of *G. villosa*. *G. dinhamensis* is generally smaller with a lower L/D ratio (see Text-fig. 33) and possesses a flat base.

Global occurrence. This species was reported from strata of a similar late Ludfordian age on Gotland (Harma and Sundre Beds) by Laufeld (1974, p. 96). It has also been reported from the late Ludlow of Estonia (Kuressaare Regional Stage) by Nestor (1990, p. 83).

**Gotlandochitina** sp. aff. *villosa* Laufeld, 1974 Pl. 18, figs 1-4, 10, 11.

*Occurrence in the Ludlow area.* Only encountered rarely. 12 specimens from the Lower Bringewood Formation on Deer Park Road (DPR1&2-Text-fig. 41) and one specimen from the Todding sections (LT11, Text-fig. 43).

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). DPR1(3); DPR2(1); LT11(1). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig 33. All measurements in μm.

<table>
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<td>65-116</td>
<td>89-110</td>
<td>3.0-3.5</td>
<td>1.8-2.5</td>
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</tbody>
</table>

Discussion. The ornament style and overall vesicle form of this species is similar to *G. villosa*. It is separated by its ovoid body, less ordered ornament, longer neck and higher L/D ratio (see Text-fig 33). It is possible that *G. sp. aff.villosa* represents an ancestral form of *G. villosa*. The longitudinal arrangement of ornament separates this species from any within *Angochitina*.

**Gotlandochitina sp. A** Pl. 18, figs 5-9

Occurrence in the Ludlow area. Encountered sporadically from SH15, immediately below the base of the Ludfordian at Sunnyhill Quarry (Text-fig. 46) to W45, 2.4m above the base of the Lower Whitcliffe Formation along the Whitcliffe at Ludlow (Text-fig. 55). Where present, commonly comprises up to 7% of assemblages. Preservation moderate.

Measurements. Measurements have been taken from specimens from the following sample points (values in brackets refer to the number of specimens measured). SH2(2); SH14(1); SH15(1); SH22(1); W26(2); W45(6). Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig. 33. All measurements in μm.

<table>
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<tr>
<th></th>
<th>L</th>
<th>D</th>
<th>da</th>
<th>ln</th>
<th>lb</th>
<th>L/D</th>
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<tbody>
<tr>
<td>Mean</td>
<td>173</td>
<td>53</td>
<td>33</td>
<td>65</td>
<td>107</td>
<td>3.2</td>
<td>2.6</td>
</tr>
<tr>
<td>Range</td>
<td>147-236</td>
<td>40-71</td>
<td>22-55</td>
<td>50-81</td>
<td>87-154</td>
<td>2.5-4.3</td>
<td>2.1-3.1</td>
</tr>
</tbody>
</table>

Discussion. Although the ornament of this species indicates greatest affiliation with *Gotlandochitina*, the presence of randomly distributed elements suggests an association with *Angochitina*. This species can resemble *Angochitina elongata* and *Angochitina milleri* sp. nov. All three species share a similar vesicle form and both the *Angochitina* species occasionally show ornament arranged in longitudinal rows. However, the higher degree of ornament arrangement in *G.* sp. A distinguishes it from both *Angochitina* species and places it within *Gotlandochitina*.

Genus **SPHAEROCHITINA** Eisenack, 1955

*Type species.* *Lagenochitina sphaerocephala* Eisenack, 1955


*Discussion.* A modified version of Eisenack's original diagnosis of 1955 is used here in preference to his expanded version of 1968 (p. 174) in which he included forms with long spines arranged in longitudinal rows. Such forms are here included within *Gotlandochitina* as was suggested by Laufeld (1974, p. 104). Forms with a mushroom shaped body are included within *Fungochitina*. 
Sphaerochitina cf. lycoperdoides Laufeld, 1974  Pl. 18, figs 12-15

cf. 1974 Sphaerochitina lycoperdoides Laufeld, p.111, figs 68a-e.

cf. 1981 Sphaerochitina lycoperdoides Laufeld; Paris, p. 271, pl. 20, figs 1-4, 6-8, 10; pl. 37, figs 3-4; pl. 41, figs 15-16.

Occurrence in the Ludlow area. Only recovered from one sample (DP25, see Text-fig. 42) from close to the top of the Lower Bringewood Formation on Deer Park Road (base of the Upper Bringewood Formation is unclear). Material moderately preserved.

Description. Body spheroidal. Neck cylindrical, flaring towards the aperture. Flexure present, shoulder broadly rounded. Convex flanks. Rounded aboral margin. Convex base. Ornament of small granules and occasional filose elements. Body 1/2 of vesicle length. Low granular ornament (around 0.5μm in diameter) evenly distributed over vesicle, no preferential development. Filose component restricted to neck (length 5μm, 0.5μm in diameter). Prosome not observed.

Measurements. Measurements have been taken from 3 specimens from DP25. Length is plotted against the ratio of length to maximum diameter of the vesicle on Text-fig 33. All measurements in μm, compared with the holotype for S. lycoperdoides Laufeld (1974, p. 112).

<table>
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<tr>
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<th>L</th>
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<th>L/D</th>
<th>L/ln</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holotype</td>
<td>97</td>
<td>57</td>
<td>25</td>
<td>-</td>
<td>-</td>
<td>1.7</td>
<td>-</td>
</tr>
<tr>
<td>Mean</td>
<td>119</td>
<td>58</td>
<td>29</td>
<td>59</td>
<td>59</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Range</td>
<td>108-127</td>
<td>49-62</td>
<td>22-38</td>
<td>54-62</td>
<td>54-66</td>
<td>1.9-2.1</td>
<td>1.9-2.0</td>
</tr>
</tbody>
</table>

Discussion. The presence of small spines affiliates the species encountered in the type Ludlow area with S. lycoperdoides rather than S. sphaerocephala (Eisenack, 1932) which shares a similar vesicle form but possess a very low, inconspicuous ornament. It is not possible to directly assign this species to S. lycoperdoides due to the low numbers of individuals encountered. Laufeld (1974, p. 112) reported S. lycoperdoides from the upper part of the Mulde Beds to near the top of the Klinteberg Beds on Gotland, a range
of approximately middle Homerian (Wenlock) to lower Gorstian (Ludlow). Paris (1981, p. 272) reported S. lycoperdoides from the Upper Wenlock of Portugal in the Formation de Sazes. Within the Ludlow area, S. cf. lycoperdoides shows greatest similarities to A. sp. aff. echinata. The two species are separated on the basis of ornament, which shows a greater development in A. sp. aff. echinata and the degree of sphericity of the body, which is more pronounced in S. cf. lycoperdoides.
FAUNAL CHARACTERISTICS AND BIOSTRATIGRAPHY

PRESERVATION

Preservation varies greatly. In general lithology influences preservation, with more carbonate rich lithologies possessing the most delicately preserved material. However, excellently preserved material has also been isolated from more argillaceous material (e.g. GR22-25; Text-fig. 39; pl. 11, figs 6-12). Specimens recovered from shale horizons tend to flattened.

Specimens from the top of the Wenlock and base of the Ludlow at Pitch Coppice are generally flattened but still possess delicate structures such as appendices. Preservation is poor throughout the Lower Elton Formation with specimens often only identifiable to generic level. Preservation is good throughout the Middle Elton Formation; intact chains of *Cingulochitina* (pl.5, figs 1, 6) and delicately preserved *Ancyrochitina* and graptolite fragments are common. Preservation is highly variable throughout the rest of the Gorstian but is generally good in the Lower Bringewood Formation. Excellently preserved three dimensional material is common at the base of the Ludfordian at Sunnyhill Quarry. Preservation is good to moderate throughout the remainder of the Lower Leintwardine Formation. With the exception of specimens recovered from the base of the Lower Whitcliffe Formation, preservation is poor throughout the upper Ludfordian. Parasite borings occur randomly throughout the succession.

