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A diverse chitinozoan record from the Upper Ordovician (Katian) of the Cincinnati region (Kentucky, USA)

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Abstract

Biostratigraphic characterization of the Upper Ordovician in the Cincinnati region is complicated by several issues including provincialism of conodonts and graptolites, their facies dependence, the lack of biostratigraphical resolution for conodonts, and the absence of graptolites from many sections. Our study of the MY-14-01 core from Maysville (Kentucky, USA), type area for the Maysvillian Regional Stage of the Cincinnatian Series, suggests that chitinozoan biostratigraphy has the potential to strengthen the existing biostratigraphic framework based on conodonts and graptolites. Our samples usually yielded abundant, well-preserved chitinozoans in diverse populations. Many of these taxa are present in biostratigraphic reference sections from other parts of the Laurentian paleocontinent (Quebec and Anticosti Island, Canada, and Nevada, USA) and Avalonia (England and Wales). Here we provide systematic descriptions of selected chitinozoan taxa, including those of 12 new species: *Conochitina rudis*, *Tanuchitina hooksae*, *Belonechitina laciniata*, *Hercochitina andresenae*, *Hercochitina anningae*, *Hercochitina edingerae*, *Hercochitina krafftae*, *Hercochitina polygonia*, *Hercochitina tharpae*, *Clathrochitina mangle*, *Angochitina bascomae*, and *Nevadachitina soufianei*. One new name combination is proposed: *Belonechitina duplicitas* (Martin, 1983). This study provides a robust starting point for further advancing the Katian chronostratigraphic framework of the U.S. midcontinent.

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Non-technical Summary

Renowned for their outstanding fossil preservation and abundance, the strata of the Cincinnati region (USA) provide an important reference for Upper Ordovician (ca. 458–443 million years ago) studies around the globe. A group of extinct organic microfossils, chitinozoans are important components of Upper Ordovician assemblages globally, and are found across a broad spectrum of marine environments. Many chitinozoan species were abundant, short-lived taxa that are easy to recognize and geographically widespread, making them excellent biostratigraphical markers. This work focus on the taxonomy of chitinozoan assemblages for the Cincinnati region. Sixty-six samples were studied from the MY-14-01 core (drilled near Maysville, the type area of the North American Maysvillian Stage). Those samples yielded abundant, well-preserved, and diverse populations of chitinozoans, which allowed the identification of 50 chitinozoan species: 17 species are already known in the literature, 21 species that remain in open nomenclature, and 12 new species are defined. Several key chitinozoan species stand out in the MY-14-01 core in terms of their biostratigraphical potential, some of which are used to define biozones in other parts of Laurentia, and Avalonia paleocontinents. Our work unveils the unrealized potential of chitinozoans in the wider area and is a robust starting point for establishing a chitinozoan biostratigraphic framework for the Cincinnati region.

Introduction

Renowned for their outstanding fossil preservation and abundance, the strata of the Cincinnati region (USA) provide an important reference for Upper Ordovician studies around the globe. Patterns of sedimentary cyclicity, faunal migrations, and paleoecology are well documented in these Katian Stage strata (e.g., Holland, 1993; Brett et al., 2020; Stigall, 2023). Unfortunately, questions remain about the precise chronostratigraphic correlation of these strata with other basins of the Laurentian paleocontinent and those on other paleocontinents. Fully integrating

Cincinnatian studies into the global picture of Late Ordovician events requires advances in age assessment of these and other Upper Ordovician strata.

Upper Ordovician biostratigraphic studies in the Cincinnati region primarily utilized conodonts and graptolites. Conodonts are highly abundant in some carbonate intervals within the Cincinnati region with studies yielding nearly a quarter of a million elements (e.g., Bergström and Sweet, 1966). They typically show outstanding mineralogical preservation and internal structure but are commonly fragmented. Graptolites by contrast are much less abundant and show a broad range of preservation. They are most common in dark-gray to brown shales north of Cincinnati, but even in these facies they have a sporadic stratigraphic distribution (Mitchell and Bergström, 1991; Goldman and Bergström, 1997). When graptolites are found it is typically on bedding planes choked with flattened, flow-aligned, monospecific assemblages, surrounded by centimeters to meters of barren shale. Poor preservation is not uncommon on these bedding planes with the best-preserved specimens typically coming from adjacent limestone beds.

Despite the relatively large specimen yields, the distribution of zonally significant conodont and graptolite taxa in the Cincinnati region is patchy and many collections are plagued by low-diversity assemblages dominated by long-ranging lineages (e.g., Sweet, 1984; Goldman and Bergström, 1997). Provincialism in both graptolite and conodont faunas has also created difficulties for interregional chronostratigraphic correlation (e.g., Bergström, 1990; Goldman et al., 2013). Ultimately, the integrated biostratigraphic framework of conodonts and graptolites in the Katian strata of the Cincinnati region is highly reliant on a few key sections, such as the core at Middletown, Ohio. This core not only contains zonally significant conodonts of both the Baltic (i.e., North Atlantic) and Midcontinent zonal schemes, but also zonally important graptolites of the *Orthograptus ruedemanni* through *Geniculograptus pygmaeus* zones (Bergström and Sweet, 1966; Mitchell and Bergström, 1991; Richardson and Bergström, 2003). Layering other biostratigraphic and chemostratigraphic techniques upon this foundation of conodont and graptolite biostratigraphy in the Cincinnati region (e.g., Bergström et al., 2010) provides an opportunity to test and refine regional and global chronostratigraphic correlations.

Chitinozoans are important components of Upper Ordovician biostratigraphy globally (e.g., Achab, 1989; Paris, 1990; Vandenbroucke, 2008a), and are found across a broad spectrum of marine facies (Vandenbroucke et al., 2010). However, chitinozoan studies in the Katian strata of the Cincinnati region are relatively limited. Eisenack (1959) was the first to describe new species of chitinozoans—*Hyalochitina hyalophrys* (Eisenack, 1959) and *Cyathochitina makromyka* Eisenack, 1959—from Cincinnati (Ohio, US). Grahn and Bergström (1985) studied the chitinozoans from the Ordovician–Silurian boundary. Additionally, three master's theses were written about Upper Ordovician chitinozoans of the Cincinnati region. Miller (1976) completed the first detailed study of chitinozoans in the area, mainly focused on the Maysvillian strata in the type region of the Cincinnatian Series. Knabe (1980) studied chitinozoans from the Kirkfieldian and Shermanian sub-stages (i.e., Chatfieldian Regional Stage) to the Edenian Regional Stage. Lastly, Velleman (2016) completed a preliminary study of the chitinozoans spanning the interval from the uppermost Tyrone Formation to the Bull Fork Formation from two drill cores. The data from one of these cores were revised and integrated here.

This study presents the rich, diverse, and well-preserved chitinozoan fauna from the MY-14-01 core drilled near Maysville, Kentucky. The main focus of the paper is to identify and describe the chitinozoans occurring in this core and to define the new species encountered in order to increase their potential for biostratigraphical and paleogeographical analyses.

Geological setting

The Jessamine dome is a broad, irregular, and gentle structure, nowadays marked by a faulted topographic high, that brings Ordovician rocks to the surface in Indiana, Ohio, and Kentucky (Fig. 1) (Borella and Osborne, 1978; Weir et al., 1984). The Cincinnati region, as referred to here, is largely synonymous with the Jessamine Dome but also includes adjacent features in the shallow subsurface of southern Kentucky, southwestern Ohio, and southeastern Indiana.

During the Late Ordovician, a shallow epicontinental sea covered much of Laurentia, and the Taconic orogeny was active along its southern margin (Rowley and Kidd, 1981; Stanley and Ratcliffe, 1985; Macdonald et al., 2017). More than 400 km north of the subduction zone, the Cincinnati region was relatively stable and situated at approximately 20–25° S latitude (Scotese and McKerrow, 1990). The Cincinnati region is the North American reference standard for the Upper Ordovician, including the regional Cincinnatian Series (e.g., Sweet and Bergström, 1971), which is divided into the Edenian, Maysvillian, Richmondian, and Gamachian (defined on Anticosti Island, Canada; Twenhofel, 1927) Regional stages (Bergström in Ross et al., 1982, and references therein).

The MY-14-01 core was drilled (38.621461°N, 83.671719°W) on the outskirts of Maysville, Kentucky, approximately 90 km southeast of Cincinnati, Ohio (Fig. 1). The total core length exceeds 500 m and the upper 224 m were donated by the Carmeuse Maysville Plant for this study (archived at the Illinois State Geological Survey). The top of the Millbrig K-bentonite, which marks the base of the regional Chatfieldian Stage (Bergström et al., 2004; Sell et al., 2013), occurs 8 cm below the base of the Lexington Limestone in this core (1019.8 ft/310.8 m). Our study interval begins near the top of the Point Pleasant Formation (785 ft/239.3 m), continues through the Kope (Edenian), the Fairview (Maysvillian), and Grant Lake (Maysvillian) formations, and ends near the top of the Bull Fork Formation (Richmondian; 50 ft/15.2 m). The locally mapped *Grewingkia* bed occurs in the core around the 45 m mark (147 ft; Schilling and Peck, 1967). The Ordovician–Silurian boundary is estimated to occur 24 m (80 ft) above the top of the core.

Material and methods

Benchtop study of the MY-14-01 core included documentation of the lithologic and macrofossil succession to provide links to the extensive mapping and conodont studies previously published from the Maysville area. Sixty-six samples from the MY-14-01 core were studied for chitinozoan biostratigraphy. Between 15 and 25 g of each sample were processed for chitinozoans using hydrochloric (HCl) and hydrofluoric (HF) acids, following a protocol based on classic palynological procedures (e.g., Paris, 1981) at the palynological laboratory of Ghent University, Belgium (see De Backer et al., 2024, for specifics). The core samples were crushed into fragments of about 0.5 cm diameter, treated with 6% HCl until decarbonated, then heated to 65°C with 150 mL 40% HF for 48 hours. Any newly formed fluorosilicates were removed using a second 6% HCl treatment, at 65°C. Samples were neutralized and filtered at 53 μm. The organic fraction larger than 53 μm of each sample was hand-picked for chitinozoans using a Zeiss Discovery

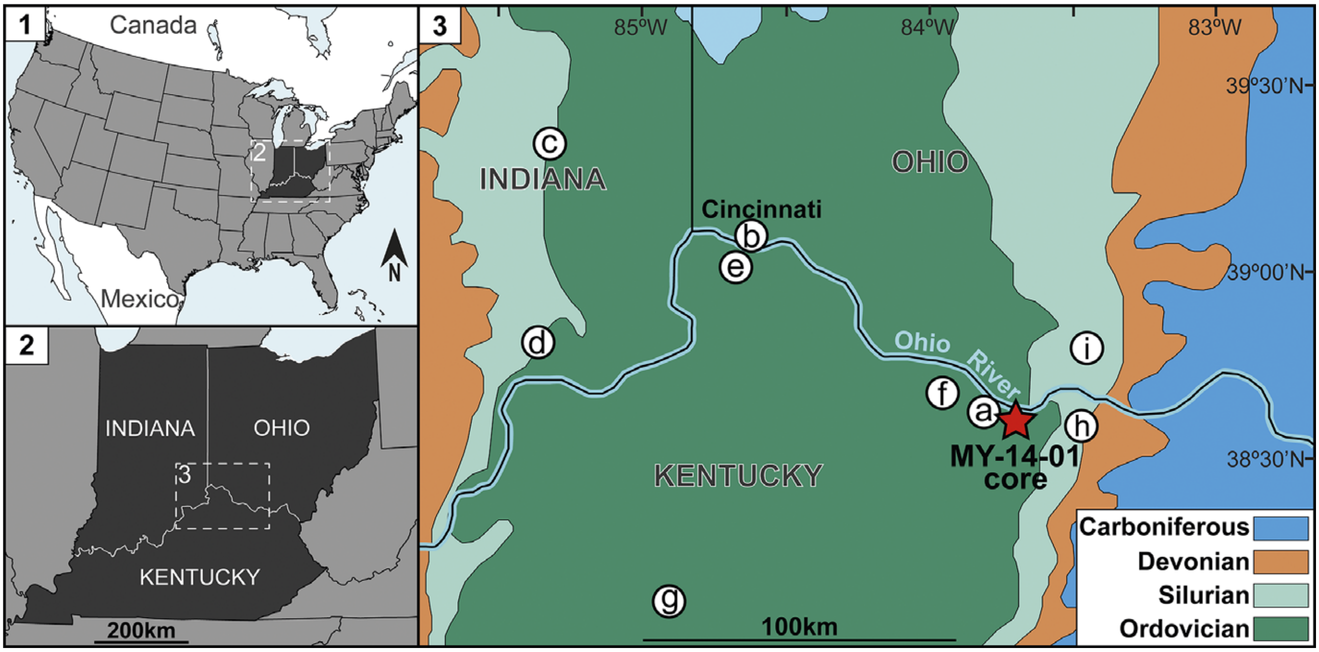

Figure 1. Location maps. (**1**) U.S.A. map highlighting the study area. (**2**) Map highlighting the states of Indiana, Ohio, and Kentucky, with the Cincinnati region outlined. (**3**) Generalized geologic map of the Cincinnati region (modified from Coogan, 1996). The red star marks the MY-14-01 drill core. Other relevant sections are marked by a circled letter: a, Maysville section; b, Cincinnati section; c, Indiana Geological Survey Drill Hole no. 124; d, China section (a–d are sections previously studied by Miller, 1976); e, Covington section; f, CA-38 core; g, Frankfort sections (e–g are successions studied by Knabe, 1980); h, Tollesboro section; i, Brush Creek section (h and i were studied by Grahn and Bergström, 1985).

V20 Stereomicroscope at ~50× magnification and mounted for scanning electron microscope (SEM) imagery and identification using a TESCAN field emission TIMA3-X GMU. All the samples studied from the MY-14-01 core were productive and most yielded assemblages of abundant and well-preserved chitinozoans. Co-occurring with the chitinozoans in the organic residues are acritarchs, graptolite fragments, melanosclerites, and scolecodonts.

Chitinozoan diversity was calculated for this core and displayed in a graphic (Fig. 2) similar to the one used by Colmenar and Rasmussen (2018). Sample-based diversity consists of the number of different species present in each sample. For constructing the cumulative diversity curve, the complete ranges of the taxa have been considered, even if a specific taxon does not occur in that sample.

Repositories and institutional abbreviations. The holotypes and holotype assemblages have been mounted on permanent microscopy slides to be stored in the collections of the Royal Belgian Institute of Natural Sciences in Brussels (RBINS), for permanent curation (RBINS collection numbers b 10041 to b 10052). The remaining specimens, stubs, sample residues, and rock samples are stored in the collections of the Department of Geology, Ghent University, Krijgslaan 281 S8, Belgium. The MY-14-01 core is archived at the Illinois State Geological Survey (ISGS) sample library.

Systematic paleontology

Fifty different chitinozoan taxa were identified from the organic residues (Fig. 2; chitinozoan counts in Supplementary Data 1). Of these, 17 species are already known in the literature, 21 species remain in open nomenclature, and 12 new species are defined (Figs. 3–13): *Conochitina rudis* n. sp., *Tanuchitina hooksae* n. sp., *Belonechitina laciniata* n. sp., *Hercochitina andresenae* n. sp., *Hercochitina anningae* n. sp., *Hercochitina edingerae* n. sp., *Hercochitina krafftae* n. sp., *Hercochitina polygonia* n. sp., *Hercochitina tharpae* n. sp., *Clathrochitina mangle* n. sp., *Angochitina bascomae* n. sp., and *Nevadachitina soufianei* n. sp. Additionally, one new name combination is proposed: *Belonechitina duplicitas* (Martin, 1983).

Some species are present throughout almost all or more than half of the studied interval (i.e., long-ranging species): *Plectochitina* cf. *Pl. sylvanica* (Jenkins, 1970a), *Cyathochitina brevis* Martin, 1983 (Fig. 4.8), *Desmochitina minor* Eisenack, 1931 (Fig. 4.18), *Kalochitina multispinata* Jansonius, 1964 (Fig. 4.22), *Pterochitina hymenelytrum* Jenkins, 1969 (Fig. 4.20, 4.21), *Conochitina minnesotensis* (Stauffer, 1933) (Fig. 4.1), *Ancyrochitina barbescens*? Martin, 1975, *Ancyrochitina* aff. *Anc. corniculans* Jenkins, 1969, *Plectochitina spongiosa* (Achab, 1977b), *Desmochitina cocca* Eisenack, 1931 (Fig. 4.17), *Cyathochitina kuckersiana* (Eisenack, 1934) (Fig. 6.11), *Calpichitina lata* (Schallreuter, 1963) (Fig. 6.22), *Cyathochitina latipatagium* Jenkins, 1969 (Fig. 9.20), and *Angochitina* cf. *Ang. capillata* Eisenack, 1938. Other species have relatively short ranges in the core and may be valuable for biozonation. The highest diversity is found in the lower Kope Formation and drops significantly upward through the core with only a few species present near the top of the Bull Fork Formation (Fig. 2).