DIVERSITY AND ABUNDANCE

Frequency is recorded as the number of chitinozoans extracted per gram of sample. The calculation is made using a corrected value of sample weight which takes into account the amount of undissolved rock in each processed sample. Diversity is calculated using the index of Fisher *et al.* (1943):
\[ S = \alpha \log_e (1 + N/\alpha) \]

Where \( S \) is the number of species, \( N \) the number of individuals and \( \alpha \) the index of diversity. Diversity and abundance data are presented on Text-fig. 35.

Diversity is moderate at the top of the Much Wenlock Limestone Formation (\( \alpha = 0.7-1.4 \)), falls throughout the Lower Elton Formation and lower Middle Elton Formation and rises again in the central parts of the Middle Elton Formation (\( \alpha = 1.3 \) in GR24, 46m above the base of the Middle Elton Formation). No major trends are observed through the Upper Elton Formation (\( \alpha = 0.5-1.0 \)) but an increase occurs in the Lower Bringewood Formation peaking at \( \alpha = 2.2 \) in GR65, 14m above the base. No trends in diversity are noted from the Upper Bringewood Formation to Upper Leintwardine Formation apart from a very distinctive peak at the base of the Ludfordian where \( \alpha \) reaches a value of 2.6 in SH3, 12cm above the base of the Lower Leintwardine Formation. Diversity falls in the Lower and Upper Whitcliffe Formation (\( \alpha = 0.3-0.8 \)) with occasional peaks for example W45, 2.4m above the base of the Upper Whitcliffe Formation, where \( \alpha = 1.3 \).

Abundance does not directly reflect peaks in diversity. Between 1 and 9 chitinozoans per gram were recorded from the top of the Much Wenlock Limestone Formation. Abundance is poor within the Lower Elton Formation and lower Middle Elton Formation where samples are commonly barren or possess less than 1 chitinozoan per gram. Abundance rises sharply in the central part of the Middle Elton Formation and peaks at 93 chitinozoans per gram in GR23, 44m above the base. This is not accompanied by a similar dramatic increase in diversity. After GR23 abundance falls rapidly with no major trends observed through the Upper Elton Formation and Lower Bringewood Formation apart from two brief peaks 15m below (GR47) and 4.8m above (GR59) the base of the Lower Bringewood Formation where 28 chitinozoans per gram were recovered. Abundance increases at the top of the Lower Bringewood Formation, close to the base of the Upper Bringewood Formation, with 32 chitinozoans per gram recovered from DP20. Abundance peaks at 35 chitinozoans per gram in A5, 4m below the top of the Upper Bringewood Formation at Aymestrey but then falls steadily.
TEXT-Fig. 35. Chitinozoan diversity and abundance from the Gorstian and Ludfordian sediments around Ludlow plotted along a proposed sea level curve based on Dornig (1981a) and Lawson (1975).
throughout the Lower and Upper Leintwardine formations. The peak in diversity at the base of the Ludfordian is not reflected in a similar increase in abundance. Abundance is high in the lower part of the Lower Whitcliffe Formation and peaks at 69 chitinozoans per gram in W32, 1.9m below the top of the Formation. Abundance falls through the Upper Whitcliffe Formation with no chitinozoans recovered from the top metre of the formation at Aston Munslow.

**BIOSTRATIGRAPHY**

The distribution of chitinozoan species throughout the sampled sections is shown on Text-figs 37-56.

Chitinozoans have not been regarded as useful biostratigraphic tools in the type Ludlow area (Lawson & White 1989). This is challenged by the data presented here. A resolution greater than a simple two-fold division based on Gorstian and Ludfordian assemblages is possible. Given the durability of chitinozoans, and their presence in strata where macrofossils are very poorly preserved (for example the base of the Ludlow Series at Pitch Coppice) the use of chitinozoans in the type Ludlow Series cannot be overlooked. The following is a review of some of the characteristic chitinozoans that have been recovered from the type Ludlow. This data is summarised in Text-fig. 36.

*Late Wenlock and early Gorstian.* (Lower Elton Formation). Characterised by the presence of *Conochitina*, particularly *Conochitina edjelensis elongata*? and *Conochitina pachycephala*.

*Early Gorstian.* (Middle Elton Formation). *Conochitina* persists into the Middle Elton Formation but is less dominant. *Cingulochitina* is common.

*Late Gorstian.* (Upper Elton Formation, Lower and Upper Bringewood formations). Characterised by the presence of *Belonechitinia* and *Eisenackitina toddingensis*.
TEXT-FIG. 36. Chitinozoan ranges through the type Ludlow Series from Ludlow and surrounding areas, and provisional chitinozoan biozonation.
**Early Ludfordian.** (Lower and Upper Leintwardine formations). Recognised by the increased importance of *E. lagenomorpha* and appearance of *Calpichitina* sp. aff.(*Calpichitina*) *hemiensis*.

**Late Ludfordian.** (Lower and Upper Whitcliffe formations). Recognised by the high abundance and frequency of *Eisenackitina philipi*. No Chitinozoans were recovered from the top of the Upper Whitcliffe Formation at Aston Munslow (Text-fig. 56). Richardson & Rasul (1990) have illustrated a chitinozoan from the upper part of the Upper Whitcliffe Formation at Weir Quarry near Downton which they have referred to *Eisenackitina barrandei* Paris.

It is important that biostratigraphical units are not defined by their position in the lithostratigraphical scheme. A chitinozoan biozonal scheme has been attempted by Dorning (1981c). The earliest of Dorning’s Ludlow assemblages covers the Middle Elton Formation to the Upper Elton Formation and is identified by the presence of *Conochitina* [1] *latifrons*, *Angochitina elongata*, *Angochitina echinata* (possibly *Angochitina* sp. aff. *echinata* of this study) and *Ancyrochitina desmea* (possibly *Gotlandochitina swifti*). The later assemblage covers the Ludfordian and is identified by *Eisenackitina lagenomorpha*, *Sphaerochitina spherocephala* (Eisenack, 1932) and *Sphaerochitina acanthifera* Eisenack, 1955 (no *Sphaerochitina* species were recognised from the Ludfordian in this study). A greater biostratigraphical resolution is now possible and 12 chitinozoan biozones have been identified in the type Ludlow on the basis of the appearances (and 1 disappearance) of various chitinozoan taxa. The top of each zone is defined by the base of the zone above it. As the validity of these biostratigraphical divisions has not been tested outside of the Ludlow area formal names have not been erected and instead the zones have been numbered 1-12. The biozones are shown in Text-fig. 36.

**Biozone 1.** The base of biozone 1 lies within the Much Wenlock Limestone Formation. It covers 14.8m of the Lower Elton Formation. Biozone 1 is characterised by an assemblage including *Ancyrochitina gogginensis*, *Ancyrochitina cf. pachyderma*,
TEXT-FIG. 37. Chitinozoan ranges at Pitch Coppice Quarry.
TEXT-FIG. 38. Chitinozoan ranges along the Goggin Road (section based on White & Lawson 1978 and Siveter et al. 1989). Continued on Text-fig. 39 and 40.
TEXT-FIG. 39. Chitinozoan ranges along Goggin Road (section based on White and Lawson 1978 and Siveter et al. 1989). Continued from Text-fig. 38 and continued on Text-fig. 40. Measurements are taken above the adjusted Wenlock/Ludlow boundary illustrated on Text-fig. 38.
MEF - Middle Elton Formation

- Mud/siltstone with calcareous nodules
- Siltstone
- Siltstone with calcareous nodules
- No exposure

TEXT-FIG-41. Chitinozoan ranges from the Deer Park Road section.
TEXT-FIG. 42. Chitinozoan ranges from the Deer Park Road section (detail of area from Text-fig. 41).
TEXT-FIG. 43. Chitinozoan ranges from sections around Lower Todding.
TEXT FIG. 44. Chitinozoan ranges from the Lower Bringewood Formation exposure along the A4113 in the Todding area.
Figure 45. Chitinozoan ranges at Beechenbank main quarry, Aymestrey.
TEXT-Fig. 46. Chitinozoan ranges at Sunnyhill Quarry (continued on Text-fig. 47).
TEXTFIG. 47. Chitinozoan ranges at Sunnyhill Quarry. Continued from Text-fig. 46, continued on Text-fig. 48.
TEXT-FIG. 48. Chitinozoan ranges at Sunnyhill Quarry. Continued form Text-fig. 47, continued on Text-fig. 49.
TEXT-FIG. 49. Chitinozoan ranges at Sunnyhill Quarry. Continued from Text-fig. 48, continued on Text-fig. 50.
TEXT-FIG. 50. Chitinozoan ranges at Sunnyhill Quarry. Continued from Text-fig. 49.
TEXT-FIG. 51. Chitinozoan ranges from the upper Lower Leintwardine Formation and the low Upper Leintwardine Formation exposed along the Whitcliffe (see Text-fig. 11 for location). Continued on Text-fig. 52.
TEXT-FIG. 52. Chitinozoan ranges from the Upper Leintwardine Formation and the lower Lower Whitcliffe Formation exposed along the Whitcliffe (see Text-fig. 11 for location). Continued from Text-fig. 50, continued on Text-fig. 53.
TEXT-FIG. 53. Chitinozoan ranges from the Lower Whitcliffe Formation exposure along the Whitcliffe (see Text-fig. 11 for location). Continued from Text-fig. 52, continued on Text-fig. 54.
TEXT-FIG. 54. Chitinozoan ranges at Whitcliffe Quarry (see Text-fig. 11 for location). Continued from Text-fig. 53, continued on Text-fig. 55.
TEXT-FIG. 55. Chitinozoan ranges at Whitcliffe Quarry. (see Text-fig. 11 for location)
Continued from Text-fig. 54.
No chitinozoans recovered from this section

TEXTFIG. 56. The base of the Downton Castle Sandstone Formation exposed at Aston Munslow.

Biozone 2. The base of the zone is defined by the disappearance of Conochitina sp. aff. elegans at GR9, 14.8m above the base of the Ludlow Series. The biozone contains very few characteristic chitinozoan taxa but Conochitina sp. A can be recognised in the lower part

Biozone 3. The base of biozone 3 is defined by the first occurrence of Cingulochitina gorstyensis at GR19, 27m above the base of the Middle Elton Formation. In addition to C. gorstyensis, assemblages also contain Bursachitina sp. A, Cingulochitina convexa and Cingulochitina sp. A. A. gogginensis, C. edjelensis elongata? and C. cf. proboscifera forma truncata, recorded from biozone 1, reappear in biozone 3.

Biozone 4. The base of biozone 4 is defined by the first occurrence of Angochitina elongata at GR30, 71m above the base of the Middle Elton Formation. Angochitina sp. aff. echinata, Belonechitina lauensis and Eisenackitina intermedia occur for the first time in the same horizon. Eisenackitina toddingensis is common through biozone 4. C. convexa and Cingulochitina sp. A disappear 6 and 2m respectively above the base of biozone 4. C. edjelensis elongata? is last recorded 4.8m below the top of biozone 4.

Biozone 5. The base of biozone 5 is defined by the first occurrence of Ancyrochitina ancyrea and A cf. primitiva at GR45, 18.8m below the top of the Upper Elton Formation. Belonechitina latifrons and Ancyrochitina aymestreyensis are recorded sporadically throughout the upper half of biozone 5. C cf. proboscifera forma truncata disappears 6m above the base of biozone 5.

Biozone 6. The base of biozone 6 is defined by the first occurrence of Gotlandochitina swifti at GR62, 8m above the base of the Lower Bringewood Formation. B. lauensis, E intermedia, A. elongata, A. sp. aff. echinata and E. toddingensis are common throughout biozone 6. Conochitina pachycephala is last recovered from biozone 6.
**Biozone 7.** The base of biozone 7 is defined by the brief appearance of *Gotlandochitina* sp. aff. *villosa* at DPR2, approximately 25m below the top of the Lower Bringewood Formation (the top of the Upper Bringewood Formation is not clear on Deer Park Road). *Belonechitina mortimerensis* is common throughout zone 7.

**Biozone 8.** The base of biozone 8 is defined by the first occurrence of *Cingulochitina* sp. aff. *cingulata* in DP15, approximately 2.5m below the top of the Lower Bringewood Formation. *Calpichitina (Calpichitina) granosa* and *Fungochitina cf. pistilliformis* occur in the same horizon. Biozone 8 covers the majority of the Upper Bringewood Formation and, although rich initially, is very sparse in characteristic chitinozoans. The last positively identified specimen of *A. cf primitiva* is identified 2.1m above the base of this zone. *A. aymestreyensis* and *G. swifti* disappear 2 and 8m respectively below the top of zone 8.

**Biozone 9.** The base of biozone 9 is defined by the appearance of *Gotlandochitina* sp. A immediately below the base of the Lower Leintwardine Formation (coincident with the base of the Ludfordian). The species recorded from the base of biozone 8 are common in the first meter of biozone 9. *Eisenackitina lagenomorpha* becomes particularly important in biozone 9 and *Calpichitina (Calpichitina) sp. aff. hemsiensis* is recognised in the lower parts of the unit. *Ancyrochitina* sp. A and *A. gogginensis* disappear just 60cm and 20cm respectively inside zone 9.

**Biozone 10.** The base of biozone 10 is defined by the appearance of *Angochitina milleri* in SH25, 8m above the base of the Lower Leintwardine Formation. *Eisenackitina lagenomorpha*? is common in biozone 10. *A. elongata* and *A sp. aff. echinata* last occur 9.96m above the base of zone 10. *Bursachitina* sp. A is last recognised 3m below the top of biozone 11.

**Biozone 11.** The base of biozone 11 is defined by the first occurrence of *Gotlandochitina villosa* in W1, 84cm from the top of the Lower Leintwardine Formation. *Calpichitina (Calpichitina) gregaria*? is a common component of assemblages in biozone 11. *C. (Calpichitina) sp. aff. hemsiensis* disappears 33cm below the top of biozone 11.
Biozone 12. The base of biozone 12 is defined by the first occurrence of *Eisenackitina philipi* in W20, 46cm below the top of the Upper Leintwardine Formation, the top of the biozone has not been defined. In addition to *E. philipi* zone 12 records the first occurrence of *Gotlandochitina dinhamensis* 46cm above its base. *G* sp. A is quite common throughout the unit.

Two radiation events can be distinguished within the Ludlow succession, the gradual appearance of species within the Middle Elton Formation and the sudden influx of species at the base of the Ludfordian. The latter case is accompanied by a rise in diversity. A sharp diversity peak is not apparent in the Middle Elton Formation as species are introduced in a more gradual manner (Text-fig. 36). The assemblage that occurs across the base of the Ludfordian, 30cm below and 80cm above the base of the Lower Leintwardine Formation, is characterised by; *Ancyrochitina narcissus*, *C. (Calpichitina) granosa, F. cf. pistilliformis*, *C* sp. aff. *cingulata* and an increased importance of *A. elongata*. This distinctive assemblage also occurs, briefly, in a thin shale unit close to the top of the Upper Bringewood Formation along Deer Park Road (DP15, Text-fig. 42).