The chitinozoan generic and suprageneric classification scheme of Paris et al. (1999) is used herein, and their morphological terminology has been used as closely as possible. Open nomenclature is used following the recommendations of Bengtson (1988). The measurements of the chitinozoan specimens described below may be found in the Supplementary Data 2. The measurements recorded (when applicable) are: L – total length of the vesicle; D – maximum diameter of the chamber; Da – diameter of the aperture; Lch – length of the chamber (base to flexure); Ln – length of the neck (flexure to lip); L carina – maximum length carina; L collarette

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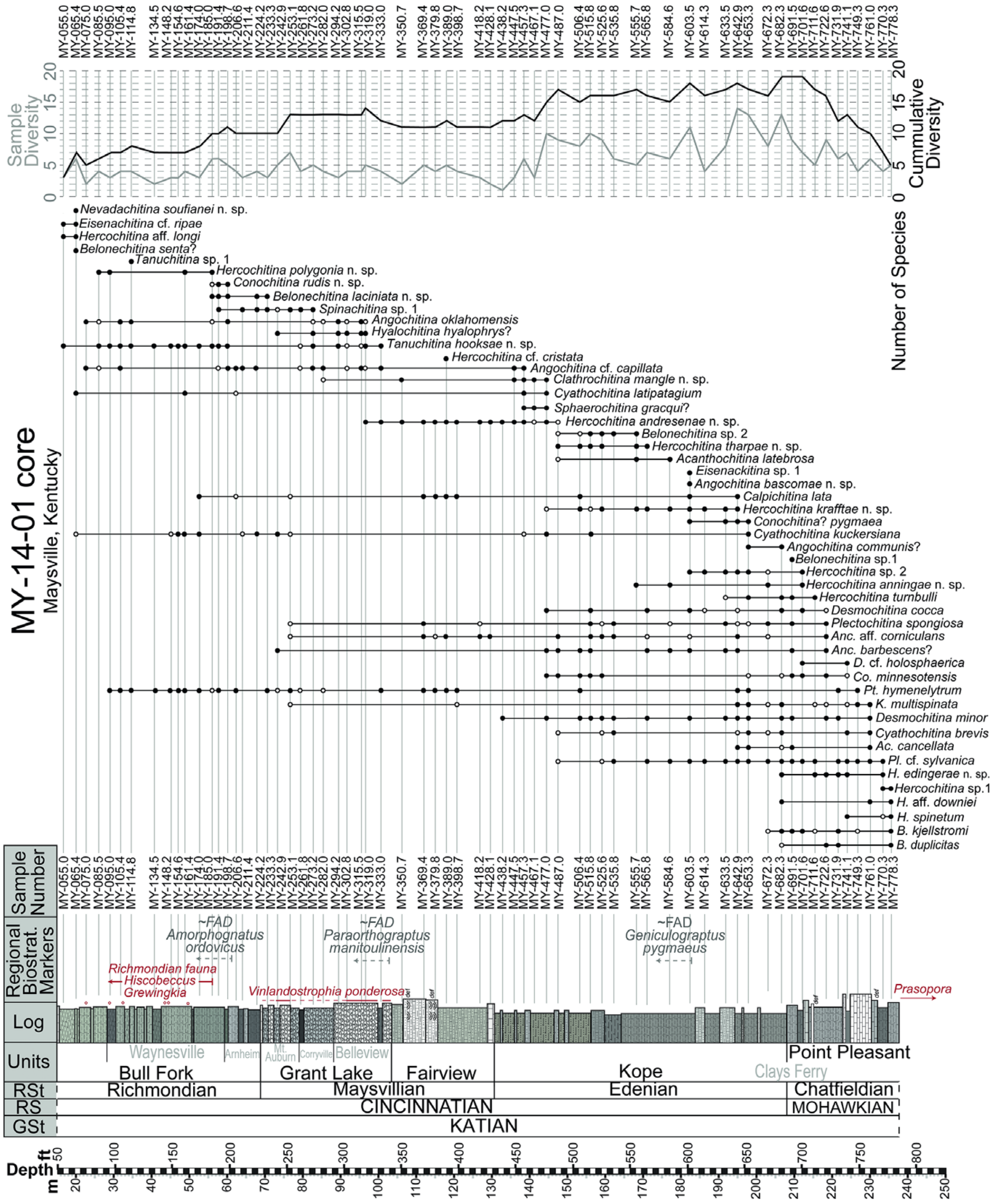

Figure 2. Log of the MY-14-01 core showing the lithologies, stratigraphic positions of the samples studied, the chitinozoan ranges of selected species, and species diversity curves. Closed and open circles represent certain and uncertain identifications, respectively. Abbreviations and acronyms: def = deformed beds; FAD = first appearance datum; GSt = Global Stage; RS = Regional Series; RSt = Regional Stage; *B. = Belonechitina*; *H. = Hercochitina*; *Pl. = Plectochitina*; *Ac. = Acanthochitina*; *K. = Kalochitina*; *Pt. = Pterochitina*; *Co. = Conochitina*; *D. = Desmochitina*; *Anc. = Ancyrochitina.*

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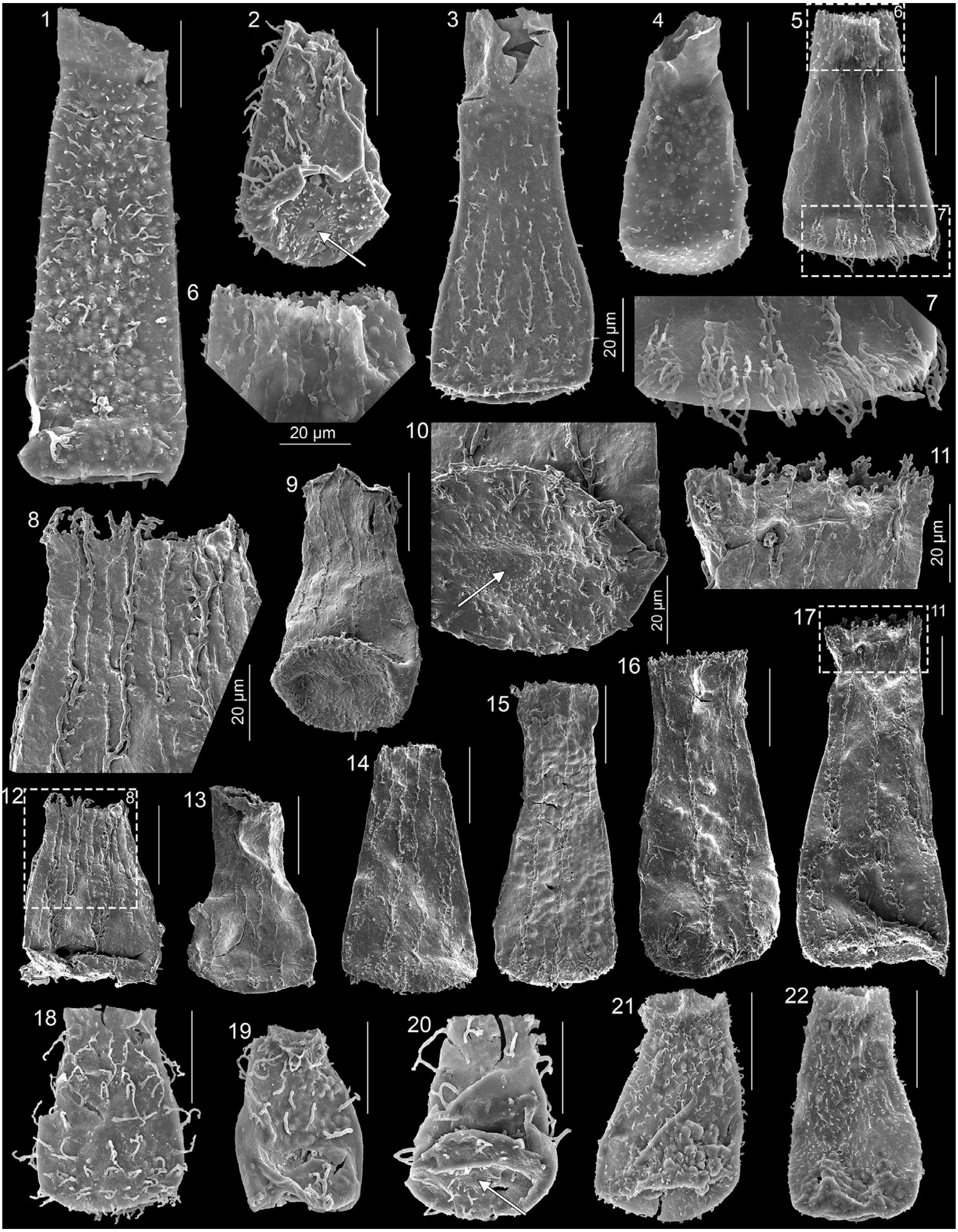

Figure 3. Scanning electron images of relevant species from the Point Pleasant Formation, with sample reference. (**1, 2**) *Belonechitina duplicitas* (Martin, 1983) n. comb.: (**1**) MY-731.9 ft (223.1 m), (**2**) MY-778.3 ft (237.2 m), note the ornamentation on the base and the arrow in (**2**), pointing to the pit with a mucron. (**3**) *Hercochitina spinetum* Melchin and Legault, 1985, MY-778.3 ft (237.2 m). (**4**) *Belonechitina kjellstromi* (Martin, 1975) MY-731.9 ft (223.1 m). (**5–17**) *Hercochitina edingerae* n. sp.: (**5–7**) MY-731.9 ft (223.1 m); (**8–17**) MY-770.3 ft (234.8 m), where the detailed images (**6, 8, 11**) display the gently sinuous, complex crests bifurcating towards the aperture, and the elaborated ornamentation on the lip, (**7**) is a closeup of the complex spines on the margin, and (**10**) is a base view, displaying the ornamentation decreasing towards the center, where a pit without a mucron is highlighted with an arrow, (**11, 17**) holotype, RBINS b 10046. (**18–20**) *Hercochitina* aff. *H. downiei* Jenkins, 1967, MY-778.3 ft (237.2 m), note the ornamentation on the base and the arrow in (**20**), pointing to the pit with a mucron. (**21, 22**) *Hercochitina* sp. 1, MY-778.3 ft (237.2 m). All scale bars = 50 µm, except when another value is indicated on the figure.

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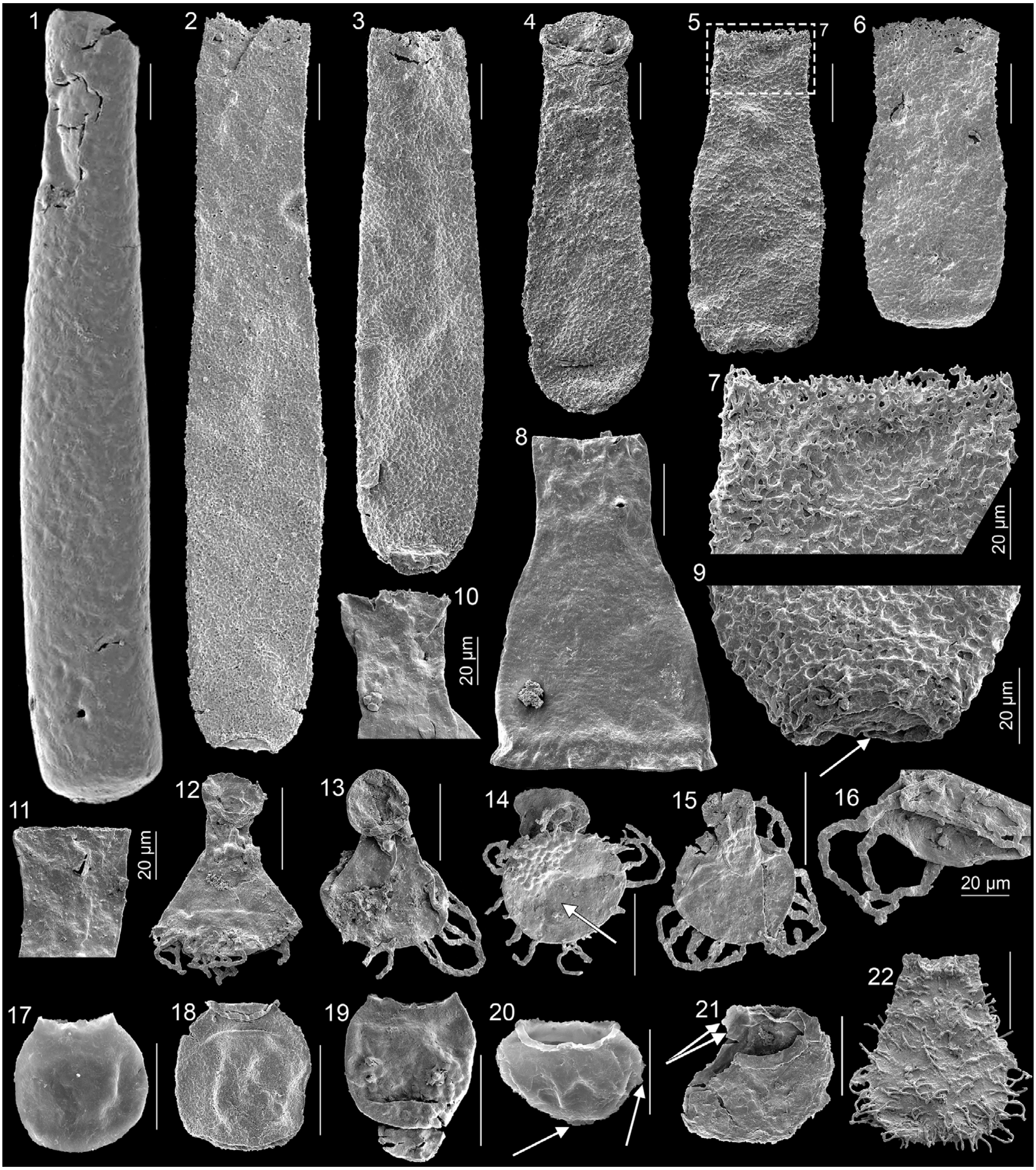

Figure 4. Scanning electron images of relevant species from the Point Pleasant and Kope formations, with the sample and formation reference. (**1**) *Conochitina minnesotensis* (Stauffer, 1933), MY-722.6 ft (220.2 m), Point Pleasant Formation. (**2–7, 9**) *Acanthochitina cancellata* Martin, 1983: (**2 –4, 6, 9**) MY-761.0 ft (232.0 m), Point Pleasant Formation, (**5, 7**) MY-642.9 ft (196.0 m), Kope Formation), (**7**) closeup of the lip ornamentation of (**5**), (**9**) view of the margin and base, where an arrow points to the pit with a mucron. (**8**) *Cyathochitina brevis* Martin, 1983, MY-761.0 ft (232.0 m), Point Pleasant Formation. (**10–16**) *Plectochitina* cf. *Pl. sylvanica* (Jenkins, 1970a), MY-761.0 ft (232.0 m), Point Pleasant Formation: (**10, 11**) detailed views of the granulate neck and gently fimbriated lips, (**14**) arrow highlighting the discrete concentric rings at the base, (**16**) closeup of the long, anastomosed processes. (**17**) *Desmochitina cocca* Eisenack, 1931, MY-682.3 ft (208.0 m), Kope Formation. (**18**) *Desmochitina minor* Eisenack, 1931, MY-691.5 ft (210.8 m), Point Pleasant Formation. (**19**) *Desmochitina* cf. *D. holosphaerica* Eisenack, 1968, MY-741.1 ft (225.9 m), Point Pleasant Formation. (**20, 21**) *Pterochitina hymenelytrum* Jenkins, 1969, Point Pleasant Formation: (**20**) MY-731.9 ft (223.1 m), arrows highlighting separation of the outer membrane from the vesicle wall, (**21**) MY-749.3 ft (228.4 m), broken specimen with arrows indicating the outer membrane and the vesicle wall. (**22**) *Kalochitina multispinata* Jansonius, 1964, MY-761.0 ft (232.0 m), Point Pleasant Formation. All scale bars = 50 µm, except when another value is indicated in the figure.

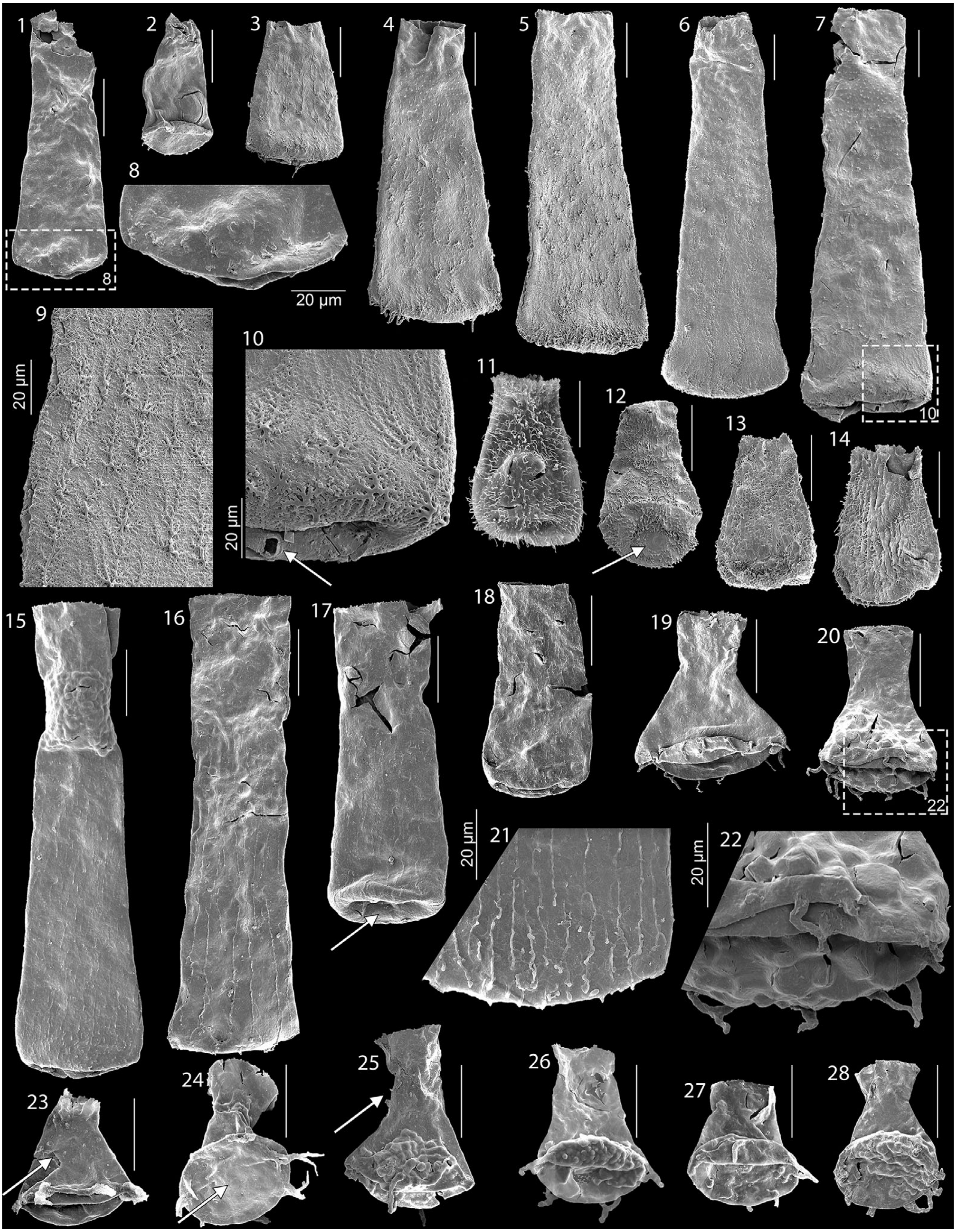

Figure 5. Scanning electron images of relevant species from the Point Pleasant and Kope formations, with the sample and formation reference. (**1, 2, 8**) *Belonechitina* sp. 1, MY-691.5 ft (210.8 m), Point Pleasant Formation, (**8**) closeup of the lowermost part of the specimen (**1**), displaying the variety of spines ornamenting the lowermost part of the chamber. (**3–7, 9, 10**) *Hercochitina anningae* n. sp.: (**3, 4**) MY-555.7 ft (169.4 m), Kope Formation, (**5, 6**) MY-672.3 ft (204.9 m), Kope Formation, (**5**) holotype, RBINS b 10045, (**7, 9, 10**) MY-701.6 ft (213.8 m), Point Pleasant Formation, (**9**) detail of the crests on the chamber, (**10**) close up of the crests on the lowermost of the vesicle and margin of specimen (**7**), with the arrow pointing to the pit with a mucron and concentric rings surrounding them. (**11–14**) *Hercochitina turnbulli* Jenkins, 1969, Point Pleasant Formation: (**11, 12**) MY-711.6 ft (216.9 m), (**12**) arrow pointing at the concentric rings and pit with a mucron at the center of the base, (**13, 14**) MY-691.5 ft (210.8 m). (**15–18, 21**) *Hercochitina* sp. 2, Kope Formation: (**15, 17, 18**) MY-642.9 ft (196.0 m), (**17**) arrow highlighting the faint pit with a mucron at the center of the base, (**16**) MY-614.3 ft (187.2 m), (**21**) MY-672.3 ft (204.9 m), detailed image displaying the fine crests ending in simple spines on the margin. (**19, 20, 22**) *Ancyrochitina barbescens*? Martin, 1975, MY-603.5 ft (183.9 m), Kope Formation: (**22**) detailed image of specimen (**20**), displaying the numerous, fine, and spongy processes characteristic of this species. (**23–25**) *Ancyrochitina* aff. *Anc. corniculans* Jenkins, 1969, MY-722.6 ft (220.2 m), Point Pleasant Formation: (**24**) arrow points to the faint concentric rings at the base, (**23, 25**) arrows pointing at the ornamentation on the vesicle. (**26–28**) *Plectochitina spongiosa* (Achab, 1977b): (**26**) MY-633.5 ft (193.1 m), Kope Formation, (**27**) MY-672.3 ft (204.9 m), Kope Formation, (**28**) MY-691.5 ft (210.8 m), Point Pleasant Formation. All scale bars = 50 μm, except when another value is indicated in the figure.