**COMPARISON OF THE CHITINOZOANS OF THE TYPE LUDLOW WITH COEVAL SECTIONS.**

A statistical comparison of the type Ludlow chitinozoans with coeval sections would be desirable but sampling of other sections has been much less detailed than that completed in the type Ludlow. A direct comparison with this broader stratigraphical work is not possible as dissimilarities may arise simply as a product of differing sampling strategies. With this limitation, some comparisons may be made with information from the available literature.

**Gotland.** The chitinozoans from the Island of Gotland, Sweden, have been studied extensively by Eisenack (for example 1955 and 1964) and Laufeld (1974). The Ludlow sections of Gotland share a number of species in common with those of the stratotype Ludlow: *Gotlandochitina villosa, Eisenackitina intermedia, Eisenackitina lagenomorpha,*
Eisenackitina philipi, Cingulochitina convexa, Belonechitinia lauensis, Angochitina elongata, Belonechitinia latifrons, and Conochitina pachycephala. Forms resembling Gotland species were also recovered from Ludlow; Angochitina sp. aff. echinata, Calpichitina (Calpichitina) sp. aff. hemsiensis and Sphaerochitina cf. lycoperdoides. On Gotland all but C. pachycephala were found to be restricted to Ludlow strata. C. pachycephala also ranges down into the Wenlock in the Ludlow area. Laufeld (1974, p. 127) noted a faunal turnover within the Hemse Beds, at least an approximate correlative of the Middle Elton Formation in the Ludlow area where an influx of chitinozoan species also occurs. At specific level, the chitinozoans are not directly comparable, each section possessing forms not found in the other, but both share C. convexa and B. lauensis. Unlike the type Ludlow, a faunal turnover is not recorded around the base of the Ludfordian on Gotland, although the presence and importance of E. lagenomorpha at this point is apparent from both sections. Both areas contain Gotlandochitina villosa in the higher Ludfordian. In the Ludlow area the range of E. intermedia is extended to include forms recovered from the Gorstian. E. intermedia is restricted to the upper Ludfordian on Gotland. In Ludlow E. philipi is restricted to the Ludfordian, but in Gotland it is also found in Gorstian strata. Some species from the Gorstian and Ludfordian of Ludlow show affinities with species from the Wenlock and Llandovery of Gotland, for example: Cingulochitina sp. aff. cingulata Ancyrochitina gogginensis sp. nov. (resembling Ancyrochitina gutnica from Gotland) Conochitina cf. proboscifera forma truncata and Ancyrochitina cf. pachyderma.

Estonia. The Ludlow of Estonia shares the following species with the type area; Belonechitinia latifrons, Angochitina elongata, Belonechitinia lauensis, Eisenackitina lagenomorpha, Eisenackitina philipi, Eisenackitina intermedia and Gotlandochitina villosa (Nestor 1990, pp. 81, 83). A faunal turnover is also apparent at a point that roughly correlates with the Middle to Upper Elton formation (Gorstian Stage). Nestor (1990, p. 83) reported that E. lagenomorpha in Estonia shows a similar increase in significance around the base of the Ludfordian as they do in the Welsh Borderlands and
Gotland. *G. villosa* was taken by Nestor as being at late Ludfordian species; this is concordant with the range of this species in Ludlow and Gotland.

**Brabant Massif.** As a result of the very poor preservation of material from the Brabant Massif it is very difficult to make direct comparisons. Even so, Verniers (1981) recognised a form he described as *Conochitina edjelensis elongata* in the early to middle Ludlow. A form resembling *C. edjelensis elongata* is also found in the lower Gorstian around Ludlow. The same author recorded the presence of *Cingulochitina convexa* from the early or middle Ludlow.

**South West Europe.** Although the recorded number of Ludlow chitinozoans is low it would appear from the work of Paris (1981, p. 348) that new species emerge in the middle to upper Gorstian of South West Europe. Paris recorded the presence of *Cingulochitina* sp. aff. *serrata* (named *Cingulochitina gorstyensis* here) and two species, *Cingulochitina* cf. *convexa* and *Angochitina* cf. *echinata* both of which have counterparts at a similar level in the type Ludlow. Paris also recorded the emergence of new species close to the contact with the Pridoli which are not recorded in the upper Ludfordian of the type Ludlow area. Cramer (1967, p.76) placed the base of the Ludlow Series at the top of the range of the *Conochitina edjelensis* complex in northern Léon, Spain, on the basis of similar forms recovered from the the Much Wenlock Limestone Formation in the Ludlow area. Forms resembling *C. edjelensis elongata* have also been recovered from lower Gorstian strata in the type Ludlow area and are named *C. edjelensis elongata*?

**South East Poland.** Very few comparisons are possible with the chitinozoans from SE Poland. Wrona (1980b) recorded the presence of forms similar to those recovered from the type Ludlow but no equivalent species are reported. Amongst these species are *Ancyrochitina* cf. *primitiva* (Ludlow, 'Mielnikian Stage'), *Belonechitinia* cf. *latifrons* and *Belonechitinia* cf. *intermedia* (upper Ludlow, 'Siedlce Stage'), and *Cingulochitina* cf. *cingulata* (upper 'Siedlce Series,' Ludfordian?). The chitinozoans from Wrona's work were extracted from discontinuous borehole sections. This has to be taken into account when considering the apparent lack of comparability of the chitinozoan faunas.


North Africa. Very little similarity exists with the chitinozoans of the type Ludlow and those described in the literature from the Sahara (Taugourdeau & Jekhowsky 1960 & 1964).

CHITINOZOANS AND ENVIRONMENTAL CHANGE.

Variations in chitinozoan assemblages are set against a background of lithological and sea level change. It would appear that influxes of chitinozoan species are often associated with argillaceous units, for example within the Middle Elton Formation (9 additional species with the re-introduction of 3 from lower in the succession, see Text-fig. 36) and 30cm below to 80cm above the base of the Lower Leintwardine Formation (4 additional species with the re-introduction of 8 species, see Text-fig. 36). However, not all silty or shaly formations are rich in chitinozoans; few additional chitinozoan species were recorded from the Lower and lower Middle Elton formations and within the main body of the Lower Leintwardine Formation.

The faunal turnover in the Middle Elton Formation and at the base of the Ludfordian are contemporaneous with the proposed sea level rises of Lawson (1975) and Dorning (1981a) (see Text-fig. 35). Sea level curves are often constructed using the premise that the increased argillaceous content of any unit may be equated with an increase in water depth. Changes in brachiopod communities are also commonly used in water depth studies. Both methods fail to take into account the effects that increase terrestrial input, water clarity and temperature may have on both lithological and faunal characteristics. Variations may depend upon the interaction of many factors, sea level being only one. It is therefore simplistic to label chitinozoans that occur in argillaceous formations as deep water forms, and those that occur in more carbonate rich lithologies as being adapted to shallow conditions.

A model proposed by Jeppsson (1990) attempts to explain variations in the lithological and faunal character of a succession in terms of oceanic cyclicity, regulated by oceanic CO₂ storage capacity. Jeppsson defined two distinct periods identified by
TEXT-FIG. 57. Some of the characteristics of a typical P and S episode (taken from Jeppsson 1990).
their lithological and faunal characters. Cycles are interpreted as driven by changes between dryer low latitude and warmer high latitude climates (S-episodes) and wetter low latitude and cooler high latitude climates (P-episodes). Some of the characteristics of a P and S-episode are shown in Text-fig. 57. Jeppsson argued that in an S-episode higher temperatures would reduce oceanic CO$_2$ storage capacity, thus increasing atmospheric levels of the greenhouse gas and perpetuating higher global temperatures. With warm surface waters unable to replace deep salinity dense water a salinity stratified ocean would be created in which oceanic circulation would be greatly reduced. Poor oceanic circulation restricts the availability of nutrients in the upper waters and the dry climate during an S-episode would reduce terrestrial runoff, ensuring clear water shelf conditions. Such warm, clear and nutrient poor waters would be excellent for the production of pure limestones but less satisfactory for high rates of planktonic productivity. An S-episode could therefore be recognised by a number of features including carbonate production and poor planktonic productivity. Such conditions would persist until CO$_2$ within the ocean had been depleted (by the production of biogenic carbonates) to such an extent that CO$_2$ could once again be taken from the atmosphere into the ocean. Under Jeppsson's model the warmer climatic conditions during an S-episode would result in a slight transgression due to the thermal expansion of sea water, this contradicting the generally held view that the presence of limestones is necessarily indicative of regressive conditions.

The cooler, wetter conditions during a P-episode would increase oceanic storage capacity of CO$_2$. This greenhouse gas depletion would perpetuate cooler global temperatures and maintain the episode until the oceanic storage capacity was exceeded and conditions reverted to an S-state. A P-episode would be characterised by higher rates of oceanic circulation, the result of temperature dense water replacing salinity dense water, and a corollary increase in the availability of nutrients on the shelf. The wetter conditions during a P-episode would also increase terreginous input. The colder, cloudier and more nutrient rich shelf conditions would be less favourable for pure limestone production but would promote higher planktonic productivity. The global
temperature drop during a P-episode may be sufficient to initiate glaciation in high latitudes resulting in glacially controlled eustatic changes. The shift of benthic communities up shelf, formerly interpreted as a response to increased water depth, could be explained as a movement of light dependent benthos to shallow shelf areas. Sunlight penetration would be reduced during a P-episode due to increased turbidity and cloudiness of sea water on the shelf (Jeppsson, 1990).

It is possible that the influx of new species in the Middle Elton Formation and at the base of the Ludfordian in the Ludlow area (and perhaps in the European sections recorded above) could be explained by such changes in environmental conditions. Jeppsson's model fits the latter case most satisfactorily. In the model, the limestones of the Upper Bringewood Formation, recording only moderate chitinozoan diversities, would be indicative of an S-episode whilst the more argillaceous sediments at the base of the Lower Leintwardine Formation, supporting diverse chitinozoan faunas (at least initially), would represent a P-episode. The assemblage including *A. narcissus*, *C. (Calpichitina) granosa*, *C. sp. aff. cingulata* and *F. cf. pistilliformis*, would therefore represent P-dependent taxa. Such an assumption would suggest that conditions during a P-episode, such as enhanced nutrient availability, would be of advantage to chitinozoans. This would be reflected in the presence of higher diversity assemblages, with hardy taxa being found during harsher periods dominated by S-state conditions. This, however, does not explain the disappearance of taxa from the Upper Bringewood Formation at Aymestrey (*A. aymestreyensis* and *G. swifti*). If these species were 'hardy taxa' they might also be expected to be present in sediments deposited during a P-episode. It is possible that their absence reflects increased competition or a specific dependence upon conditions developed during an S-episode, identifying these species as S-dependent taxa. Another problem with the model is the lack of high diversity assemblages, or even significant numbers of additional species, within the main body of the Lower Leintwardine Formation. Under Jeppsson's model this could be explained as changes in environmental factors not reflected lithologically, possibly a local effect. It must be noted that such an identification of P and S-dependent taxa and the assignment
of lithological units to a P or S-episode is speculative and would require the investigation of many additional sections to test its validity. The situation within the Middle Elton Formation is more difficult to explain in terms of Jeppsson's model as there is neither a dramatic increase in diversity or a lithological change. However, it can be seen that the change in character of chitinozoan assemblages is not purely facies related as the appearance of new chitinozoan species occurs within a relatively homogeneous lithological unit.

Another feature of Jeppsson's model is an explanation of the occurrence of Lazarus taxa. The re-emergence of species absent from large portions of the succession may happen when either P or S conditions recur allowing characteristic species, perhaps confined meanwhile to isolated 'refugia', to re-populate a wider area. Lazarus chitinozoans were found throughout the Ludlow succession, the most obvious being those recovered from 30cm below to 80cm above the Lower Leintwardine Formation at Sunnyhill Quarry (Text-fig. 46). A very similar assemblage is recorded from a thin shale horizon within the Lower Bringewood Formation on Deer Park Road (DP15, Text-fig. 42) but is absent throughout most of the Upper Bringewood Formation. It is possible that these species are missing from the limestones of the Upper Bringewood Formation because of unfavourable environmental factors, but occur at the base of the Ludlowian where conditions are once again suitable. Some Ludlow species show striking similarities to chitinozoans regarded as Wenlock and Llandovery forms. These include C. edjelensis elongata? (similar to C. edjelensis elongata from the Llandovery), C. sp. aff. cingulata (similar to the Wenlock form C. cingulata) and A. gogginensis (similar to Ancyrochitina gutnica from the Wenlock). It is possible that these are also Lazarus taxa.

As has already been indicated, it is important to consider the effects that local factors would have upon any larger scale cyclicity. In the late Ludlowian the infilling of the Welsh Basin would probably have had considerable effect upon any processes of a more global nature. The high abundance, low diversity assemblages from the Lower Whitcliffe Formation (Text-fig, 35) may indicate that chitinozoans came under greater environmental pressure, perhaps from an increased freshwater influence, as the Welsh
basin shallowed. By the latest Ludfordian conditions may have become virtually intolerable, reflected in the increased occurrence of low yield or barren samples. The limited lithological and faunal evidence from the Ludlow succession in the type area is not sufficient for a full evaluation of the validity of Jeppsson's model. As noted above, to adequately test this theory in terms of chitinozoans would require the investigation of parallel sections from elsewhere on the shelf and in the basin as well as in other parts of the world. It is possible that additional factors are involved in the production of the observed pattern of chitinozan extinction and radiation.

SUMMARY OF CONCLUSIONS

As morphological features such as ornamentation are often undetectable under the transmitted light microscope, the enhanced resolution provided by the scanning electron microscopy is regarded as essential in the study of Chitinozoa. Also the use of stereo-photography is invaluable, particularly when applied to chitinozoans that possess structurally complex elements such as Ancyrochitina and Gotlandochitina.

As chitinozoans are hermetically sealed units, they are not considered to represent the active stage of a marine protist. This, and the chain forming habit of the group, suggests that chitinozoans possibly represent the eggs of some (unknown) marine metazoan.

Preservation varies greatly and, although specimens from shale horizons tend to be flattened, the quality of preservation was found to be unrelated to lithology.

Chitinozan diversity declines throughout the Lower Elton Formation and increases in the Middle Elton Formation. A peak in diversity is recognised at the base of the Lower Leintwardine Formation (base of the Ludfordian Stage). In general, diversity falls throughout the Ludfordian Stage. Abundance follows a similar pattern to diversity.

Chitinozoans are a useful biostratigraphical tool in the Ludlow Series of the type area. Due to this enhanced resolution it is possible to erect a chitinozan biozonal scheme consisting of 12 numbered zones.
Comparison of chitinozoans from the type Ludlow Series with coeval sections reveals that greatest similarity occurs with collections from the island of Gotland (Sweden), Estonia and with the Brabant Massif. Little similarity occurs with South West Europe, Poland and North Africa.

Two chitinozoan radiation events are distinguished within the Ludlow succession; the first in the Middle Elton Formation and a second at the base of the Lower Leintwardine Formation (base of the Ludfordian Stage). The event in the Middle Elton Formation occurs within a lithologically homogeneous unit; thus it is concluded that the change in chitinozoan assemblages are not purely facies related. The influx of new species is regarded as being the result of a change of environmental conditions, particularly nutrient availability. Such changes are held responsible for the emergence of Lazarus taxa.
REFERENCES


----- 1972. Chitinozoen und andere mikrofossilien aus der Bohrung Leba, Pommern. ibid., 139, 64-87, 20pls.