– maximum length collarette; L processes – maximum length processes; H crests – maximum height crests; H mesh – maximum height mesh; and H spines – maximum height spines. Supplementary Data 3 has an alphabetical list of the identified species in the MY-14-01 core.

Incertae sedis Group **Chitinozoa** Eisenack, 1931
Order **Prosomatifera** Eisenack, 1972
Family **Conochitinidae** Eisenack, 1931 emend. Paris, 1981
Subfamily **Conochitininae** Paris, 1981
Genus ***Conochitina*** Eisenack, 1931, emend. Paris et al., 1999

Type species. Conochitina claviformis Eisenack, 1931; lost holotype in Eisenack, 1931, p. 84, pl. 1, fig. 17, from erratic graptolitic rocks ('Graptolithengestein'); neotype in Eisenack, 1968, p. 159, pl. 25, fig. 5, from erratic graptolitic rocks, early Ludlow, Silurian (Paris et al., 1999).

Conochitina rudis new species
Figure 11.1–11.6

Holotype. Illustrated in Figure 11.4 (RBINS collection number b 10041); dimensions: L: 154 μm; D: 120 μm; Da: 84 μm; L/D: 1.28; D/Da: 1.43; sample MY-198.7 ft (60.6 m), Bull Fork Formation (Maysville, Kentucky, USA).

Diagnosis. Stout subcylindrical to subconical species with a distinctively ornamented lip, fimbriated and usually with some perforations. The vesicle wall is composed of two layers, somewhat separated, with the outer membrane being peculiarly rough, with an irregular aspect.

Occurrence. From sample MY-198.7 ft to MY-185.0 ft (60.6–56.4 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle varies from subcylindrical to subconical. Flanks straight to slightly convex. The flexure can be inconspicuous, without a clear separation between the chamber and neck (Fig. 11.3). When a gentle flexure is observed, it separates the conical chamber from the subcylindrical to flaring neck (Fig. 11.6). Lip distinctively ornamented, fimbriated, and sometimes also perforated. When slightly broken, it is possible to observe that the vesicle wall is composed of two layers, somewhat individualized (Fig. 11.5). Throughout the entire vesicle, the outer layer has a rough, rugose ornamentation that, in extreme examples, can look like scales (Fig. 11.2, 11.3). This results in a homogenously irregular surface wall. In long specimens, the neck appears smooth. Rounded margin. The base has the same rough ornamentation; a pit with a mucron is situated at its center (Fig. 11.1).

Etymology. 'Rudis' means 'raw, rude, scratchy, or rough' in Latin. The name refers to the diagnostic rough vesicle wall.

Materials. *N* = 50 specimens.

Dimensions. L: 95–164–242 μm; D: 75–99–120 μm; Da: 56–73–97 μm; L/D: 1.10–1.67–2.44; D/Da: 1.19–1.36–1.68 (*n* = 25).

Remarks. Although visibly ornamented, the vesicle surface of our material is still considered glabrous, one of the diagnostic features of the genus *Conochitina*. No other species of *Conochitina* is known to have this characteristic vesicle shape, and a wall with two layers that appear only to be poorly fused (Fig. 11.5), with the outer layer having a rough, rugose ornamentation.

Conochitina? pygmaea Achab, 1987
Figure 6.1–6.3

1987 *Conochitina pygmaea* n. sp.; Achab, p. 1216–1218, pl. 9, figs. 1–10.
?2001 *Conochitina? pygmaea*; Ottone et al., p. 102, pl. 3, fig. 4.

Holotype. GSC85479, sample from St-Roch n°1 core, 1700 ft (518 m), Utica Group, Katian, Upper Ordovician; near Sorel-Tracy city, SW Quebec Province, Canada (Achab, 1987, p. 1216, pl. 9, fig. 1).

Occurrence. From sample MY-653.3 ft to MY-603.5 ft (199.1–183.9 m), Kope Formation, MY-14-01 core, Kentucky, USA. Also from upper Utica Group, near Sorel-Tracy city, SW Quebec Province (St-Roch n°1 core), and Macasty Shale, Anticosti Island (LGPL and LGCP cores), Canada (Riva, 1969; Achab, 1987, 1989).

Description. The vesicle's overall shape is stout and subconical, with convex flanks. In specimens without a neck, the vesicle is inflated and subconical, with the flanks tapering towards the aperture (Fig. 6.1). Other specimens have a gentle flexure between a short neck, tapering towards the aperture, and an inflated and subconical chamber (Fig. 6.2). At the end of the spectrum, some specimens show a more pronounced flexure separating the neck (~1/3 of the total length) from the inflated, subconical chamber (Fig. 6.3). The sealing structure has been observed close to the aperture. The lip is mildly fimbriated and can be finely and randomly perforated. Rounded margin. Vesicle wall usually smooth but can display randomly distributed granules (Fig. 6.2). Base frequently invaginated. Rarely, probable pits with a mucron were observed at the center of the base; however, these structures were very small and discrete, preventing a clear assessment of this feature.

Materials. *N* = 27 specimens.

Dimensions. L: 84–108–131 μm; D: 69–79–92 μm; Da: 27–36–46 μm; L/D: 1.03–1.36–1.62; D/Da: 1.84–2.22–3.00 (*n* = 13).

Remarks. Specimens can have a large variability in vesicle shape and outline across the population within the same sample. We consider our material to be conspecific with the specimens described and figured by Achab (1987) as *Conochitina pygmaea.* Given the overall shape of the vesicle (short and inflated, more common in genera of the Family Desmochitinidae) in both Achab's (1987) and our material, the uncertainties about the apical structures, and that the sealing structure has been observed near the aperture, we have some doubt about the attribution of this species to the genus *Conochitina.* Although Ottone et al. (2001) also questioned the attribution of this species to the genus *Conochitina*, their specimen is poorly preserved (fractures, folds, and pyrite marks present) and it appears to have randomly distributed granules and spines.

In the Province of Quebec, *Co. pygmaea* is one of two nominal species of a biozone defined by Achab (1989), in strata of the *Geniculograptus pygmaeus* graptolite Biozone (GBz; Riva, 1969; Achab, 1987).

Subfamily **Tanuchitininae** Paris, 1981
Genus ***Hyalochitina*** Paris and Grahn in Paris et al., 1999

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Figure 6. Scanning electron images of relevant species from the Kope Formation, with sample reference. (**1–3**) *Conochitina*? *pygmaea* Achab, 1987: (**1**) MY-603.5 ft (183.9 m), (**2**) MY-642.9 ft (196.0 m), (**3**) MY-653.3 ft (199.1 m). (**4–10**) *Hercochitina krafftae* n. sp., MY-642.9 ft (196.0 m): (**4**) closeup highlighting the organization of the crests and the spines on the margin, (**5, 6**) short specimens, arrows indicate sealing structures, (**7**) holotype, RBINS b 10047, (**9**) arrow indicates discrete pit with a mucron. (**11**) *Cyathochitina kuckersiana* (Eisenack, 1934), MY-653.3 ft (199.1 m). (**12–17**) *Angochitina bascomae* n. sp., MY-603.5 ft (183.9 m): (**13**) arrow indicates cylindrical prosome partially ejected, (**14**) holotype, RBINS b 10051, displays an unusual structure at the aperture, still partially attached to the lip, that could be part of a prosome, (**15**) long specimen, (**16**) short specimen, (**17**) closeup of ornamentation at the lower part of the holotype specimen in (**14**), with arrows indicating the bifurcated spines. (**18–21**) *Eisenackitina* sp. 1, MY-603.5 ft (183.9 m): (**18**) long specimen, (**18, 19**) specimens with an operculum partially ejected, (**21**) short specimen. (**22**) *Calpichitina lata* (Schallreuter, 1963), MY-642.9 ft (196.0 m). All scale bars = 50 µm, except when another value is indicated in the figure.

Type species. By original designation, *Cyathochitina hyalophrys* Eisenack, 1959; holotype in Eisenack, 1959, p. 11–12, pl. 2, fig. 6, from the Upper Ordovician of Cincinnati, Ohio, USA.

***Hyalochitina hyalophrys*?** (Eisenack, 1959)
Figure 11.7–11.9

Occurrence. From sample MY-319.0 ft to MY-242.9 ft (97.2–74.0 m), Grant Lake Limestone, MY-14-01 core, Kentucky, USA.

Materials. *N* = 36 specimens.

Dimensions. L: 336–423–500 μm; D: 84–109–134 μm; Da: 69–74–79 μm; L carina: 5–8–11 μm; L/D: 3.02–3.95–5.54; D/Da: 1.21–1.47–1.83 (*n* = 9).

Remarks. This species has a short original description and has not been reported frequently in the literature. The specimens in our population are frequently broken as these long vesicles seem to have a fragile wall. For identification of this morphotype, we focused on a few characteristic features (Eisenack, 1959): population with an elongated subconical vesicle (total length 276–382–528 μm), neck that can be distinctly flaring, carina on the margin (L carina 5–10 μm), and lack of ornamentation. The dimensions of the specimens in our population also fall within the range of values provided for the type population.

The *Hyalochitina hyalophrys*? specimens are usually longer than *Tanuchitina hooksae* n. sp. specimens and without ornamentation on the vesicle. This population also can be separated from *Tanuchitina* sp. 1, given that the specimens of *Tanuchitina* sp. 1 are always longer and wider and their carina is always clearly below the margin. However, because of the imperfect preservation of our specimens, we decided to keep them in open nomenclature.

Miller (1976) identified *Hy. hyalophrys* in the upper Fairview Formation, Miamitown Shale, Grant Lake Limestone, Mt. Auburn, and Dillsboro formations, from Ohio, Kentucky, and Indiana, USA. In Canada, *Hy. hyalophrys* is the nominal species of a biozone defined by Achab (1989) above the *Conochitina* sp. 2 Biozone, the latter partially equivalent to the *Paraorthograptus manitoulinensis* GBz (Riva, 1969; Achab, 1987).

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

Type species. *Tanuchitina ontariensis* Jansonius, 1964; lost holotype (Michelle Coyne, pers. comm., 2023) in Jansonius, 1964, p. 910–911, pl. 1, fig. 6 (Imp. 4309-306-7-112.1 x 17), cuttings from Imperial-Calvan Anderson no. 9-6 borehole, depth 738 m (2420 ft), Maeford-Dundas Formation, Katian, Upper Ordovician, Anderdon Township, Essex County, Ontario, Canada; neotype not yet designated.

Tanuchitina hooksae new species
Figure 10

Holotype. Illustrated in Figure 10.13 (RBINS collection number b 10042); dimensions: L: 175 μm; D: 70 μm; Da: 50 μm; L carina: 4 μm; L/D: 2.50; D/Da: 1.39; sample MY-185.0 ft (56.4 m), Bull Fork Formation (Maysville, Kentucky, USA).

Diagnosis. *Tanuchitina* species with low but distinct ornamentation propagated throughout the entire vesicle—typically granules, that can coexist with small spines, crest-like and/or mesh-like structures. The ornamentation of the vesicle delicately spreads to the carina below the margin (< 14 μm), typically perforated and with an irregular outline.

Occurrence. From sample MY-333.0 ft (101.5 m), Grant Lake Limestone, to sample MY-055 ft (16.8 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicle's overall shape is subcylindrical to conical, with straight to convex flanks. In specimens with an inconspicuous flexure, the vesicle is conical, with the flanks tapering towards the aperture (Fig. 10.4, 10.7, 10.9, 10.10, 10.12, 10.13). When a gentle flexure is present, it separates the subcylindrical, somewhat short neck from the conical chamber (Fig. 10.1, 10.3). The maximum width is located at the rounded margin or closely above it. The lip is always fimbriated and can also display perforations and spines (Fig. 10.1, 10.7). Low-rise but distinctive ornamentation spread over the whole vesicle. The most prevalent type comprises vesicles with randomly distributed, individualized granules (Fig. 10.1, 10.10, 10.13–10.15). Rarely, vesicles with granules display bands of densely distributed, thicker granules and spines, alternating with areas with more spaced, small granules (Fig. 10.2, 10.3). There are rare specimens with granules connected by lines, giving the ornamentation a polygonal-mesh appearance (Fig. 10.4, 10.5, 10.9). In some vesicles, the granules can be well-developed and coexist with small spines (Fig. 10.12). Some specimens show fine lines, subparallel to the long axis of the chitinozoan vesicle, creating a crest-like appearance (Fig. 10.7, 10.8). The ornamentation on the vesicle delicately spreads to the carina below the margin, with a variable length (3–14 μm), commonly perforated and always with an irregular outline (Fig. 10.5, 10.8, 10.16–10.18). The base is gently ornamented with granules, with a pit with a mucron at its center, surrounded by concentric rings (Fig. 10.6, 10.18).

Etymology. Named after the pen name 'bell hooks' used by Gloria Jean Watkins, an African-American educator, author, and social critic born in Kentucky.

Materials. *N* = 821 specimens.

Dimensions. L: 98–195–367 μm; D: 56–82–116 μm; Da: 44–59–100 μm; L carina: 3–7–14 μm; L/D: 1.44–2.42–4.07; D/Da: 1.13–1.40–1.68 (*n* = 46).

Remarks. Frequently, *Tanuchitina* specimens with distinct ornamentation coexist in the same sample and are considered part of the same population. The intraspecific variation of dimensions and ornamentation in this morphotype is notable, as demonstrated in Figure 10.

Tanuchitina alborzensis Ghavidel-Syooki, 2017, of the Ghelli Formation, Iran, resembles the new species described here due to its granulate ornamentation. However, *T. alborzensis* usually is longer than our material, the density of its granules decreases towards the aperture, the ornamentation on the lip is not described or observed, no perforations are observed in the carina, and, while the carina length is not provided, we calculated it from the plate with the type material as no longer than 5 μm. Additionally, intraspecific variation in the ornamentation of specimens is not mentioned for *T. alborzensis.* From our material, the specimens with a gentle flexure (e.g., Fig. 10.1, 10.3) may display an overall shape similar to *Tanuchitina ontariensis* Jansonius, 1964, first described from the Maeford-Dundas Formation, currently assigned to the Georgian Bay Formation (Ontario, Canada; Liberty, 1969; Zhang et al., 2011).

In contrast, *T. ontariensis* has a more pronounced hourglass shape, with the flaring neck approximately half of the total length of the vesicle, and, importantly, the vesicles are not described as having ornamentation nor is it observed in the specimen figured by Jansonius (1964). Although *T. ontariensis* is the type species of the genus *Tanuchitina*, it was succinctly described, only one complete specimen was figured, and no SEM images were ever made, which hinders assessing the morphological characters of the entire population and their variation. It remains possible that, in the absence of SEM studies of the type assemblage of *T. ontariensis*, these type specimens do contain subtle ornamentation, which could make them fall within the intraspecific variability we describe here for *Tanuchitina hooksae* n. sp. Unfortunately, further studies are impossible, as the holotype of *T. ontariensis* is considered lost (Michelle Coyne, pers. comm., 2023), and the type stratum (collected in well cuttings) is inaccessible. Thus, we separate our ornamented specimens from *T. ontariensis* to emphasize the presence of ornamentation.

Another species showing similarities with the material described here is *Tanuchitina laurentiana* Soufiane and Achab, 2000b, given its outline and dimensions. However, the *T. laurentiana* population has clear convex flanks, giving the vesicles an inflated aspect, and, while this is not described, the longitudinal axis of the type specimens figured is slightly curved. Also, for *T. laurentiana*, the ornamentation on the lip, vesicle, or carina and the presence of apical structures have not been described or observed.

***Tanuchitina* sp. 1**
Figure 12.1, 12.2, 12.10

Occurrence. Sample MY-114.8 ft (35.0 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. Elongated, subcylindrical vesicle shape. Gentle flexure between the short, slightly flaring neck, and long, subcylindrical and inflated chamber (Fig. 12.1, 12.2). Maximum width at the lower half of the chamber. Carina below the rounded margin. Lip gently fimbriated. Vesicle wall glabrous, varying from smooth to rugose in appearance, the latter especially noticeable in the lowermost part of the chamber of some specimens. At the transition between chamber and carina, fine folds can be observed, parallel or oblique to the longitudinal axis of the vesicle (e.g., Fig. 12.10). In parts where the carina is well preserved, it is long and complete (i.e., without perforations), without distinct ornamentation. The carina seems to tear easily (Fig. 12.10); therefore, the carina wall is considered thin and fragile, and the irregular outline of the carina is not considered diagnostic since it could be damaged. In a few specimens, the carina seems multi-layered (Fig. 12.2). When observed, the base of the vesicle always displays a rugose aspect, with a pit with a mucron at its center (Fig. 12.10).

Materials. $N = 5$ specimens.

Dimensions. L: 602–659 μm; D: 145–156 μm; Da: 116–118 μm; L carina: 16–18 μm; L/D: 4.16–4.22; D/Dp: 1.24–1.33 ($n = 2$).

Remarks. Our specimens display similarities with *Tanuchitina anticostiensis* (Achab, 1977a) and *Tanuchitina agrestis* (Jenkins, 1970a) in terms of vesicle and carina length and vesicle shape. The maximum diameter and absence of rough ornamentation in our material are more compatible with the features of *T. anticostiensis* than with *T. agrestis.* However, some ornamentation has been observed in our specimens, which is incompatible with *T. anticostiensis*: the vesicle wall appears rugose, particularly at the lowermost part of the chamber (Fig. 12.1), carina, and base (Fig. 12.10). In contrast to our material, the carina of *T. anticostiensis* appears robust, not damaged and with a wavy outline. Additionally, many characteristics of *T. anticostiensis* and *T. agrestis* display significant overlap (vesicle shape, dimensions, age), and their main difference (i.e., the rough ornamentation of *T. agrestis*) cannot be fully evaluated given that there are no SEM images known of this taxon. Given our limited population and all the uncertainties expressed, the use of open nomenclature is preferred.