*Geoscience and Man I*, Baton Rouge, Louisiana.


APPENDIX 1 : SAMPLE DESCRIPTIONS

Hand specimens of all the following are held at the University of Leicester.

PITCH COPPICE. (Text-fig. 37).


GOGGIN ROAD. (Text-figs 6, 38-40 ).


DEER PARK ROAD. (Text-figs 9, 41-42).


LOWER TODDING (LT) AND TODDING (T). (Text-figs 7, 43, 44).


AYMESTREY. (Text-figs 8, 45).

SUNNYHILL QUARRY (Text-figs 10, 46-50).


THE WHITCLIFFE. (Text-figs 11, 51-55).

ASTON MUNSWOW. (Text-figs 12 and 56).

PLATE 1

Fig. | Page | Description
--- | --- | ---
1 & 2. | 23 | *Bursachitina* sp. A. Lateral view, N36/PC13(iv) x400, Much Wenlock Limestone Formation; surface detail x3085.
3 & 4. |  | Lateral view, H39-4/LT3(ii) x400, Lower Leintwardine Formation; aboral margin x1500.

*Bursachitina* sp. B.

5. | 24 | Lateral view, S48/GR25(i) x250, Middle Elton Formation.
6. |  | Lateral view, 048/GR25(ii) x250, Middle Elton Formation.

*Calpichitina (Calpichitina) granosa* sp. nov.

7 & 8. | 26 | Chain of three individuals, P36/SH3(ii) x250, Lower Leintwardine Formation; holotype, Lateral view x500.

*Calpichitina (Calpichitina) gregaria* ?Paris, 1984

9 & 10. | 27 | Oral view, F46/W19(i) x500, Upper Leintwardine Formation; oblique oral view x500.
11 & 12. |  | Oral view, O31-1/W1 x500, Lower Leintwardine Formation; oblique oral view x500.

*Calpichitina (Calpichitina) sp. aff. hemsiensis* (Laufeld, 1974)

13. | 28 | Oblique oral view, N39/SH17(v) x500, Upper Bringewood Formation.
14 & 15. |  | Oblique oral view N35/SH3(ii)x500, Lower Leintwardine Formation; oral detail x1020.

*Eisenackitina intermedia* (Eisenack, 1955)

16 & 17. | 30 | Surface detail, k33/SH3(ii) x1020, Lower Leintwardine Formation; lateral view x250.
18. |  | Lateral view, O35/GR35 x250.
# PLATE 2

<table>
<thead>
<tr>
<th>Fig.</th>
<th>Description</th>
<th>Page</th>
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<tbody>
<tr>
<td>1 &amp; 2.</td>
<td><em>Eisenackitina intermedia</em> (Eisenack, 1955) Lateral view Q34-4/SH25(i) x400, Lower Leintwardine Formation; oblique aboral, x925.</td>
<td>30</td>
</tr>
<tr>
<td>3 &amp; 4.</td>
<td>Lateral view, F37-4/SH15(ii) (stereo pair) x250, Upper Bringewood Formation; oblique aboral view x615.</td>
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<td>5, 6 &amp; 7.</td>
<td>Lateral view M35/DPR1(i) x250, Lower Bringewood Formation; oblique aboral view x1000; oral view x800.</td>
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<tr>
<td>8, 9, 10 &amp; 11.</td>
<td><em>Eisenackitina lagenomorpha</em> (Eisenack, 1931) Lateral view, N36/SH3(ii) x250, Lower Leintwardine Formation; oblique oral view x500; oblique aboral view x500; aboral margin x1000.</td>
<td>32</td>
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<tr>
<td>12.</td>
<td>Lateral view, P37/DPR3(i) x250, Lower Bringewood Formation.</td>
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<tr>
<td>13 &amp; 14.</td>
<td>Lateral view, S39-1/SH3(ii) x250, Lower Leintwardine Formation; aboral margin x765.</td>
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<td>15.</td>
<td><em>Eisenackitina lagenomorpha?</em> (Eisenack, 1931) Lateral view, O35-2/SH3(ii) x500, Lower Leintwardine Formation.</td>
<td>34</td>
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<td>16.</td>
<td>Lateral view, P45-1/W0 x500, Lower Leintwardine Formation.</td>
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PLATE 3

Fig. 1 & 2. *Eisenackitina lagenomorpha*? (Eisenack, 1931) Lower Leintwardine Formation; aboral margin x1800.

Fig. 3 & 4. *Eisenackitina philipi* Laufeld, 1974 Lower Whitcliffe Formation; base detail x950.

Fig. 5. Lower Whitcliffe Formation.

Fig. 6, 7, 8 & 9. *Eisenackitina toddingensis* sp. nov. Lower Whitcliffe Formation; vesicle wall x900; aboral margin x1200; oblique aboral view x500.

Fig. 10. *Eisenackitina toddingensis* sp. nov. Lower Bringewood Formation x400.

Fig. 11, 12 & 13. Lower Bringewood Formation; oblique aboral view x800; oblique oral view x1000.
PLATE 4

**Eisenackitina toddingensis** sp. nov. 37

1. Lateral view, J39/LT5(i) x400, Lower Bringewood Formation.

2. Oblique aboral view, S38-1/LT2(i) x400, Lower Bringewood Formation.

**Cingulochitina** sp. aff. *cingulata* (Eisenack, 1937) 39

3 & 4. Lateral view, N48-2/SH16(iii) (stereo pair) x400, Lower Leintwardine Formation; oblique aboral x900.

5 & 6. Lateral view, J45/SH16(iii) (stereo pair) x400, Lower Leintwardine Formation; oblique aboral view x900.

**Cingulochitina convexa** (Laufeld, 1974) 40

7 & 8. Lateral view, P43-3/GR21(i) (stereo pair) x400, Middle Elton Formation; aboral margin x2500.

9. Lateral view, L32-4/GR23(i) x400, Middle Elton Formation.

10. Lateral view, O41-2/GR23(ii) x400, Middle Elton Formation.

11. Lateral view, M36-3/GR30 x400, Middle Elton Formation.

12. Lateral view, M27/GR22 x400, Middle Elton Formation.

**Cingulochitina gorstyensis** sp. nov. 42

13. Lateral view, S51-3/GR23(iii) x400, Middle Elton Formation.

14. Lateral view, T39-1/GR23(i) (stereo pair) x400, Middle Elton Formation.

15. Lateral view, M45-2/GR28(i) x400, Middle Elton Formation.
PLATE 5

_Cingulochitina gorstyensis_ sp. nov.

1, 2 & 3. Holotype (topmost) in chain of 3 individuals, K38/GR31(i) x400, Middle Elton Formation; holotype, oblique oral view x1400; holotype, oblique aboral view x750.

4 & 5. Lateral Pair, J40/GR31(ii) x400, Middle Elton Formation; operculum detail x1200.

6 & 7. Chain, J49/GR25(ii) x200, Middle Elton Formation; detail of one individual, x400.

_Cingulochitina_ sp. A

8 & 9. Lateral view, P40-2/GR23(ii) x400, Middle Elton Formation; aboral margin x1700.

10. Lateral pair, E44-4/GR25(ii) x400, Middle Elton Formation.

11, 12 & 13. Lateral view, O48-2/GR25(i) x400, Middle Elton Formation; detail of base x1300; detail of oral part of the specimen x2800.
PLATE 6

Fig.   Page

Belonechitina lauensis (Laufeld, 1974) 47
1 & 2. Lateral view, J41/SH25(i) (stereo pair) x250, Lower Leintwardine Formation; aboral margin x3000.
3. Lateral view, P47-1/A5(i) x250, Upper Bringewood Formation.
4 & 5. Lateral view, O32-1/LT11(ii) x250, Lower Bringewood Formation; aboral margin x1200.
6 & 7. Lateral view, S37-1/LT3(ii) x250, Lower Bringewood Formation; detail of base in oblique aboral view x1200.

Belonechitina latifrons (Eisenack, 1964) 45
8, 9 & 10. Lateral view, L36/T7(i) x250, Lower Bringewood Formation; oblique aboral view x500; base detail x1500.
11, 12 & 13. Lateral view, P43-1/GR66 x250, Lower Bringewood Formation; oblique aboral view x440; base detail x1650.

Belonechitina mortimerensis sp. nov. 49
PLATE 7

Fig. 1, 2 & 3. Lateral view, U37-3/SH20(ii) (stereo pair) x250, Lower Bringewood Formation; oblique aboral view x740; oral neck detail x930.

Fig. 4. Lateral view, M38-4/DP10 x250, Lower Bringewood Formation.

Fig. 5 & 6. Holotype lateral, T41/DP10(ii) (stereo pair) x250, Lower Bringewood Formation; aboral detail x600.

Fig. 7 & 8. Lateral view, G36-2/DP24(ii) x250, Lower Bringewood Formation; oblique aboral view x490.

Fig. 9. Lateral view, H30-1/GR25(ii) x250, Middle Elton Formation.

Fig. 10. Lateral view, P45-3/GR1(v) x250, Much Wenlock Limestone Formation.

Fig. 11 & 12. Lateral view, N43-3/PC11(iii) x250, Much Wenlock Limestone Formation; base detail x1000.

Fig. 13. Lateral view, F40/PC10(iv) x250, Much Wenlock Limestone Formation.

Fig. 14. Lateral view, T39/GR5(ii) x250, Lower Elton Formation.
## PLATE 8

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<tr>
<td>Lateral view, R32-2/PC13(v) (stereo pair) x250, Much Wenlock Limestone Formation; base in oblique aboral view x930.</td>
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<td>Lateral view, L40/GR9(i) x250, Lower Elton Formation; oral neck detail x900.</td>
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<td>5 &amp; 6.</td>
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<td>Lateral view, O39/GR9(i) x250, Lower Elton Formation; base in oblique aboral view x600.</td>
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<td>7 &amp; 8.</td>
<td>54</td>
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<td>Lateral view, P43-2/PC10(iv) x250, Much Wenlock Limestone Formation; base in oblique aboral view x680.</td>
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<td>9 &amp; 10.</td>
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<td>Lateral view, M36-4/PC1(iv) x250, Lower Elton Formation; base detail x480.</td>
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<td>11, 12 &amp; 13.</td>
<td>54</td>
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<tr>
<td>Lateral view, N44/GR2(ii) x250, Much Wenlock Limestone Formation; oral neck detail x1230; aboral detail x740.</td>
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<td>14 &amp; 15.</td>
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<td>Lateral view, O43/PC4(iii) x250, Lower Elton Formation; base in oblique aboral view x740.</td>
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**PLATE 9**

**Conochitina pachycephala** Eisenack, 1964  

1 & 2. Lateral view, M39/PC6(v) x250, Much Wenlock Limestone Formation; base in oblique aboral view x600.

3. Lateral view, H47-2/PC10(iv) x250, Much Wenlock Limestone Formation.

**Conochitina cf. proboscifera forma truncata** Laufeld, 1974  

4 & 5. Lateral view, U38/PC2(iv) (stereo pair) x250, Lower Elton Formation; base in oblique aboral view x590.

6 & 7. Lateral view, T41/GR25(i) x250, Middle Elton Formation; aboral margin x1200.

8 & 9. Lateral view, K44/GR20(v) x250, Middle Elton Formation; aboral detail x600.

**Conochitina sp. A**  

10 & 11. Lateral view, M41/GR8(i) x250, Lower Elton Formation; base in oblique aboral view x600.

12. Lateral view, P46/GR9(ii) x250, Lower Elton Formation.

13. Lateral view P42-1/GR8(i) x250, Lower Elton Formation.

**Rhabdochitina wakefieldi** sp. nov.  

14, 15 & 16. Holotype lateral view, M32-3/LT11(i) x250, Lower Bringewood Formation; base in oblique aboral view x600; oral neck detail x925.
PLATE 10

Fig. | Page
---|---

*Rhabdochitina wakefieldi* sp. nov.

1 & 2. Lateral view, Q25-2/LT11(ii) x250, Lower Bringewood Formation; oblique aboral x500.

3 & 4. Lateral view M33-3/LT6(i) x250, Lower Bringewood Formation; oblique aboral x600.

Chitinozoan indet.

5 & 6. Lateral view, P40-1/DP25(i) x250, Lower Bringewood Formation; aboral margin, note parasite borings x925.

*Ancyrochitina ancyrea* (Eisenack, 1931)

7 & 8. Lateral view, P38-4/GR60 (stereo pair) x300, Lower Bringewood Formation; aboral margin x1230.

9. Lateral view, L43-1/W0 x300, Lower Leintwardine Formation.

10. Lateral view, L43/A7(i) x300, Upper Bringewood Formation.

11. Lateral view, L46-1/SH1(ii) x300, Lower Leintwardine Formation.

12. Lateral view, N44-3/GR47(i) x300, Upper Elton Formation.

13. Lateral view, N32/GR49(i) x300, Upper Elton Formation.

*Ancyrochitina* cf. *ansarviensis* Laufeld, 1974

14 & 15. Oblique oral view, O36-1/SH3(ii) x600, Lower Leintwardine Formation; oral view x600.
PLATE 11

Fig.  

Ancyrochitina aymestreyensis sp. nov.  

1, 2 & 3. Lateral view, Specimen lost /A5(ii) (stereo pair) x430, Upper Bringewood Formation; oblique oral view x 300; oblique aboral x500.

4. Holotype lateral view, O35-1/A5(i) x300, Upper Bringewood Formation.

5. Lateral view, O41/GR66(i) x300, Lower Bringewood Formation.

Ancyrochitina gogginensis sp. nov.  

6. Lateral view, O36-2/GR23(ii) (stereo pair) x300, Middle Elton Formation.

7, 8 & 9. Lateral view, J43-2/GR25(ii) (stereo pair) x300, Middle Elton Formation; oral neck detail, note emergent prosome x1000; aboral margin x1100.

10, 11 & 12. Holotype lateral view, J36/GR23(ii) (stereo pair) x300, Middle Elton Formation; appendice x2500; oral neck detail x1850.
**PLATE 12**

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<td>1. Lateral view, F37/GR24(i) x300, Middle Elton Formation.</td>
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<td>2. Lateral view, G45-4-1/PC9(ii) (stereo pair) x300, Much Wenlock Limestone Formation.</td>
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<tr>
<td>3. Lateral view, P46-2/GR24(i) x300, note emergent prosome, Middle Elton Formation.</td>
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<td>4. Lateral view, T34/GR23(i) x300, Middle Elton Formation.</td>
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*Ancyrochitina gogginensis* sp. nov. 65

5, 6, 7 & 8. Holotype lateral view, L35/SH3(ii) x300, Lower Leintwardine Formation; oblique oral view x500; base x500; oblique aboral view x300; oblique aboral view x300.

9, 10, 11 & 12. Lateral view O48/SH2(iii) (stereo pair) x300, Lower Leintwardine Formation; oblique oral view x300; oblique aboral view x300; petalloid neck ornament x1200.

13. Lateral view, K38-3-2/DP15 (stereo pair) x300, Lower Bringewood Formation.

*Ancyrochitina narcissus* sp. nov. 67
PLATE 13

Ancyrochitina narcissus sp. nov. 67
1. Lateral view, K35-1/SH2(ii) x300, Lower Leintwardine Formation.
2. Lateral view, M27-1/SH15(ii) (stereo pair) x300, Upper Bringewood Formation.