Subfamily **Belonechitininae** Paris, 1981
Genus ***Acanthochitina*** Eisenack, 1931

Type species. Acanthochitina barbata Eisenack, 1931; lost holotype in Eisenack, 1931, p. 82–83, pl. 1, fig. 10, from erratic limestone from the Baltic ('Ostseekalk'); neotype in Nõlvak, 1980, pl. 29, fig. 1, Hullo borehole, 21.0 m, Baltoscandian late Vormsi Stage, Katian, Upper Ordovician, Estonia (Paris et al., 1999).

Remarks. The genus *Acanthochitina* was erected as monospecific, with *Acanthochitina barbata* as the type species (Eisenack, 1931). Before the 1970s, it was difficult to fully understand the details of ornamentation without advanced imaging techniques. For decades, many specimens with a second layer elevated from the vesicle were attributed to *Ac. barbata* (see below, in the remarks of the *Acanthochitina* species, mention of possible misidentifications). Now that SEM is a standard technique in chitinozoan studies, differentiation among species of *Acanthochitina* is easier and advances are being made (see Vandenbroucke, 2008b).

Acanthochitina cancellata Martin, 1983
Figure 4.2–4.7, 4.9

1983 *Acanthochitina*? *cancellata* Martin, p. 11, pl. 3, fig. 19; pl. 4, figs. 14, 28, 29.
1987 *Acanthochitina cancellata*; Achab, p. 1213, pl. 2, figs. 1–4.
?**2000** *Acanthochitina cancellata*; Asselin et al., pl. 1, figs. 4, 5, 7, 8.
?**2004** *Acanthochitina cancellata*; Asselin et al., pl. 1, fig. 10.

Holotype. CGC 55810, sample NEP-9-2, Delisle unit, Lotbinière Formation, Utica Group, Portneuf County, Quebec, Canada (Martin, 1983, p. 11, pl. 4, fig. 14).

Occurrence. Discontinuously from samples MY-761.0 ft (232.0 m) to MY-642.9 ft (196.0 m), Point Pleasant and Kope formations, MY-14-01 core, Kentucky, USA. *Acanthochitina cancellata* also occurs from the Neuville Formation (Trenton Group) to the Lotbinière Formation (Utica Group), St-Lawrence Lowlands, Quebec, and in the Macasty Formation, Anticosti Island, Canada (Martin, 1983; Achab, 1987).

Materials. $N = 87$ specimens.

Dimensions. L: 253–390–645 μm; D: 91–110–150 μm; Da: 65–83–106 μm; H mesh: 2–4–5 μm; L/D: 1.97–3.58–5.21; D/Da: 1.10–1.34–1.71 ($n = 33$).

Remarks. Despite some specimens of our population surpassing the dimensions of the type material of Martin (1983) and the specimens attributed by Achab (1987) to this species, the remaining morphological characters fit within the diagnostic range given by Martin

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(1983). The variability of dimensions we encountered in our population likely is related to the greater number of specimens found (n = 87), in contrast with the number of specimens studied by Martin (1983, n = 4) and Achab (1987, n = 8).

Achab (1987) reassigned specimens identified as *Acanthochitina barbata* Eisenack, 1931, from the Kope Formation, Kentucky (Miller, 1976), to *Ac. cancellata.* However, we suggest those specimens fit better within *Acanthochitina latebrosa* Vandenbroucke, 2008b. Additionally, we question the specific attribution of the specimens figured in Asselin et al. (2000, 2004). On the specimens from the lower Amadjuak Formation (south Baffin Island, Canada; Asselin et al., 2000), the mesh ornamenting the vesicle seems considerably elevated from the vesicle wall, particularly in Asselin et al. (2000, pl. 1, figs. 7, 8 [corrected from the original figure caption]), a feature more compatible with *Ac. latebrosa.* However, due to the limited resolution of the published images, this suggestion cannot be confirmed. These specimens, as well as the one represented in Asselin et al. (2004, pl. 1, fig. 10) are incomplete and broken, which prevents us from fully evaluating their dimensions. While the latter-mentioned specimen has a vesicle and ornamentation outline suggestive of *Ac. cancellata*, its image was obtained in transmitted light microscopy and does not allow clear observation of its diagnostic mesh.

In Quebec Province, *Ac. cancellata* is the index species of a biozone defined by Achab (1989) and occurs in levels that have yielded fossils of the *Orthograptus ruedemanni* GBz and of the lower part of the *Diplacanthograptus spiniferus* GBz (Riva, 1969; Martin, 1983), which is partially correlative with the *Diplacanthograptus caudatus* GBz (Maletz, 2021[2023]), the international marker of the GSSP for the base of the Katian (Goldman et al., 2007).

Acanthochitina latebrosa Vandenbroucke, 2008b
Figure 7.1–7.5, 7.10

1967 *Acanthochitina barbata* Eisenack in Jenkins, p. 443–445, pl. 68, figs. 1–9, text-fig. 3.
1976 *Acanthochitina barbata*; Miller, p. 98–105, pl. 1, figs. 1–7.
?**1980** *Acanthochitina barbata*; Knabe, p. 62–64, pl. 1, figs. 1, 3, 5, 6 (non pl. 1, figs. 2, 4).
1997 *Acanthochitina barbata*; Ancilletta, p. 9, pl. 6, fig. 12; pl. 11, figs. 2–5; pl. 20, figs. 1–12, pl. 22, fig. 12.
2008b *Acanthochitina latebrosa* Vandenbroucke, p. 31–33, pl. 15, figs. 1–14; pl. 25, figs. 1, 2, 12–15.
2009a *Acanthochitina latebrosa*; Vandenbroucke et al., fig. 14(e).

Holotype. UGent repository number: SV9-0009; RBINS repository number: b5049; sample 90-17, stub II; Cliff section, Onny Valley, Shropshire, UK; Onny Formation, British Streffordian Stage, lower Katian (Vandenbroucke, 2008b, p. 31–33, pl. 15, fig. 1).

Occurrence. In the USA, *Ac. latebrosa* has been identified with certainty in the Kope Formation, Kentucky (Miller, 1976; this work, samples MY-584.6 ft/178.2 m, MY-555.7 ft/169.4 m, and MY-487.0 ft/148.4 m). In England, *Ac. latebrosa* occurs in the Onny Formation, British Streffordian Stage, lower Katian (Vandenbroucke, 2008b, and references therein). In Turkey, this species has been identified in well cuttings CEYLANPINAR 1 and GIRMELLI 1, Katian (Paris et al., 2007).

Materials. N = 30 specimens.

Dimensions. L: 186–268–353 μm; D: 76–88–109 μm; Da: 53–65–83 μm; H mesh: 5–10–13 μm; L/D: 2.36–3.06–3.72; D/Da: 1.11–1.36–1.61 (n = 13).

Remarks. The specimens of the Kope Formation from the MY-14-01 core display the same claviform-cylindrical vesicle outline, with its maximal width more or less halfway up the chamber, as *Ac. latebrosa* from the Onny Valley (England; Vandenbroucke, 2008b; Vandenbroucke et al., 2009a). In addition, the polygonal mesh-like ornamentation considerably elevated from the vesicle by small spines, the carina-like structure (Fig. 7.10), and their dimensions are all similar to the characteristics of the type assemblage.

Specimens from the Kope Formation in Maysville, Kentucky, have been identified as *Acanthochitina barbata* Eisenack, 1931 (Miller, 1976, pl. 1, figs. 1–7). Later, these were reassigned by Achab (1987, p. 1213) to *Acanthochitina cancellata* Martin, 1983. However, given their vesicle outline, ornamentation characteristics, and dimensions (similar to the specimens from the upper Kope Formation in the MY-14-01 core), we propose reassigning these to *Ac. latebrosa.* Additionally, Knabe (1980) identified *Ac. barbata* from the Lexington Limestone, Point Pleasant, Clays Ferry, and Kope formations (Kentucky), but the described morphological features are more aligned with the diagnosis of *Ac. latebrosa.* Unfortunately, the images of the figured specimens are not sharp enough to allow a certain reassignment.

In the British Avalonia, *Ac. latebrosa* is one of two nominal species of a biozone defined by Vandenbroucke (2008a), in strata correlated with the *Dicellograptus morrisi* Subzone of the *Dicranograptus clingani* Biozone (lower Katian; e.g., Zalasiewicz et al., 1995).

Genus ***Belonechitina*** Jansonius, 1964

Type species. By original designation, *Conochitina micracantha* subsp. *robusta* Eisenack, 1959; holotype in Eisenack, 1959, p. 9–10, pl. 3, fig. 4, from the Saku Member of the Wasalemma Formation, Katian, Upper Ordovician, Estonia.

Belonechitina duplicitas (Martin, 1983) new combination
Figure 3.1, 3.2

1983 *Hercochitina*? *duplicitas* Martin, p. 17, pl. 1, fig. 11; pl. 2, figs. 8, 11, 12; pl. 3, fig. 2; pl. 4, figs. 5, 33; pl. 5, figs. 15, 37.
1987 *Hercochitina*? *duplicitas*; Achab, p. 1224, pl. 8, figs. 1, 2 (non pl. 8, figs. 3, 4).
?**2001** *Hercochitina*? *duplicitas*; Malo et al., p. 31, 34, pl. 1, figs. 5, 6.
?**2004** *Hercochitina duplicitas*; Asselin et al., p. 494, pl. 1, fig. 15.

Holotype. CGC 55874, sample CBE-2, Saint-Casimir unit, Neuville Formation, Trenton Group, Charlesbourg Ltée quarry, Quebec County, Canada (Martin, 1983, p. 17, pl. 4, fig. 33).

Occurrence. In this work, *Belonechitina duplicitas* n. comb. occurs discontinuously from sample MY-778.3 ft to MY-682.3 ft (237.2–208.0 m), Point Pleasant Formation and Kope Formation, MY-14-01 core, Kentucky, USA. *Belonechitina duplicitas* n. comb. also occurs in several formations of the Trenton, Ottawa, and Utica groups, Québec City, Montréal, and Ottawa regions (Martin, 1983; Achab, 1987), and in the Macasty Shale of the LGPL core, Anticosti Island (Riva, 1969; Achab, 1987), Canada.

Materials. N = 11 specimens.

Dimensions. L: 215–242–272 μm; D: 78–91–98 μm; Da: 55–63–67 μm; H spines: 11–18–23 μm; L/D: 2.45–2.67–2.8; D/Da: 1.42–1.45–1.47 (n = 3).

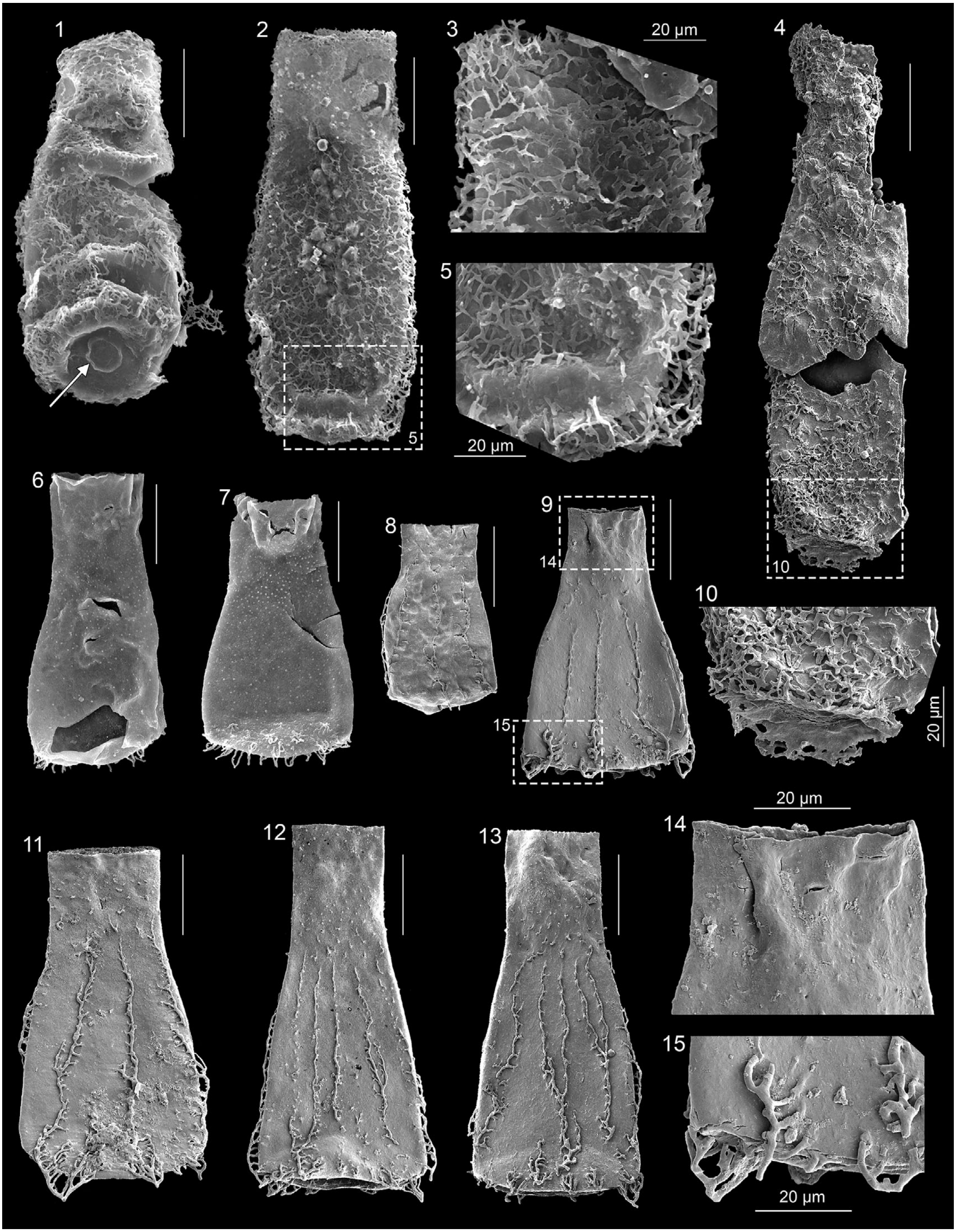

Figure 7. Scanning electron images of relevant species from the Kope Formation, with sample reference. (**1–5, 10**) *Acanthochitina latebrosa* Vandenbroucke, 2008b: (**1 –3, 5**) MY-584.6 ft (178.2 m), (**1**) arrow pointing at the pit with a mucron, (**3**) closeup of an aperture and the ornamentation on the vesicle, (**5**) closeup of the ornamentation on the margin of specimen in (**2**), (**4, 10**) MY-555.7 ft (169.4 m), (**4**) long specimen, (**10**) closeup of (**4**) displaying the ornamentation on the margin and the basal structure comparable to a carina, as described by Vandenbroucke (2008b). (**6, 7**) *Belonechitina* sp. 2, MY-535.8 ft (163.3 m). (**8, 9, 11–15**) *Hercochitina tharpae* n. sp.: (**8**) short specimen, MY-555.7 ft (169.4 m), (**9, 11, 12, 14, 15**) MY-506.4 ft (154.4 m), (**13**) MY-515.8 ft, 157.2), (**11**) holotype, RBINS b 10049, (**14**) closeup of (**9**) showing discrete ornamentation on the upper part of the neck and gently ornamented lip, (**15**) closeup of (**9**) showing the crests ending in complex spines on the margin, expanding laterally. All scale bars = 50 µm, except when another value is indicated in the figure.

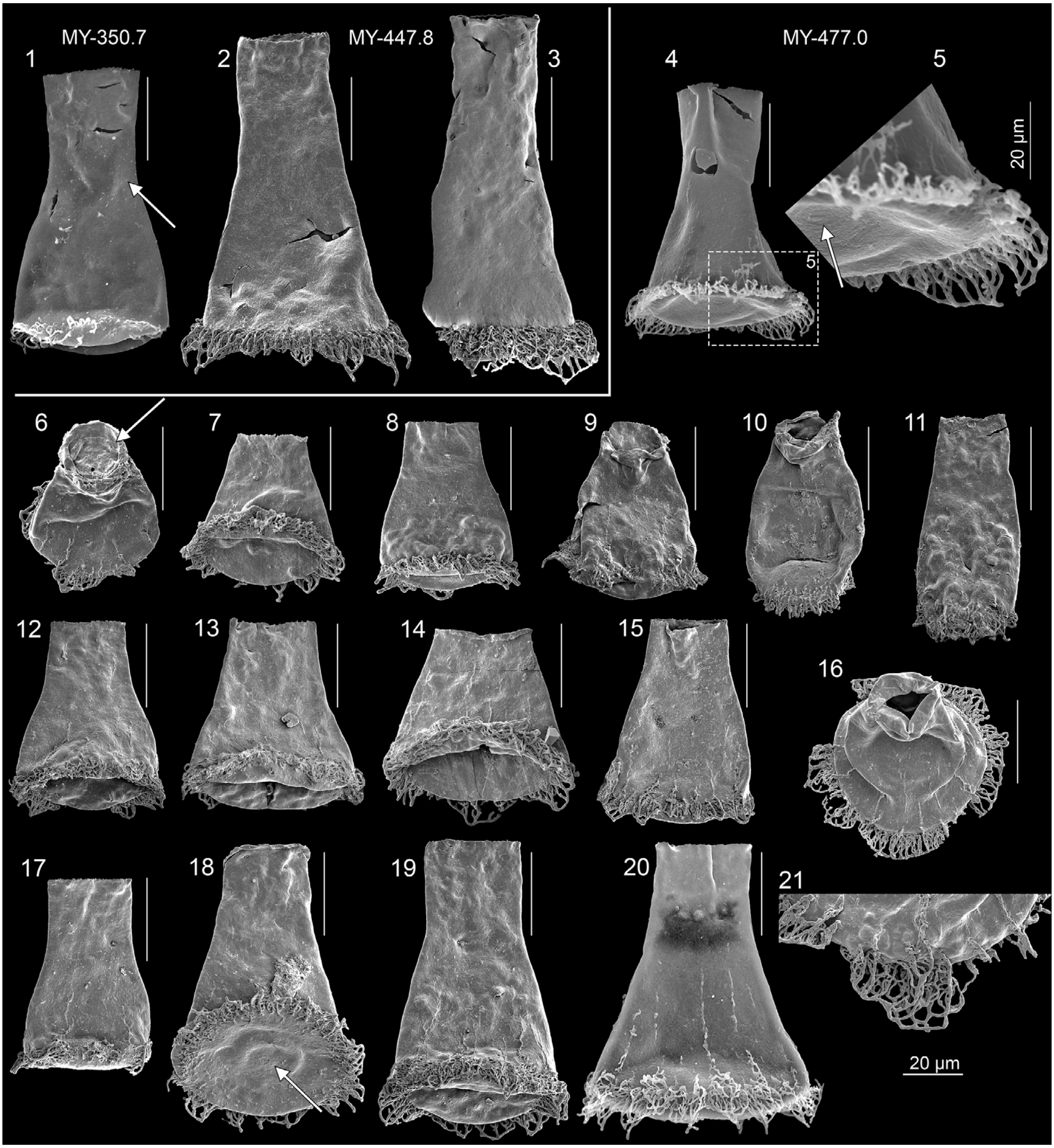

Figure 8. Scanning electron images of the *Clathrochitina mangle* n. sp., displaying the variability of this taxon, all specimens from the Kope Formation, with exception of specimen (**1**), MY-350.7 ft (106.9 m), Fairview Formation: (**1**) arrow indicating granules on the flexure area; (**2, 3**) anastomosing processes well contained on the margin of the conical vesicles, with smooth (**3**) or granulated (**2**) walls; (**4, 5**) small crests distributed throughout the conical chamber, more developed at its base, connecting with the anastomosing processes, arrow in (**5**) highlights the pit with a mucron and the concentric rings at the base; (**4, 6, 9–21**) specimens with crests on the chamber, of variable number and size, probable remnants of the possible ancestor of this species, *Hercochitina tharpae* n. sp., these two species being part of morphological lineage 1; (**6, 16**) apertural view of specimens, (**6**) arrow indicates the sealing structure visible inside the vesicle, at the base of the neck, displaying perforations in the sealing structure, and on the vesicle wall; (**7, 14**) specimens with inconspicuous necks; (**10, 11**) rare vesicles with an underdeveloped or folded base; (**18**) arrow highlights the pit with a mucron at the center of the base, surrounded by concentric rings; (**19**) *Clathrochitina mangle* n. sp. holotype, RBINS b 10050; (**21**) closeup of the anastomosing processes: numerous, fine, and densely packed. All scale bars = 50 μm, except when another value is indicated in the figure.