Ancyrochitina cf. pachyderma Laufeld, 1974 69
3 & 4. Oblique aboral view, F40-4/PC7(vii) x700, Much Wenlock Limestone Formation; lateral view x300.
5 & 6. Oblique oral view, Q42-4/PC2(v) x600, Lower Elton Formation; oral view x600.
7. Lateral view, G41/PC13(v) x300, Much Wenlock Limestone Formation.
9. Lateral view, L42/PC13(iv) x300, Much Wenlock Limestone Formation.

Ancyrochitina cf. primitiva Eisenack, 1964 70
8. Lateral view, L45/DP23(i) x300, Lower Bringewood Formation.
10. Lateral view, O40-3/DP21(i) x600, Lower Bringewood Formation.
11. Lateral view, L39-3/GR51(i) x600, Upper Elton Formation.

Ancyrochitina sp. A 71
12, 13 & 14. Lateral view, L43-3/PC6(iv) x300, Much Wenlock Limestone Formation; oral neck detail x800; aboral margin x1050.
15, 16, & 17. Lateral view, N39-3/PC3(vi) x300, Lower Elton Formation; appendice scar x1200; oral neck detail x800.
**PLATE 14**

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<th>Ancyrochitina sp. A</th>
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<td>Lateral view, P36/LT5(i) x300, Lower Bringewood Formation; vesicle surface x1200.</td>
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<td>3.</td>
<td>Lateral view, P53-3/SH8(ii) x600, Lower Leintwardine Formation.</td>
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<td>4.</td>
<td>Lateral view, P31-4/LT5(ii) x300, Lower Bringewood Formation.</td>
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<tr>
<td>5.</td>
<td>Lateral view, J46-4/GR24(i) x300, Middle Elton Formation.</td>
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<tr>
<td>6.</td>
<td>Lateral view, O36-1/DPR3(i) x300, Lower Bringewood Formation.</td>
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<tr>
<td>7.</td>
<td>Lateral view, M35/LT5(ii) x300, Lower Bringewood Formation.</td>
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<thead>
<tr>
<th>Angochitina sp. aff. echinata Eisenack, 1931</th>
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<tbody>
<tr>
<td>8 &amp; 9.</td>
<td>Lateral view, Q40-4/SH30(vi) (stereo pair) x300, Lower Leintwardine Formation; ornament detail x1200.</td>
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<td>10 &amp; 11.</td>
<td>Lateral view, N38-3/GR30 x300, Middle Elton Formation; surface detail x1200.</td>
</tr>
<tr>
<td>12.</td>
<td>Lateral view, M52-4/GR30 (stereo pair) x300, Middle Elton Formation.</td>
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<tr>
<th>Angochitina elongata Eisenack, 1931</th>
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<tr>
<td>13.</td>
<td>Lateral view, Q39-2/GR36(i) x300, Middle Elton Formation.</td>
</tr>
<tr>
<td>14 &amp; 15.</td>
<td>Lateral view, Q36-3/GR45(ii) (stereo pair) x300, Upper Elton Formation; surface detail x925.</td>
</tr>
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</table>
PLATE 15

Angochitina elongata Eisenack, 1931

1, 2 & 3. Lateral view, R51-2/SH16(iii) (stereo pair) x300, Upper Bringewood Formation; oral neck detail x740; oblique oral view x740.

4 & 5. Lateral view, H22/SH15(ii) x300, Upper Bringewood Formation; oral neck detail x600.

Angochitina milleri sp. nov.

6 & 7. Lateral view, L40/SH31(ii) x300, Lower Leintwardine Formation; ornament detail x1300.

8 & 9. Holotype lateral view, R29/SH26 (stereo pair) x300, Lower Leintwardine Formation; ornament detail x900.

10. Lateral view, P47/SH25(i) x300, Lower Leintwardine Formation.

11 & 12. Lateral view, O47-1/SH31(ii) (stereo pair) x300, Lower Leintwardine Formation; ornament detail x900.
**PLATE 16**

**Fungochitina cf. pistilliformis** (Eisenack, 1931) 79

1. Lateral view, O32-4/SH3(ii) x400, Lower Leintwardine Formation.

**Gotlandochoitina swifti** sp. nov. 82

2, 3 & 4. Holotype lateral view, P39/DP6(i) (stereo pair) x300, Lower Bringewood Formation; neck ornament detail x600; appendice detail x1000.

5. Lateral view, P43/GR62 x300, Lower Bringewood Formation.

6, 7 & 8. Lateral view, P42/DP6(iii) (stereo pair) x300, Lower Bringewood Formation; neck ornament detail x800; aboral margin x700.

9 & 10. Lateral view, Q34-3/A8 x300, Upper Bringewood Formation; oblique oral view x400.

11. Lateral view, J52/DP23(i) x600, Lower Bringewood Formation.

12. Lateral view, R38-3/A8 x600, Upper Bringewood Formation, note parasitic borings.
PLATE 17

Fig.    Page

1.      81
Lateral view, H38-2/W25 x600, Lower Whitcliffe Formation.

2 & 3.  81
Holotype lateral view, O30/W25 x300, Lower Whitcliffe Formation; aboral margin x1200.

4 & 5.  81
Lateral view, G47-1/W26 x300, Lower Whitcliffe Formation; aboral margin x1200.

6.      81
Lateral view, K45/W26 x300, Lower Whitcliffe Formation.

7, 8 & 9.  84
Lateral view, P41-3/W25 (stereo pair) x300, Lower Whitcliffe Formation; aboral ornament detail x1000; neck detail x1500.

10, 11 & 12  84
Oral neck detail, O38-1/W25 x1100, Lower Whitcliffe Formation; lateral (stereo pair) x300; ornament detail x1500.

13.     84
Lateral view, K39-1/W45 x300, Upper Whitcliffe Formation.

14.     84
Lateral view, O35-1/W21 x600, Upper Leintwardine Formation.

*Gotlandochitina dinhamensis* sp. nov.

*Gotlandochitina villosa* Laufeld 1974
### PLATE 18

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<tr>
<th>Fig.</th>
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<td><strong>Gotlandochitina</strong> sp. aff. <em>villosa</em> Laufeld, 1974</td>
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</tr>
<tr>
<td>1, 2 &amp; 3. Lateral view, L38-4/DPR1(i) (stereo pair) x300, Lower Bringewood Formation; oblique oral view x300; body x700.</td>
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<tr>
<td>4. Lateral view, M34-2/LT11(ii) x300, Lower Bringewood Formation.</td>
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<tr>
<td>10 &amp; 11. Lateral view, O34-1/DPR1(i) x300; ornament detail x1300.</td>
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<td><strong>Gotlandochitina</strong> sp. A.</td>
<td>86</td>
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<tr>
<td>5 &amp; 6. Lateral view, N34-1/SH15(ii) (stereo pair) x300, Upper Bringewood Formation; ornament detail x1200.</td>
<td></td>
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<tr>
<td>7 &amp; 8. Lateral view, O42/SH9(ii) x300, Lower Leintwardine Formation; oblique aboral view x755.</td>
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<td><strong>Sphaerochitina</strong> cf. <em>lycoperdoides</em> Laufeld, 1974</td>
<td>88</td>
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<tr>
<td>12. Lateral view, O43/DP25(i) x600, Lower Bringewood Formation.</td>
<td></td>
</tr>
<tr>
<td>13, 14 &amp; 15. Lateral view, R43-4/DP25(i) x600, Lower Bringewood Formation; aboral ornament detail x1850; ornament detail on neck x1300.</td>
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