Remarks. *Belonechitina duplicitas* n. comb. was originally assigned to the genus *Hercochitina* with doubt (Martin, 1983), and in subsequent studies as well (Achab, 1987, 1989; Achab and Asselin, 1995; Malo et al., 2001). Asselin et al. (2004) seem to confirm its attribution to that genus (i.e., *Hercochitina*). However, in the type material of this species, the multirooted spines are randomly distributed, a feature compatible with the diagnosis of the genus *Belonechitina.* We consider attribution of the specimens in Malo et al. (2001, pl. 1, figs. 5, 6) to this species questionable since we do not distinguish ornamentation in their vesicles. We also doubt that the specimen of Asselin et al. (2004, pl. 1, fig. 15) could be *B. duplicitas* due to the limited height of its ornamentation, contrasting with the type material (e.g., Martin, 1983, pl. 2, figs. 11, 12).

In the Province of Quebec, *B. duplicitas* n. comb. is one of the nominal species of a biozone defined by Achab (1989).

Belonechitina laciniata new species
Figures 11.10–11.16, 14.7

Holotype. Illustrated in Figure 11.12, 11.16 (RBINS collection number b 10043); dimensions: L: 189 µm; D: 88 µm; Da: 73 µm; H spines: 4 µm; L/D: 2.14; D/Da: 1.22; sample MY-233.3 ft (71.1 m), Grant Lake Limestone (Maysville, Kentucky, USA).

Occurrence. From sample MY-233.3 ft (71.1 m; Grant Lake Limestone) to MY-185.0 ft (56.4 m; Bull Fork Formation), MY-14-01 core, Kentucky, USA.

Diagnosis. Stout *Belonechitina* species with an exceptionally ornamented lip, deeply lobed, (sub)cylindrical vesicle densely ornamented with randomly distributed simple spines—fine, short, with pointy tips and broad bases, usually longitudinally aligned but never connected with the surrounding spines.

Description. Stout cylindrical to subcylindrical vesicles with generally straight flanks. Flexure inconspicuous (Fig. 11.14, 11.16). Exceptionally ornamented lip, deeply lobed, with the lobes being drawn out and giving the lip an overall pitchfork appearance. Usually, the lip also displays numerous large perforations (Fig. 11.12, 11.16) and/or long spines (Fig. 11.10, 11.13). Maximum width situated at the rounded margin. Entire vesicle densely ornamented with randomly distributed simple spines. These spines are fine, with broad bases, usually longitudinally aligned, but never connecting to the surrounding spines, and ending in pointed tips. The spines are typically short in most of the vesicle (< 5 µm), slightly thicker at the margin, and become shorter towards the aperture or are substituted by granules (Fig. 11.10). The spiny ornamentation on the base becomes scarcer and smaller towards the center of the base, where a pit with a mucron, surrounded by concentric rings has been observed (Fig. 11.15).

Etymology. Named after its lip ornamentation, resembling laciniate leaves with deep lobes.

Materials. *N* = 145 specimens.

Dimensions. L: 131–192–266 µm; D: 71–101–133 µm; Da: 50–75–101 µm; H spines: 2–3–5 µm; L/D: 1.46–1.92–2.38; D/Da: 1.13–1.35–1.62 (*n* = 23).

Remarks. A line drawing of the holotype, to illustrate the ornamentation of this new species more clearly, can be found in Figure 14.7. *Belonechitina laciniata* n. sp. is the second element of the morphological lineage 2 (Fig. 14) containing, from older to younger: *Hercochitina andresenae* n. sp., *B. laciniata* n. sp., and *Hercochitina polygonia* n. sp. These species have similar size ranges and mostly discrete ornamentation. However, *H. andresenae* n. sp. can be differentiated by having crests ornamented with several spines and perforations, which resemble lacework in the more elaborate cases (Fig. 9.4, 9.10, 9.11). Additionally, specimens of *H. andresenae* n. sp. usually have subconical vesicles, gentle but well-marked flexures, and mildly ornamented lips.

Belonechitina laciniata n. sp. differs from *H. polygonia* n. sp. as the latter has small crests connecting the short spines and thorn-like projections (frequently < 2 µm in height) and dense and complex ornamentation on the margin, resulting in a polygonal mesh appearance (Fig. 12.9). Also, the ornamentation (shape, size, and density) of *B. laciniata* n. sp. is similar to *Belonechitina brittanica* Vandenbroucke, 2008b (Sandbian and lower Katian, UK). However, the latter species is characterized by its claviform vesicle and ovoid to ovoid-conical, swollen chamber and commonly has lambda spines, which are absent in our material.

***Belonechitina senta*?** (Achab, 1978a)
Figure 13.1

Occurrence. Sample MY-065.4 ft (19.9 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Dimensions. L: 97 µm; D: 74 µm; Da: 34 µm; H spines: 2 µm; L/D: 1.30; D/Da: 2.18 (*n* = 1).

Materials. *N* = 1 specimen.

Remarks. Like the type material, this specimen has a narrow and short neck, well differentiated from the subconical chamber with convex flanks, short and conical spines randomly distributed on the entire vesicle, which give it a grainy appearance, and the greatest width located at the rounded margin. This specimen is smaller than the eight specimens measured by Achab (1978a). However, due to the limited populations measured by Achab (1978a) and found here, and the fact that the ratios of our specimen fall within the ratios of the type material, we consider it possible that our material could represent a short specimen of this taxon.

***Belonechitina* sp. 1**
Figure 5.1, 5.2, 5.8

Occurrence. Sample MY-691.5 ft (210.8 m), Point Pleasant Formation, MY-14-01 core, Kentucky, USA.

Description. Subconical vesicle. Gentle to inconspicuous flexure. When the flexure is present, it separates the gently conical chamber from the subcylindrical neck. Maximum width is situated at the rounded margin. Straight flanks. Lip finely fimbriated. The lowermost part of the chamber and margin are ornamented with granules and numerous simple, two-legged, or thin, multirooted spines (around 40), ending in a simple tip (Fig. 5.8). The remaining vesicle is smooth. A pit with a mucron has been observed in the base, also ornamented with randomly distributed, small granules.

Materials. *N* = 12 specimens.

Dimensions. L: 73–142–216 µm; D: 57–70–84 µm; Da: 32–43–64 µm; H spines: 2–6–9 µm; L/D: 1.07–1.99–2.99; D/Da: 1.06–1.73–2.08 (*n* = 6).

Remarks. Our material is very similar to the specimens described as *Conochitina* sp. 2 by Achab (1987), of the Lorraine Group, near Sorel-Tracy city, SW Quebec Province, Canada, which defines a Katian biozone (Achab, 1989). Our specimens differ by having seemingly thinner walls and more complex spines. Both Achab's

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Figure 9. Scanning electron images of relevant species that occur in the Kope, Fairview, and Grant Lake formations, with sample references. (**1–8, 10, 11**) *Hercochitina andresenae* n. sp.: (**1**) MY-398.7 ft (121.5 m), Fairview Formation, (**2, 3, 5**) MY-369.4 ft (112.6 m), Fairview Formation, (**4, 6**) MY-418.2 ft (127.5 m), Fairview Formation, (**7, 10, 11**) MY-333.0 ft (101.5 m), Grant Lake Limestone, (**8**) MY-457.3 ft (139.4 m), Kope Formation, (**1–3**) short specimens, (**1**) arrows indicate two lines of ornamentation that can be observed—one being the fimbriated lip and the other just below the lip, with numerous spines, (**3**) arrow points to the pit with a mucron, surrounded by concentric rings, with disorganized crests, and an unidentified external piece that seems fused to the lip of the vesicle, (**5**) tubular prosome ejected from the vesicle, (**6, 8**) long specimens, with arrow in (**6**) highlighting the partially covered pit with a mucron and the ornamented base, (**8**) *Hercochitina andresenae* n. sp. holotype, RBINS b 10044, (**10**) arrow points to the discrete pit with a mucron, surrounded by concentric rings, (**7**) apertural closeup of (**10**), highlighting the fimbriated lip and the size and morphology of the crests, (**11**) lateral detail of (**10**), showing the more-developed crests on the chamber. (**9, 12–14**) *Hercochitina* cf. *H. cristata* Achab, 1987, MY-389.0 ft (118.6 m), Fairview Formation: (**9**) short specimen, with crests extending beyond the lip, (**13**) specimen compressed like an accordion, shows a clear view of the ornamented base, and a pit with a mucron at its center (feature not described or illustrated in the type population) highlighted by arrow, (**14**) long specimen. (**15–18**) *Angochitina* cf. *Ang. capillata* Eisenack, 1938: (**15, 18**) MY-447.4 ft (136.4 m), (**18**) short specimen, (**15**) detailed view of the upper part of the chamber of (**18**), ornamented with randomly distributed broad-base spines, some being two-legged (arrow), (**16, 17**) MY-457.3 ft (139.4 m), (**16**) long specimen. (**19**) *Sphaerochitina gracqui*? Martin, 1983, MY-477.0 ft (145.4 m), Kope Formation. (**20**) *Cyathochitina latipatagium* Jenkins, 1969, MY-477.0 ft (145.4 m), Kope Formation, with a small acritarch near the flexure. All scale bars = 50 μm, except when another value is indicated in the figure.

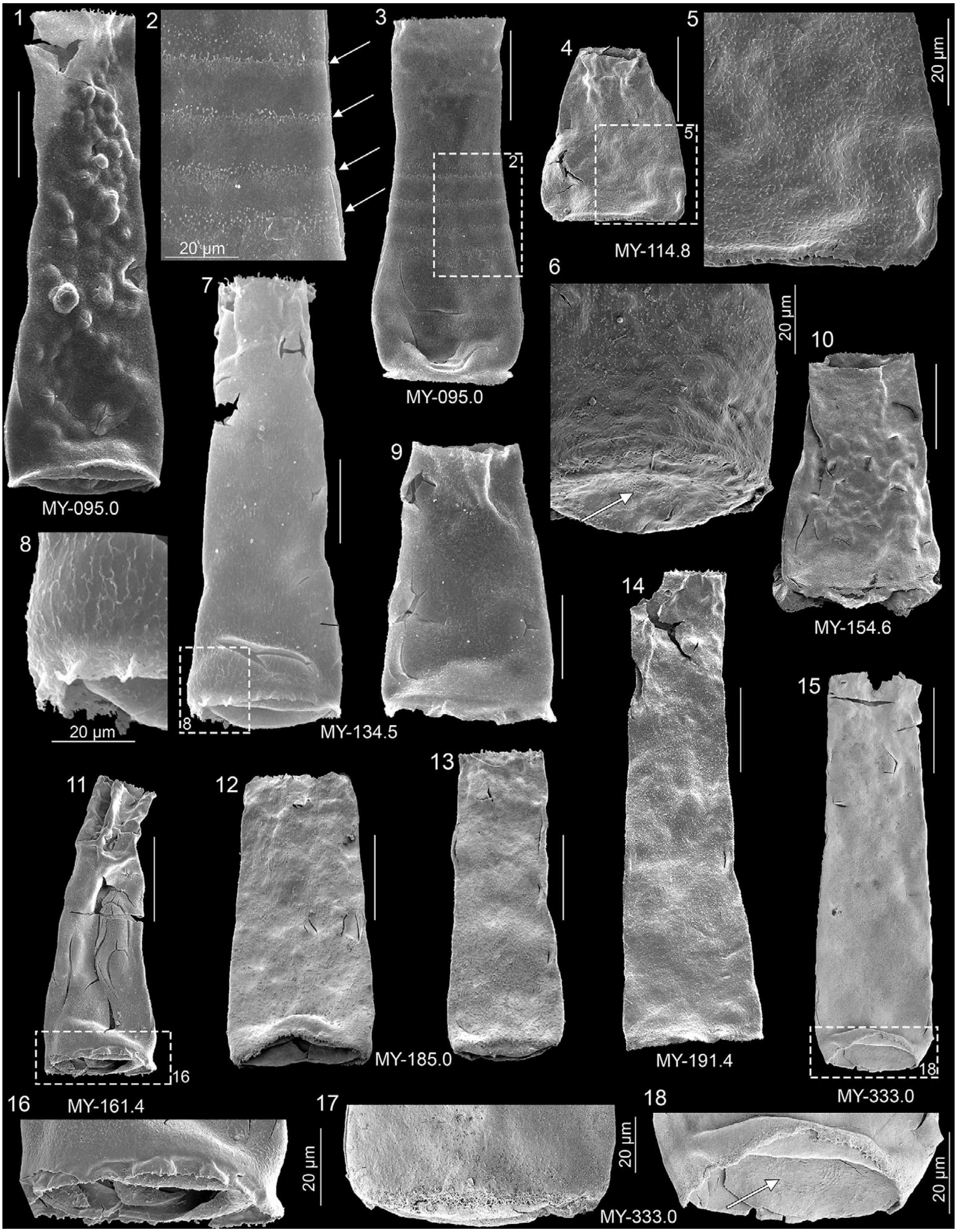

Figure 10. Scanning electron images of *Tanuchitina hooksae* n. sp., showing how the ornamentation of this this taxon can vary, samples are from the Bull Fork Formation, except sample MY-333.0 ft (101.5 m), which is from the Grant Lake Limestone. (**1–3**) Specimens from sample MY-095.0 ft (29.0 m): (**1**) long specimen with typical granulate ornamentation throughout the vesicle, fimbriated lip, and carina with irregular outline, (**2, 3**) specimen with areas of sparser and denser ornamentation, (**2**) lateral detail of (**3**), arrows highlighting the areas of denser ornamentation, consisting of granules, spines, and perforations; (**4, 5**) MY-114.8 ft (35.0 m), short specimen, with lines between the granules, connecting them into a polygonal mesh on the vesicle wall and the characteristic carina with perforations and irregular outline, details better observed in (**5**); (**6**) MY-114.8 ft (35.0 m), arrow indicating the concentric rings and pit with a mucron at the base; (**7–9**) specimens with elaborate ornamentation, MY-134.5 ft (41.0 m), (**7**) longitudinally aligned, crest-like ornamentation on the vesicle, and an finely perforated carina with a notable irregular outline, especially clear in the detailed image (**8**), (**9**) rugose mesh ornamentation on the vesicle and carina; (**10**) MY-154.6 ft (47.1 m), specimen densely ornamented with small granules and with a long, intensely perforated carina; (**11, 16**) MY-161.4 ft (49.2 m), specimen densely ornamented with small granules, distinct in the detailed image (**16**), where a perforated carina with an irregular outline is also noteworthy; (**12, 13**) MY-185.0 ft (56.4 m), specimens with fine spines and granules on the vesicle, and a short but intensely ornamented carina; (**13**) *Tanuchitina hooksae* n. sp. holotype, RBINS b 10042; (**14**) MY-191.4 ft (58.3 m), long specimen with granules on the vesicle and carina; (**15, 17, 18**) MY-333.0 ft (101.5 m), lowest occurrences of this taxon in the section, with sparse, small granules on the vesicle, and its characteristic ornamented carina, with granules, perforations and irregular outline. All scale bars = 50 µm, except when another value is indicated in the figure.

Figure 11. Scanning electron images of relevant species from the Grant Lake and Bull Fork formations, with sample reference. (**1–6**) *Conochitina rudis* n. sp., Bull Fork Formation: (**1**) MY-191.4 ft (58.3 m), short specimen, arrow marks faint pit with a mucron at the center of the ornamented base, (**2–6**) MY-198.7 ft (60.6 m), (**4**) holotype, RBINS b 10041, (**5**) partially broken specimen, arrows highlight vesicle wall composed of two layers. (**7–9**) *Hyalochitina hyalophrys*? (Eisenack, 1959), Grant Lake Limestone: (**7**) MY-319.0 ft (97.2 m), (**8, 9**) MY-294.2 ft (89.7 m), (**9**) detail of a carina on the margin, preserved on the left. (**10–16**) *Belonechitina laciniata* n. sp.: (**10, 12, 13, 16**) MY-233.3 ft (71.1 m), Grant Lake Limestone, (**10**) detailed image of (**13**), displaying the elaborated ornamentation at the lip and the spines on the vesicle, (**12, 16**) holotype, RBINS b 10043, (**12**) detailed image of (**16**), showing a perforated and spiny lip, (**11, 14, 15**) MY-191.4 ft (58.3 m), Bull Fork Formation, (**11**) short specimen, (**15**) arrow highlighting the partially covered pit with a mucron at the center of the ornamented base. (**17–22**) *Spinachitina* sp. 1: (**17, 18, 20, 22**) MY-253.1 ft (77.1 m), Grant Lake Limestone, (**17**) long specimen, (**18**) arrow points to faint pit with a mucron at the center of the ornamented base, (**20**) arrow indicating the sealing structure partially ejected from the vesicle, (**22**) short specimen, (**19**) MY-224.2 ft (68.3), Bull Fork Formation, (**21**) MY-261.8 ft (79.8 m), Grant Lake Limestone. All scale bars = 50 µm, except when another value is indicated in the figure.

(1987) and our specimens are not glabrous, having spines (> 2 μm) randomly distributed on the lower chamber and margin, fitting better instead within the genus *Belonechitina*. Nevertheless, given the image resolution of the *Conochitina* sp. 2 type material and the poor preservation of the specimens studied here, we prefer to not consider these populations conspecific for now and leave our population in open nomenclature.

Belonechitina sp. 2
Figure 7.6, 7.7

Occurrence. From samples MY-555.7 ft to MY-487.0 ft (169.4–148.4 m), Kope Formation, MY-14-01 core, Kentucky, USA.

Description. Subconical vesicle. A gentle flexure separates the conical chamber with convex flanks from the neck, which flares discreetly. Lip finely fimbriated. Maximum width at the bluntly rounded margin or slightly above. Concerning its ornamentation, the vesicles can be divided into four areas. At the margin and lowermost part of the chamber, the ornamentation is more developed, in the form of long (< 14 μm) and fine multi-rooted spines that come together in a rounded tip. Most of the chamber is decorated with few, minor granules, randomly distributed and very dispersed. On the flexure, the granules are larger, more abundant, and spaced closer. The neck wall can be smooth or ornamented with few, small and dispersed granules. In only one exposed base, some short spines and granules were observed but no apical structure was recognized.

Materials. *N* = 12 specimens.

Dimensions. L: 94–153–181 μm; D: 73–84–98 μm; Da: 41–52–59 μm; H spines: 3–8–14 μm; L/D: 1.28–1.82–2.30; D/Da: 1.46–1.63–1.90 (*n* = 5).

Remarks. *Belonechitina micracantha* (Eisenack, 1931) is well known for its spines concentrated on the lower part of the chamber, originally only characterized as short. We consider that the spines of the figured type assemblage, including holotype and neotype, can also be described as having thick roots and simple tips (e.g., Eisenack, 1931, pl. 1, figs. 19–21; Eisenack, 1959, pl. 1, fig. 5). The specimens attributed here to *Belonechitina* sp. 2 also have spines concentrated on the lower part of the chamber, although they are considerably longer than those of *B. micracantha*, and multi-rooted, which is neither observable nor described in the type assemblage of the latter species. In addition to the differences in spine morphology, *B. micracantha* usually has a greater L/D ratio than *Belonechitina* sp. 2. No other *Belonechitina* species are known with similar ornamentation, consisting of only multi-rooted spines, restricted to the margin and area immediately above it, coexisting with granules in the vesicle and no other type of spine. Given that only a couple of well-preserved specimens were found in this reduced population, we prefer to use open nomenclature until more material is found.

Genus **_Hercochitina_** Jansonius, 1964

Type species. *Hercochitina crickmayi* Jansonius, 1964; holotype in Jansonius, 1964, p. 908–909, pl. 1, fig. 9, core sample from 210 m (690 ft), Gamache Princeton Lake 1 borehole, Vauréal Formation, Upper Ordovician, Anticosti Island, Canada.

Remarks. The large number of *Hercochitina* species identified here agrees with decades of work by Achab and her colleagues in Canada. Achab (1988) previously mentioned that many species of *Hercochitina* defined in Laurentia have not been reported from other paleocontinents. *Hercochitina* seems to be a genus that encompasses a great intraspecific total length variability, as discussed at length by Liang et al. (2019), reported in the dimensions section, figured by several other authors (e.g., Jenkins, 1967; Achab, 1977b; Melchin and Legault, 1985), and demonstrated within different species described here.

Hercochitina andresenae new species
Figures 9.1–9.8, 9.10, 9.11, 14.6

Holotype. Illustrated in Figure 9.8 (RBINS collection number b 10044); dimensions: L: 212 μm; D: 96 μm; Da: 78 μm; H crests: 4 μm; L/D: 2.21; D/Da: 1.23; sample MY-457.3 ft, 139.4 m, Kope Formation (Maysville, Kentucky, USA).

Diagnosis. *Hercochitina* species with 20–25 discontinuous, long, and spiny crests on the visible face. The crests lie directly on the vesicle, are frequently perforated, and are ornamented with closely spaced, blunt spines, with broad bases. When the crests are elevated and intensely perforated, they resemble lacework.

Occurrence. From sample MY-487.0 ft (148.4 m; Kope Formation) to MY-319.0 ft (97.2 m; Grant Lake Limestone), MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is subconical. A gentle and broad flexure separates the conical chamber from the subcylindrical to slightly flaring neck. Maximum width occurs at the lower half of the chamber. Lip finely fimbriated and can have a few spines and perforations (Fig. 9.7, 9.8). Numerous discontinuous, long, and spiny crests densely ornament the entire vesicle: the estimated total number of crests is 40–50 (based on the 20–25 crests counted on the visible face). The crests rest directly on the vesicle, are closely spaced, frequently perforated, and ornamented with blunt spines, with broad bases, and round tips. In parts where the crests are elevated and intensely perforated, the vesicle seems adorned with lacework (Fig. 9.4, 9.10, 9.11). In specimens where the ornamentation has been mildly eroded, the crests look wavy (Fig. 9.6). Usually, the crests are more continuous and ornamented on the lower half of the vesicle and become more discontinuous and simpler towards the aperture; granules can coexist with the small crests, immediately below the lip (Fig. 9.7, 9.8). On the rounded margin, the crests may end on a prominent simple spine (Fig. 9.5, 9.10). The base is ornamented with granules, and a discrete pit with a mucron, surrounded by concentric rings has been observed at its center (Fig. 9.3, 9.6, 9.10).

Etymology. Named after Sophia de Mello Breyner Andresen, a Portuguese poet and writer.

Materials. *N* = 964 specimens.

Dimensions. L: 63–171–238 μm; D: 67–91–118 μm; Da: 43–63–83 μm; H crests: 2–3–6 μm; L/D: 0.62–1.91–2.54; D/Da: 1.21–1.45–1.64 (*n* = 22).

Remarks. While in some specimens the ornamentation can be very discontinuous (e.g., Fig. 9.8), it is easy to spot many crests when looking at the details, thus this species fits with the diagnostic features of the genus. A line drawing of the holotype, to depict the ornamentation of *Hercochitina andresenae* n. sp. more clearly, can be found in Figure 14.6. *Hercochitina andresenae* n. sp. is the oldest element of the morphological lineage 2, containing (older to younger, Fig. 14): *H. andresenae* n. sp., *Belonechitina laciniata* n. sp., and *Hercochitina polygonia* n. sp. *Hercochitina andresenae* n. sp. can be differentiated from *B. laciniata* n. sp., which has the vesicle ornamented by individual spines, that are never connected to the surrounding spines (i.e., no crests present). Additionally, *B. laciniata* n. sp. has an inconspicuous flexure and an intensely ornamented lip that can have long spines and several perforations. *Hercochitina andresenae* n. sp. differs from *H. polygonia* n. sp. as the latter has an inconspicuous flexure, a higher number of crests, and the ornamentation is lower (frequently < 2 μm), so the crests connect spines and thorn-like projections. Importantly, the most diagnostic feature of *H. polygonia* n. sp. is the dense ornamentation at the margin, forming a polygonal mesh, which is absent in *H. andresenae* n. sp.

Although *H. andresenae* n. sp. and *Hercochitina* sp. 2 (in this study) have a somewhat similar outline and discontinuous crests, the latter specimens always have an inconspicuous flexure and fewer, lower, and more continuous, non-spiny crests. The more ornamented specimens of *H. andresenae* n. sp., with lacework-like crests (e.g., Fig. 9.10), can resemble some very ornamented *Hercochitina* species from Anticosti Island: *Hercochitina filamentosa* Achab, 1977b (Vauréal Formation, *Paraorthograptus prominens* GBz, upper Katian), and *Hercochitina florentini* Achab and Asselin in Achab et al., 2013 (Ellis Bay Formation, uppermost Katian?–Hirnantian). However, *H. filamentosa* has a narrower neck, the flanks are distinctively convex, the crests are more continuous, and the height of the crests can reach 28 μm. In *H. florentini*, the crests are more continuous and are raised from the vesicle by spines, while in our material the crests are clearly discontinuous and lie directly on the vesicle, with the spines above them.

Hercochitina anningae **new species**
Figures 5.3–5.7, 5.9–5.10, 14.9

Holotype. Illustrated in Figure 5.5 (RBINS collection number b 10045); dimensions: L: 306 μm; D: 122 μm; Da: 70 μm; H crests: 3 μm; L/D: 2.51; D/Da: 1.76; sample MY-672.3 ft (204.9 m), Kope Formation (Maysville, Kentucky, USA).

Diagnosis. Hercochitina species characterized by its numerous discontinuous, poorly individualized, and multi-rooted crests, predominantly located in the lower two-thirds of the subconical vesicle. These complex crests are composed of about 2–5 low ridges, one of them being thicker, longitudinal, and longer, like a main stem; these structures meet antiaperturalwards in a multi-rooted spine with a simple tip.

Occurrence. From sample MY-701.6 ft (213.8 m; Point Pleasant Formation) to MY-555.7 ft (169.4 m; Kope Formation), MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is conical, without a clear separation between the neck and the chamber (i.e., the flexure is inconspicuous). Maximum width situated at the rounded margin. The flanks are roughly straight. In the longer specimens, there is a gentle constriction above the margin (Fig. 5 .6, 5.7), which is absent or inconspicuous in small and medium specimens (Fig. 5.3, 5.4). Lip always fimbriated. The lower two-thirds of the vesicle covered by sets with about 2–5 low ridges, connected to the vesicle by multiple roots. These ridges coalesce antiaperturalwards, where they culminate in a multi-rooted spine with a simple tip, perpendicular to the vesicle (Fig. 5.9, 5.10). One of these 2–5 ridges is always thicker, fairly longitudinal, and longer, like the main stem of a plant. This group of features (main longitudinal stem, smaller ridges, and spine) is considered a complex, discontinuous, and poorly individualized crest. On the visible face, around 7–10 crests were counted (an estimated 14–20 crests in the whole vesicle). The crests are longer, more continuous, and complex in the lower third of the vesicle. The margin is ornamented with usually long (< 27 μm) and intensely multi-rooted spines, in a similar number to the number of crests on the vesicle. Towards the aperture, the crests become very short and evolve first into isolated multi-rooted spines and then into simple spines and granules. In the base, the ornamentation continues, first as multi-rooted and then simple spines towards the pit, which has been observed with a mucron and concentric rings (Fig. 5.10).

Etymology. Named after Mary Anning, a self-taught English paleontologist.

Materials. N = 124 specimens.

Dimensions. L: 138–296–506 μm; Dp: 98–125–155 μm; Da: 55–70–90 μm; H crests: 3–7–12 μm; L/D: 1.41–2.37–5.18; D/Da: 1.18–1.80–2.39 (n = 44).

Remarks. A line drawing of the holotype, to represent the ornamentation of this new species more clearly, can be found in Figure 14.9. Among all the *Hercochitina* species, this population presents more similarities to *Hercochitina violana* Nõlvak and Liang in Liang et al., 2019: the low and multi-rooted crests, the multi-rooted spines on the base, margin and upper third of the vesicle, and the apical structures. However, the crests of our specimens are longer, more complex, and extend farther towards the aperture on the vesicle. In *H. violana*, we counted more crests (around 12–14 on the visible face, 28 on the whole vesicle) than the ones counted in our population, the constriction near the base of *H. violana* is considered a diagnostic feature (i.e., present in most or all vesicles), while the constriction in our specimens is only recognizable in longer vesicles, and the neck of *H. violana* develops a flaring collar, a feature not present in our material. Across the literature, other specimens in open nomenclature have ornamentation similar to our population but their crests are raised higher above the vesicle wall than in our material. This is the case for one of the specimens identified as *Hercochitina* aff. *spinetum* Melchin and Legault, 1985, by Grahn and Nõlvak (2007b, fig. 4O; Baltoscandian Keila Stage/ ca. Sandbian–Katian boundary, from Estonia) and one specimen also identified as *Hercochitina* aff. *spinetum* by Bauert et al. (2014, fig. 2G; Baltoscandian Keila Stage/ ca. Sandbian–Katian boundary, from Estonia). Liang et al. (2023, fig. 6R) identified a specimen as *Hercochitina* sp. 1 from the Huadan Formation (Katian, South China) with very similar ornamentation to our specimens but the outline of their specimen is very different: a conspicuous flexure separates the short, flaring neck from the chamber with convex flanks. Due to the limited SEM images available in the literature of these similar specimens, we cannot evaluate the outline and ornamentation variability of those populations and we cannot assess if these morphotypes could be conspecific with our material.

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Hercochitina edingerae new species
Figures 3.5–3.17, 14.1

Holotype. Figure 3.11, 3.17 (RBINS collection number b 10046); dimensions: L: 220 μm; D: 97 μm; Da: 62 μm; H crests: 6 μm; L/D: 2.27; D/Da: 1.55; sample MY-770.3 ft (234.8 m), Point Pleasant Formation (Maysville, Kentucky, USA).

Occurrence. From sample MY-770.3 ft (234.8 m; Point Pleasant Formation) to MY-682.3 ft (208.0 m; Kope Formation), MY-14-01 core, Kentucky, USA.

Diagnosis. Hercochitina species bearing 6–10 main crests that are sinuous, thick, and continuous from margin to lip, many of them bifurcating towards the aperture. Smaller, simpler, and discontinuous crests can also be present, between the main crests. Presence of complex multirooted spines at the margin.

Description. The vesicle's overall shape is conical. When a gentle flexure is present, it separates the conical chamber with mildly convex flanks from the subcylindrical to slightly flaring neck. Gently (Fig. 3.5, 3.14) to strongly (Fig. 3.8, 3.11) fimbriated lip. Maximum diameter above the rounded margin. Ornamentation consists of 6–10 thick and sinuous main crests (extrapolated from the 3–5 crests counted on the visible face) connected to the vesicle by spines, single or in pairs. The crests are continuous, extending from the margin to the lip. The main crests can be identified by being thicker, more complex, and elevated from the vesicle (< 9 μm). Smaller, simpler, and discontinuous crests can occur between the main crests (Fig. 3.9, 3.15). Rarely, the main crests extend beyond the lip, in the form of complex spines (Fig. 3.8, 3.11). Many crests bifurcate towards the aperture, on the chamber, and neck (e.g., Fig. 3.5, 3.7, 3.8). One of the crests resulting from the bifurcation commonly is abandoned (e.g., Fig. 3.10, 3.13–.17). There can be more crests on the upper half (aperturalwards) of the vesicle than on its lower half (antiaperturalwards; Fig. 3.5, 3.12). The crests are thicker, more complex, and more elevated on the lower half of the vesicle. At the margin, the crests develop into complex, multirooted spines (< 18 μm long; Fig. 3.7, 3.17). The ornamentation extends to the base in the form of multirooted spines and to simple spines towards the center of the base, where a pit without a mucron can be observed (Fig. 3.10).

Etymology. Named after Johanna 'Tilly' Edinger, German-American paleontologist and the founder of paleoneurology.

Materials. N = 386 specimens.

Dimensions. L: 108–164–240 μm; D: 67–86–107 μm; Da: 42–54–70 μm; H crests: 4–6–9 μm; L/D: 1.34–1.91–2.57; D/Da: 1.15–1.62–2.00 (n = 30).

Remarks. A line drawing of the holotype, to better illustrate the ornamentation of this new species, can be found in Figure 14.1. Our material can be easily separated from most of the other species of *Hercochitina* given that its crests extend continuously from the margin to the aperture. In *Hercochitina crickmayi* Jansonius, 1964, the crests may also reach the aperture, but the number of crests is higher, the crests are more regular, and they do not bifurcate. Also, the vesicle of that species is generally longer than our material (total length of *H. crickmayi*: 230–450 μm), and its aperture is less ornamented. In *H. downiei* Jenkins, 1967, and *H.* aff. *H. downiei* (in this paper), the crests might reach the aperture, but the ornamentation elevates higher above the vesicle's surface than in the species described here. In contrast to our material, *H. normalis* Achab, 1977b, has full membranous crests (rarely with perforations on the lower half of the chamber). *Hercochitina edingerae* n. sp. is the oldest element of the morphological lineage 1. *Hercochitina edingerae* n. sp. and *Hercochitina krafftae* n. sp. have similar vesicle dimensions and both have thick crests that can bifurcate and be sinuous. However, *H. krafftae* n. sp. can be differentiated by its stout vesicle and inflated chamber, having more crests but only located on the chamber, and those crests are discontinuous, ending antiaperturalwards in a multirooted spine perpendicular to the vesicle wall, becoming smaller towards the aperture, and being substituted at the neck by spines and granules. Additionally, when present, the flexure in specimens of *H. krafftae* n. sp. is more marked, and the spines at the margin are usually shorter and have fewer roots than the ones of *H. edingerae* n. sp.

Hercochitina krafftae new species
Figures 6.4–6.10, 14.2

Holotype. Illustrated in Figure 6.7 (RBINS collection number b 10047); dimensions: L: 187 μm; D: 98 μm; Da: 55 μm; H crests: 7 μm; L/D: 1.90; D/Da: 1.80; sample MY-642.9 ft (196.0 m), Kope Formation (Maysville, Kentucky, USA).

Occurrence. From samples MY-642.9 ft to MY-477.0 ft (196.0–145.4 m), Kope Formation, MY-14-01 core, Kentucky, USA.

Diagnosis. Hercochitina species with a stout and inflated vesicle. The chamber has 5–8 low and discontinuous crests on the visible face that become higher and better developed antiaperturalwards. Each crest developed on the chamber that does not reach the margin ends in a multirooted spine that is perpendicular to the vesicle wall and has a simple tip (< 10 μm). The crests become smaller towards the aperture and are substituted by simple spines and granules in the neck. Discrete, multi-rooted spines on the margin.

Description. Stout and overall conical vesicle with convex flanks. Within the same sample, a population of this species can have considerable variability of vesicle shape and outline. In specimens without a neck, the vesicle is inflated and subconical, with the flanks tapering towards the aperture (Fig. 6.5, 6.6, 6.10). Most specimens have a gentle flexure between a subcylindrical neck and an inflated and subconical chamber (Fig. 6.7–6.9). Gently fimbriated lip. The chamber is covered by 10–16 rows of low and discontinuous crests (5–8 crests counted on the visible face), that can commonly be sinuous and bifurcate aperturalwards (Fig. 6.4, 6.7). The crests are connected to the chamber by spines, single or in pairs (Fig. 6.4), and increase in height and ornamentation in an antiapertural direction. If they do not reach the margin, the crests end in a multirooted, thick spine, somewhat perpendicular to the chamber wall, and with a simple tip (< 10 μm; Fig. 6.7–6.10). Few crests reach the rounded margin, ending as discrete, multirooted spines (L spines margin < 14 μm); the latter can be in higher numbers than the number of crests on the chamber (Fig. 6.4). The crests get smaller towards the aperture, being substituted by small spines and granules. The base is ornamented with small spines and granules, and a pit with a mucron has been observed at its center (Fig. 6.9).

Etymology. Named after Catherine 'Katia' Krafft, a French volcanologist who, together with her husband Maurice Krafft, captured videos and imagery of volcanic eruptions, raising awareness and inspiring many young women to study geology.

Materials. N = 230 specimens.

Dimensions. L: 48–142–255 µm; D: 66–84–117 µm; Da: 28–47–72 µm; H crests: 4–7–10 µm; L/D: 0.72–1.67–2.17; D/Da: 1.45–1.83–2.62 (n = 22).

Remarks. A line drawing of the holotype, to depict the ornamentation of this new species more clearly, can be found in Figure 14.2 (the arrows highlight the crests bifurcating aperturally). Similar to our material, *Hercochitina changi* Achab and Asselin in Achab et al., 2013 (Ellis Bay Formation, uppermost Katian?–Hirnantian) has discontinuous, short crests coalescing in spines. However, *H. changi* is differentiated by its subcylindrical vesicles, weak flexure, more crests (not provided in the original description but counted in the type material from the plates; Achab et al., 2013), around 11–15 on the visible face, and those crests coalesce in longer spines than in the new species described here.

Hercochitina krafftae n. sp. is the second element of morphological lineage 1. *Hercochitina edingerae* n. sp. can be differentiated from *H. krafftae* n. sp. by its slender vesicle, having fewer crests, continuous from margin to lip, and those crests never display spines on the chamber. Additionally, the crests of *H. edingerae* n. sp. are usually thicker, more sinuous, and have more bifurcations per crest, and the spines at the margin are commonly longer and more intensely multi-rooted. *Hercochitina tharpae* n. sp. only has discontinuous crests in the flexure area; its crests are continuous on the chamber and more homogeneously raised from the vesicle (H crests < 12 µm), while the crests of *H. krafftae* n. sp. are mostly low and only increase in height in the antiapertural direction, peaking at their multi-rooted spine (H crests < 10 µm). Also, *H. tharpae* n. sp. displays sets of spines at the margin: usually longer (< 22 µm) than those of *H. krafftae* n. sp., intensely multi-rooted, anastomosed, that extend laterally on the margin.

Hercochitina polygonia **new species**
Figures 12.3–12.6, 12.9, 14.8

Holotype. Illustrated in Figure 12.3 and 12.9 (RBINS collection number b 10048); dimensions: L: 256 µm; D: 98 µm; Da: 80 µm; H crests: 1.6 µm; L/D: 2.61; D/Da: 1.23; sample MY-085.5 ft (26.1 m), Bull Fork Formation (Maysville, Kentucky, USA).

Diagnosis. Stout *Hercochitina* species with fine, very discontinuous but distinctive, 76–84 crests (about 38–42 on the visible face). Crests lie on the surface of the vesicle and connect the simple or two-legged, broad-based ornaments—short spines and thorn-like projections (< 2 µm). At the margin, this ornamentation gets denser, thicker, and more complex, with a polygonal mesh appearance.

Occurrence. From sample MY-185.0 ft to MY-085.5 ft (56.4–26.1 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicle overall shape is subcylindrical to subconical, and stout. The flanks are generally straight. Inconspicuous flexure. The uppermost part of the vesicle may flare. Lip fimbriated and can have small perforations (Fig. 12.3, 12.6). The entire vesicle is densely ornamented with fine, very discontinuous, 76–84 crests (inferred from around 38–42 crests counted in the observable face). Lying directly on the vesicle, the crests connect a few short spines and thorn-like projections (< 2 µm): these can be simple or two-legged, with broad bases (Fig. 12.3, 12.5, 12.9). On the margin, the ornamentation gets bigger and more abundant, and the connections between spines get thicker and more complex—more lines occur, propagating in different directions, between the crests and spines, uniting these elements randomly; this ornamentation has the appearance of a polygonal mesh connected to the vesicle (Fig. 12.9). The ornamentation extends to the base, getting smaller towards its center, where a pit with a mucron is observed.

Etymology. From Greek πολύς - polys, 'many', and γωνία - gōnia, 'angle', the name refers to the polygonal mesh appearance of the ornamentation on the margin.

Materials. N = 31 specimens.

Dimensions. L:110–176–262 µm; D: 65–91–122 µm; Da: 51–67–87 µm; H crests: 1–1–3 µm; L/D: 1.38–1.95–2.74; D/Da: 1.23–1.35–1.51 (n = 14).

Remarks. Although the ornamentation of this species is low and fine, it is easily recognized even in eroded specimens, due to the polygonal mesh-like ornamentation on the margin (Fig. 12.4). A line drawing of the holotype, to represent the ornamentation of this new species more clearly, can be found in Figure 14.8. *Hercochitina polygonia* n. sp. is the youngest element of morphological lineage 2, with *Hercochitina andresenae* n. sp. and *Belonechitina laciniata* n. sp., as the oldest and second elements, respectively (Fig. 14). These species have similar size ranges, and their ornamentation is mostly discrete. *Hercochitina polygonia* n. sp. can be differentiated from *H. andresenae* n. sp., which has fewer spiny crests (40–50 in the entire vesicle, 20–25 in the observable face), that are generally higher (H crests < 6 µm) and can be intensely perforated, resembling lacework (Fig. 9.4, 9.10, 9.11). Additionally, the specimens of *H. andresenae* n. sp. usually have more subconical vesicles and a gentle but well-marked flexure.

Belonechitina laciniata n. sp. is distinguished by the individual spines ornamenting the entire vesicle, never connected to the surrounding spines (i.e., no crests present). Additionally, *B. laciniata* n. sp. has an intensely ornamented lip that can have long spines and several perforations (Fig. 11.10, 11.12). While the ornamentation of *H. andresenae* n. sp. and *B. laciniata* n. sp. gets thicker on the margin, it never gets complex and interconnected as in *H. polygonia* n. sp., gaining the appearance of a polygonal mesh.

Lastly, the complex ornamentation on the margin of *H. polygonia* n. sp. resembles *Hercochitina*? *bromidensis* Grahn and Miller, 1986 (Darriwilian–Sandbian; Oklahoma, USA; Laurentia). However, the mesh in *H.*? *bromidensis* has a wavy pattern while *H. polygonia* n. sp. has a more random polygonal mesh. In other differences, *H.*? *bromidensis* has broadly concave flanks, and the neck will be granulated or smooth in the specimens in which the crests stop at the upper part of the vesicle.

Hercochitina tharpae **new species**
Figures 7.8, 7.9, 7.11–7.15, 14.3

Holotype. Illustrated in Figure 7.11 (RBINS collection number b 10049); dimensions: L: 202 µm; D: 118 µm; Da: 70 µm; H crests: 10 µm; L/D: 1.71; D/Da: 1.67; sample MY-506.4 ft (154.4 m), Kope Formation (Maysville, Kentucky, USA).

Diagnosis. *Hercochitina* species with a wide conical vesicle. Six to ten continuous crests are situated only on the chamber. On the

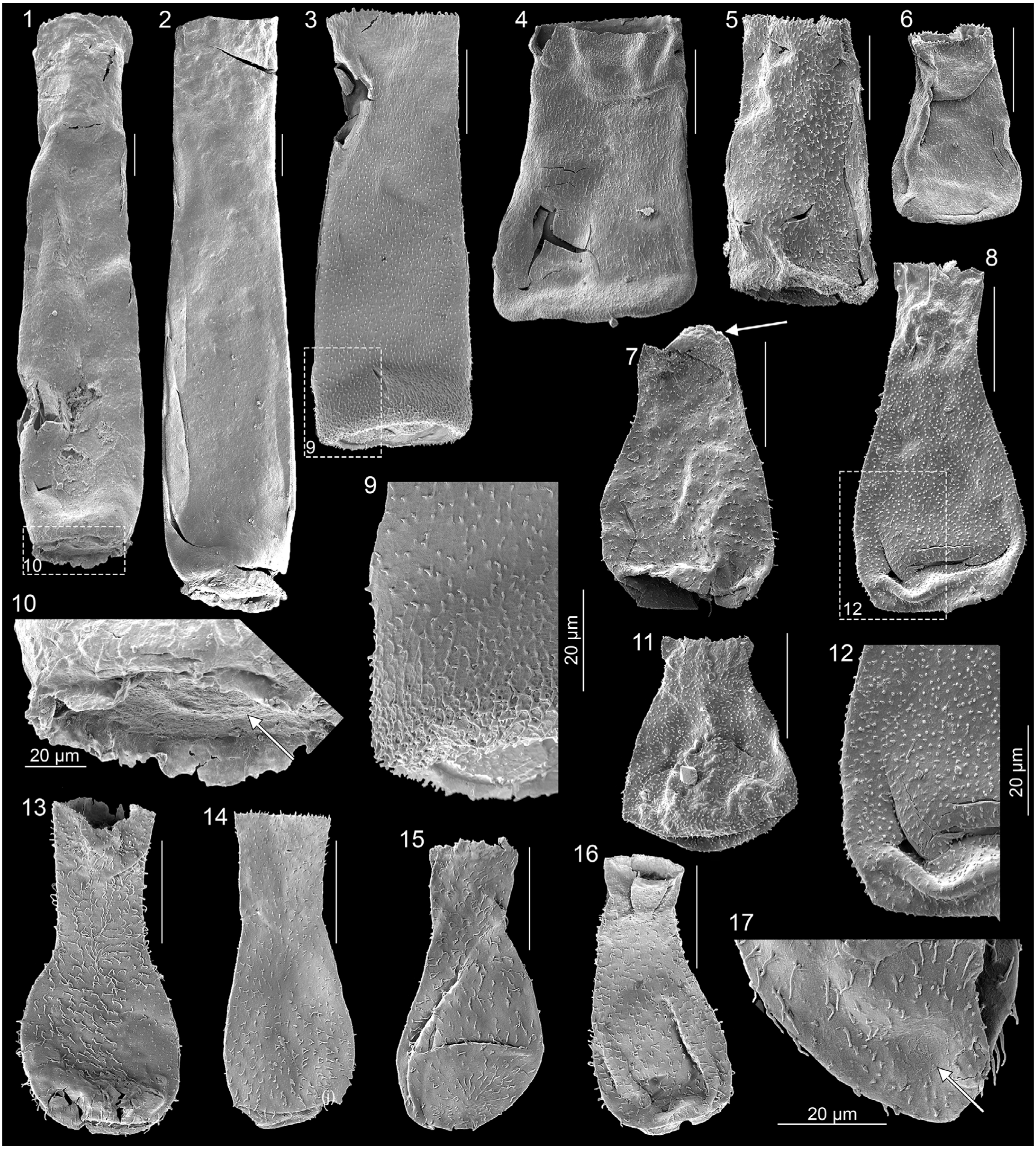

Figure 12. Scanning electron images of the relevant species from the Bull Fork Formation, with sample reference. (**1, 2, 10**) *Tanuchitina* sp. 1, MY-114.8 ft (35.0 m): (**10**) detail of the base of the specimen (**1**), arrow points to the pit with a mucron. (**3–6, 9**) *Hercochitina polygonia* n. sp.: (**3, 9**) MY-085.5 ft (26.1 m), (**3**) holotype, RBINS b 10048, long specimen, (**9**) lateral closeup of the holotype specimen (**3**), displaying elaborated ornamentation on the margin, (**4–6**) MY-161.4 ft (49.2 m), (**6**) short specimen. (**7, 8, 11, 12**) *Angochitina oklahomensis* Taugourdeau, 1965: (**7**) MY-075.0 ft (22.9 m), arrow points to the cylindrical sealing structure partially ejected from the vesicle, (**8, 11, 12**) MY-114.8 ft (35.0 m), (**8**) long specimen, (**12**) lateral closeup of the specimen in (**8**), focused on the densely packed, small spines, (**11**) short specimen. (**13–17**) *Angochitina* cf. *Ang. capillata* Eisenack, 1938, MY-085.5 ft (26.1 m): (**17**) arrow highlights a possible pit without a mucron, surrounded by disorganized lines. All scale bars = 50 μm, except when another value is indicated in the figure.

margin, these crests become sets of numerous long, multi-rooted, and anastomosing spines, which propagate antiapertu-rally, beneath the vesicle, and extend laterally on the margin, without connecting to the adjacent sets of spines.

Occurrence. From sample MY-565.8 ft to MY-487.0 ft (172.5–148.4 m), Kope Formation, MY-14-01 core, Kentucky, USA.

Description. Overall vesicle shape is conical, with a wide base. Maximum width at the margin. The marked flexure separates the conical chamber with convex flanks from the subcylindrical neck. Lip with discrete ornamentation, finely fimbriated to wavy (Fig. 7.14). Neck usually smooth but can have some randomly distributed, small granules. On and around the flexure, randomly distributed granules and short, small spines, with bases widening longitudinally (parallel to the long axis of the vesicle) are present. Rarely, in the flexure area, small discontinuous crests that are connected to the vesicle by simple spines bifurcate aperturalwards and end antiaperturalwards in a simple spine (Fig. 7.11, 7.13). On the chamber, 6–10 continuous crests (extrapolated from the 3–5 crests observed on the visible face) are connected to the chamber by spines, individually or in pairs (Fig. 7.15). Some of the crests on the vesicle commonly bifurcate aperturalwards and are gently sinuous, always ending at more or less the same height as the flexure. On the rounded margin, the crests are elevated from the chamber by their spines, which propagate antiaperturally (< 22 μm), beneath the base of the vesicle, and extend laterally on the margin—becoming sets of numerous long, multi-rooted, and anastomosed spines (Fig. 7.15). These complex spines on the margin are differentiated and they do not connect laterally with the adjacent sets of spines. The base is ornamented with some small spines and granules and, at its center, a pit with a mucron, sometimes surrounded by concentric rings has been observed.

Etymology. Named after Marie Tharp, an American geologist and oceanographic cartographer who made the first scientific map of the Atlantic Ocean floor.

Materials. *N* = 213 specimens.

Dimensions. L: 100–173–252 μm; D: 64–93–118 μm; Da: 43–53–70 μm; H crests: 6–8–12 μm; L/D: 1.11–1.86–2.67; D/Da: 1.41–1.75–2.16 (*n* = 20).

Remarks. A line drawing of the holotype, to illustrate the ornamentation of this new species more clearly, can be found in Figure 14.3. *Hercochitina tharpae* n. sp. is the third element of morphological lineage 1, composed of (older to younger, Fig. 14): *Hercochitina edingerae* n. sp., *Hercochitina krafftae* n. sp., *H. tharpae* n. sp., and *Clathrochitina mangle* n. sp. *Hercochitina krafftae* n. sp. can be differentiated from this new species by its discontinuous crests in the flexure area and chamber, which are low for most of their length but becoming higher antiaperturalwards and culminating in a spine that is perpendicular to the vesicle wall (< 10 μm), and by its spines on the margin, which are simpler and usually shorter (< 12 μm) than those of *H. tharpae* n. sp., and do not extend laterally. While *H. tharpae* n. sp. and *Cl. mangle* n. sp. have a similar outline and remarkable ornamentation on the margin, the latter has less to no ornamentation on the chamber and neck, and a crown of anastomosing processes on the margin (i.e., the ornamentation elements are densely packed and connected), while *H. tharpae* n. sp. has sets of spines that are well differentiated and do not connect laterally to other sets of spines.

Hercochitina cf. _H. cristata_ Achab, 1987
Figure 9.9, 9.12–9.14

Occurrence. Sample MY-389.0 (118.6 m), Fairview Formation, MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is conical. The gentle flexure separates the conical chamber with straight to mildly convex flanks from the short, subcylindrical neck that can sometimes slightly flare towards the aperture (Fig. 9.12, 9.14). Lip gently fimbriated. Greatest width at the rounded margin or closely above. Thick, complex, and multi-rooted crests, poorly individualized (around 8–12 on the visible face), and very well-developed on the chamber. Towards the aperture, the crests decrease in size and complexity and frequently bifurcate (Fig. 9.12, 9.14). The crests are continuous on the chamber and discontinuous on the neck, and can even change to multi-rooted, small spines or granules (Fig. 9.14). On the contrary, towards the basal margin, the crests get thicker, more elevated from the chamber, and intensely multi-rooted. The crests end on the margin in the form of complex, multi-rooted but short spines, with simple tips (< 13 μm). The ornamentation of the chamber propagates to the base, decreasing in direction to its center, where a pit with a mucron has been observed (Fig. 9.13).

Materials. *N* = 12 specimens.

Dimensions. L: 134–251–345 μm; D: 109–125–143 μm; Da: 59–80–96 μm; H crests: 5–6–7 μm; L/D: 1.12–1.97–2.48; D/Da: 1.31–1.60–2.01 (*n* = 5).

Remarks. All the specimens strongly resemble *Hercochitina cristata* Achab, 1987, from the Utica Formation (*G. pygmaeus* GBz), Montréal, Canada. However, in our small population, only occurring in one sample, the crests seem thicker, slightly higher, and more intensely multi-rooted than the ones observed in the type material. These differences favor the use of open nomenclature.

Hercochitina aff. _H. downiei_ Jenkins, 1967
Figure 3.18–3.20

Occurrence. Discontinuously present in samples MY-778.3 ft (237.2 m; Point Pleasant Formation) to MY-682.3 ft (208.0 m; Kope Formation), MY-14-01 core, Kentucky, USA.

Description. The vesicle's overall shape is conical. The chamber is conical to pyriform, with convex flanks. The neck can be inconspicuous or short and subcylindrical. When present, the flexure is gentle. The sealing structure can be close to or at the aperture (Fig. 3.19). Fimbriated lip. Maximum diameter between the middle of the chamber and the rounded margin. The ornamentation consists of continuous crests: simple, wishbone, and multirooted spines (up to 15 μm in height), arranged in 10–14 longitudinal rows around the whole vesicle (5–7 on the visible face), connected at their tips by longitudinal bars. The crests start on the neck (Fig. 3.18) or at the lip (Fig. 3.19, 3.20) and it is inferred that they extend to the margin since the crests are never entirely preserved. The crests can bifurcate aperturalwards (Fig. 3.18). The ornamentation extends to the base, in multirooted spines turning into simple spines towards the center of the base, where a pit without a mucron can be observed (Fig. 3.20).

Materials. *N* = 11 specimens.

Dimensions. L: 72–107–135 μm; D: 61–76–86 μm; Da: 33–46–55 μm; H crests: 11–13–15 μm; L/D: 1.18–1.41–1.69; D/Da: 1.39–1.73–2.57 (*n* = 11).

Remarks. The long spines are aligned in longitudinal rows, with their tips connected by continuous crests suggesting similarity to *H. downiei* Jenkins, 1967. This characteristic ornamentation enables

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this taxon to be distinguished from other *Hercochitina* species with similarly long spines such as *H. multiansata* Paris et al., 2015, from the Qasim and Sarah formations of Saudi Arabia, or *H. filamentosa* Achab, 1977b, from the upper part of the Vauréal Formation (upper Katian) of Anticosti Island, which do not develop these characteristic crests. *Hercochitina turnbulli* Jenkins, 1969, from the Viola Limestone (*Pa. manitoulinensis* GBz), Oklahoma, has shorter and more abundant spines arranged in a greater number of longitudinal rows, and the crests only occur in four or five longitudinal rows connecting a few of the spine tips (i.e., the crests are not continuous across the whole length of the vesicle; see Fig. 5.11–5.14). However, some morphological features hamper an unambiguous assignment of our material to the species *H. downiei* Jenkins, 1967: (1) the total length of specimens in our population is shorter than the type assemblage of *H. downiei* (72–107–135 µm vs. 135–153–188 µm); (2) our specimens can have fewer crests than the ones from the type assemblage (10–14 vs 12–16); (3) besides simple and wishbone spines, our specimens also have multirooted spines, not described by Jenkins (1967) and impossible to discern in the images of the type assemblage; and (4) the spines in our specimens have a maximum height of 15 µm while in the assemblage described by Jenkins (1967), the spines had a height of up to 59 µm. These four features suggest a population somewhat different from *H. downiei* (i.e., a different morphospecies).

Hercochitina* aff. *H. longi Achab and Asselin in Achab et al., 2013
Figure 13.2–13.7

Occurrence. From samples MY-065.4 and MY-055.0 (19.9–16.8 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicle shape cylindrical to subconical. Flanks straight to slightly convex. Flexure inconspicuous. Two to four crests in the observable face. The crests are slightly sinuous, and they can be thick (connected to the vesicle by pairs of spines) and display perforations (Fig. 13.3, 13.7). A considerable variation in the total length of the specimens has been observed: longer (Fig. 13.4, 13.5), shorter (Fig. 13.2), and intermediate specimens have been found in the population. This characteristic seems to condition certain morphological and ornamentation features. In longer specimens, the vesicle shape is (sub)cylindrical, the crests are continuous until around the middle part of the vesicle, then evolve towards the aperture into broad-base spines, simple spines, and granules, and the vesicle finally displays a smooth collarette that may flare (Fig. 13.4); the ornamentation on the lip is gently fimbriated (Figs. 13.4, 13.5). In the short specimens, the vesicles are subconical, the crests are continuous from the marginal spines to the lip and extend beyond it, giving a spiny ornamentation to the lip, and the flanks taper towards the aperture (Fig. 13.2, 13.3). In all specimens, the spines on the margin can be long (< 37 µm) and have an approximated triangular shape due to their broad base and simple tip (Fig.13 .2, 13.7); commonly, the number of spines at the margin is superior to the number of crests on the vesicle (Fig. 13.6). At the center of the base, which has gently rugose ornamentation, a pit with a mucron was observed, surrounded by concentric rings (Fig. 13.7).

Materials. $N = 119$ specimens.

Dimensions. L: 90–269–384 µm; D: 69–86–107 µm; Da: 54–70–94 µm; H crests: 1–3–4 µm; L/D: 1.03–3.15–4.44; D/Da: 0.92–1.25–1.72 ($n = 25$).

Remarks. Our material has some morphological characteristics in common with *Hercochitina longi* Achab and Asselin in Achab et al., 2013, from the Vauréal Formation (*Pa. prominens* GBz), eastern Anticosti Island: cylindroconical vesicle; ornamentation consisting of a few relatively long and distinct crests observed on the visible face; discontinuous crests that evolve to simple spines towards the aperture, culminating in an ornamented lip; a row of spines at the margin. However, when compared with the type material of *H. longi*, our population has a greater range of dimensions, the vesicles are usually more cylindrical, the crests are thicker and more ornamented, and the spines on the margin are longer, larger, more numerous, and complex. These differences favor the use of open nomenclature, at least until more *H. longi* specimens are illustrated, preferentially from the type locality.

***Hercochitina* sp. 1**
Figure 3.21, 3.22

Occurrence. From samples MY-778.3 ft and MY-770.3 ft (237.2–234.8 m), Point Pleasant Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicle's overall shape is conical to pyriform. Conical chamber with convex flanks. Gentle flexure. Short, subcylindrical neck. Aperture fimbriated. Ornamentation on the neck and upper half of the chamber consists of discontinuous crests of connected thorn-like and λ-spines (< 5 µm). The discontinuity of the crests makes it difficult to give an exact number but between 18 and 20 crests were counted with certainty on the visible face of the vesicles. On the lower half of the chamber, the ornamentation decreases in complexity: the discontinuous crests are shorter and smaller. At the margin, simple and λ-spines, sometimes multirooted spines, are observed and they propagate to the base (Fig. 3.21). The ornamentation transitions occur gradually. Maximum diameter located slightly above the rounded basal margin. Apical structures were not observable.

Materials. $N = 20$ specimens.

Dimensions. L: 93–108–129 µm; D: 65–74–88 µm; Da: 37–46–55 µm; H crests: 2–3–5 µm; L/D: 1.18–1.47–1.71; D/Da: 1.36–1.65–2.17 ($n = 14$).

Remarks. No other species of *Hercochitina* is known to have such a clear decrease in the ornamentation complexity on the lower half of the chamber. However, due to the small number of specimens recovered, we decided to keep this morphotype in open nomenclature until more material is found.

***Hercochitina* sp. 2**
Figure 5.15–5.18, 5.21

Occurrence. From sample MY-701.6 ft (213.8 m; Point Pleasant Formation) to MY-603.5 ft (183.9 m; Kope Formation), MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is subcylindrical to subconical. No clear separation between chamber and neck (i.e., flexure inconspicuous). Rounded margin. The flanks are overall straight. The lip is gently fimbriated. Low, fine, and numerous crests (12–18 crests on the visible face) were observed across the entire vesicle. The crests rise up to 3 µm above the vesicle wall.

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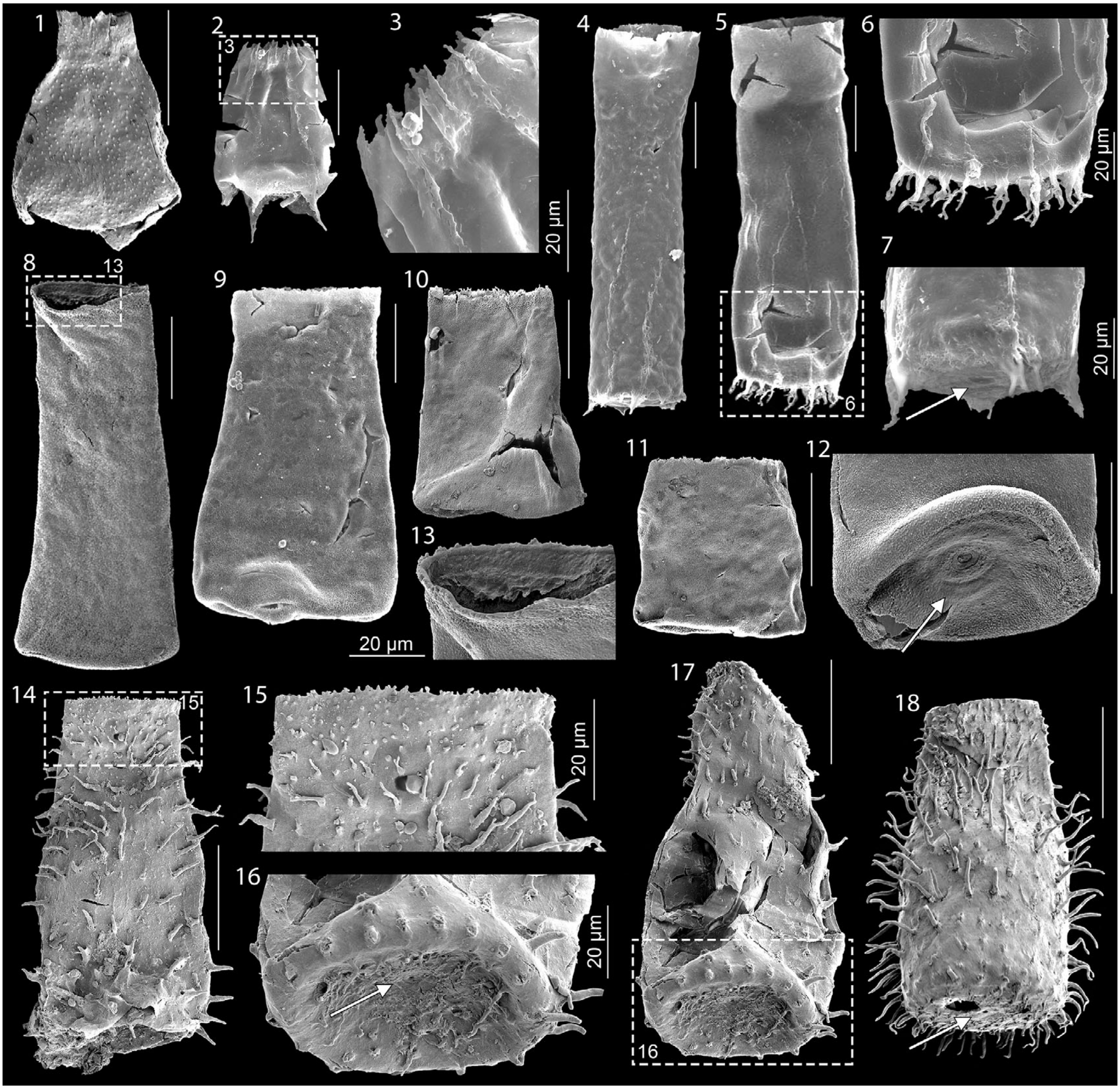

Figure 13. Scanning electron images of relevant species from the Bull Fork Formation, with sample reference. (**1**) *Belonechitina senta*? (Achab, 1978a), MY-065.4 ft (19.9 m). (**2–7**) *Hercochitina* aff. *H. longi* Achab and Asselin in Achab et al., 2013, MY-055.0 ft (16.8 m): (**2**) short specimen, (**3**) detail of the lip ornamentation in specimen (**2**), (**4, 5**) long specimens, (**6**) detail of the lower part of vesicle (**5**), showing the complexity and development of the marginal spines, and (**7**) basal view, a pit with a mucron can be observed. (**8–13**) *Eisenackitina* cf. *E. ripae* Soufiane and Achab, 2000b: (**8, 10–13**) MY-065.4 ft (19.9 m), (**9**) MY-055.0 ft (16.8 m), where (**8, 9**) represent long specimens and (**10, 11**) represent short specimens, (**12**) is a view of the ornamented base where a pit with a mucron, surrounded by concentric rings, is observed, and (**13**) is a detail of the apertural view of (**8**), showing the lip ornamentation and the possible scar of the sealing structure that has been torn away, allowing its original position to be inferred, close of the aperture. (**14–18**) *Nevadachitina soufianei* n. sp., MY-065.4 ft (19.9 m): (**15**) detailed view of the apertural part of specimen (**14**), where the lip ornamentation and morphology of the spines is observed, (**16**) closeup view of the ornamented base of specimen (**17**), where a pit with a mucron is observed and indicated with an arrow, and in specimen (**18**), holotype, RBINS b 10052, an arrow also points to the pit with a mucron at the center of the ornamented base. All scale bars = 50 μm, except when another value is indicated in the figure.

Fairly continuous in the lower half of the vesicle, the crests get tenuous and discontinuous in its upper half and usually do not reach the lip (e.g., Fig. 5.15). The crests are sometimes replaced by randomly distributed, simple spines and granules on the uppermost part of the vesicle. At the margin, the crests end in the form of simple or two-legged spines (Fig. 5.21, < 4 μm in length). The base is lightly ornamented with granules and a pit with a mucron has been observed (Fig. 5.17).

Materials. N = 140 specimens.

Dimensions. L: 148–259–348 μm; D: 64–85–104 μm; Da: 52–65–84 μm; H crests: 0.7–1.4–2.5 μm; L/D: 1.86–3.04–3.85; D/Da: 1.08–1.30–1.53 (n = 18).

Remarks. While *Hercochitina lindsayensis* Melchin and Legault, 1985, has similar ornamentation to our material, that species presents a more subconical vesicle (Dp of *H. lindsayensis*: 100–129–170 μm), a gentle flexure, and complex spines up to 8 μm long at the margin. Our material can also be differentiated from *Hercochitina longi* Achab and Asselin in Achab et al., 2013, a species with a lower number of crests, and spines on the margin. Although *Hercochitina* sp. 2 shares some features with *Hercochitina crickmayi* Jansonius, 1964 (vesicle shape and low crests), our material is differentiated by its crests becoming discontinuous towards the aperture and being replaced by spines on the uppermost part of the vesicle, low crests that barely rise above the vesicle wall, and by the absence of complex spines at the margin. These differences were also noted previously in specimens identified as "*Hercochitina* sp. aff. *H. crickmayi*" (Knabe, 1980, p. 99–101) from the Lexington Limestone, Point Pleasant, Kope, and Clays Ferry formations, from different sections in Kentucky, and thus could be conspecific with our material. In conclusion, the ornamentation in our specimens is faint, fine, and low, and we are unsure if this is an original feature or a result of poor preservation/abrasion. Therefore, this morphotype is kept in open nomenclature until more material is found from coeval levels, in other sections, and we can confirm if the delicate ornamentation is in fact an original feature.

Subfamily **Spinachitininae** Paris, 1981
Genus ***Spinachitina*** Schallreuter, 1963, emend. Paris et al., 1999

Type species. By original designation, *Conochitina cervicornis* Eisenack, 1931; lost holotype in Eisenack, 1931, p. 89, pl. 2, fig. 12, erratic calcareous sandy siltstones; neotype, *Spinachitina cervicornis*, in Nõlvak and Grahn, 1993, pl. 3, fig. A, from the Kahula Formation, Baltoscandian Keila Stage, ca. Sandbian–Katian boundary, Upper Ordovician, Estonia (Paris et al., 1999).

***Spinachitina* sp. 1**
Figure 11.17–11.22

Occurrence. From sample MY-273.2 ft (83.3 m; Grant Lake Limestone) to MY-191.4 ft (58.3 m; Bull Fork Formation), MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is subconical. A gentle flexure separates the subcylindrical to slightly flaring neck from the conical chamber with straight to mildly convex flanks. Lip fimbriated. Vesicle ornamented with randomly distributed granules of small to moderate size. Small, broad-based spines with a blunt tip may be observed on the chamber, in addition to the granules (Fig. 11.19). Crown of numerous (about 32–48), roughly aligned processes on the rounded margin (< 16 μm). These processes are multirooted, two-legged, or simple spines, thick at their roots, fine most of their length, with simple and blunt tips. The granular ornamentation extends to the base, decreasing in size towards its center, where a pit with a mucron has been observed (Fig. 11.18).

Materials. *N* = 302 specimens.

Dimensions. L: 83–132–211 μm; D: 57–79–103 μm; Da: 37–47–65 μm; L processes: 2–6–16 μm; L/D: 1.02–1.68–2.72; D/Da: 1.35–1.72–2.18 (*n* = 36).

Remarks. Although the processes on the margin do not always perfectly align in a crown, there is a significant length difference between these and the ornamentation on the lower half of the chamber. Therefore, in our opinion, it is justified to attribute this species to *Spinachitina*, instead of *Belonechitina* (Paris et al., 1999). In the Katian Stage, there are two clear groups of *Spinachitina* species: (1) the ones with thick, long, and ornamented processes (e.g., *Spi. alaticornis* Jenkins, 1967, *Spi. cervicornis* (Eisenack, 1931), and *Spi. katherinae* Vandenbroucke, 2008b); and (2) the ones with numerous fine, short spiny processes with simple tips (e.g., *Spi. bulmani* Jansonius, 1964, and *Spi. fossensis* Vanmeirhaeghe and Verniers, 2004). *Spinachitina* sp. 1 shares more morphological characteristics with the species of the second mentioned group: conical chamber and subcylindrical to slightly flaring neck, similar total length range (~100 to < 300 μm), commonly ornamented lip, and occasionally with granules present on the vesicle wall. There is substantial intraspecific variation in the ornamentation of *Spinachitina* sp. 1 specimens, including many transitional forms. This morphotype is easy to differentiate from other *Spinachitina* species only when its features are intensely developed and well preserved: thick granules coexisting with spines on the chamber and long processes on the margin (< 16 μm; e.g. Fig. 11.19). In the same population, specimens with subtle ornamentation (i.e. with small granules and shorter processes; e.g., Fig. 11.17, 11.21) may be difficult to separate from other *Spinachitina* species. Therefore, we do not consider our material to have sufficiently diagnostic characteristics to erect a new species and it is kept in open nomenclature.

Family **Lagenochitinidae** Eisenack, 1931, emend. Paris, 1981
Subfamily **Ancyrochitininae** Paris, 1981
Genus ***Ancyrochitina*** Eisenack, 1955

Type species. *Conochitina ancyrea* Eisenack, 1931, by original designation; lost holotype in Eisenack, 1931, p. 88–89, pl. 4, fig. 4, erratic limestones of the Baltic ('Ostseekalk'); neotype in Eisenack, 1955, p. 163–164, pl. 2, fig. 7, erratic *Beyrichia* limestones from the Baltic seafloor, Přídolí, Silurian (Paris et al., 1999).

***Ancyrochitina barbescens*?** Martin, 1975
Figure 5.19, 5.20, 5.22

Occurrence. From sample MY-722.6 ft (220.2 m; Point Pleasant Formation) to MY-242.9 ft (74.0 m; Grant Lake Limestone), MY-14-01 core, Kentucky, USA.

Description. Vesicle's overall shape is conical. The inflated, conical chamber is separated from the subcylindrical neck by a marked flexure without shoulders. Flanks convex. Lips fimbriated. Vesicle wall glabrous. Numerous thin and spongy processes, simple or bi-rooted, and simple, bifurcating or branching tips (Fig. 5.19, 5.22). Apical structures or ornamentation on the base have not been observed.

Material. *N* = 144 specimens.

Dimensions. L: 78–98–124 μm; D: 73–86–105 μm; Da: 33–42–54 μm; Lch: 34–60–79 μm; Ln: 28–38–70 μm; L processes: 9–15–24 μm; L/D: 0.79–1.16–1.41; D/Da: 1.67–2.07–2.98 (*n* = 20).

Remarks. While this species is rarely imaged and has only briefly been described in the literature, it has diagnostic characteristics that differentiate it from other species of *Ancyrochitina*: inflated chamber, vesicle wall smooth, and 10–27 cylindrical, spongy, and fine processes, length of 15–28 μm, with a simple or bifurcated base, and branched at the tip. The ornamentation is often broken in the specimens of this population, therefore we can rarely assess the total number of processes and observe their branching tips.

Our material is different from *Ancyrochitina merga* Jenkins, 1970a (Sylvan Shale, *Pa. manitoulinensis* and *Dicellograptus complanatus* GBzs, Oklahoma) as *Anc. merga* has a longer neck, can have spiny ornamentation on the vesicle, the processes can be longer, and usually are more elaborate and organized ("generally 1–3, rarely 4, orders of Y- or T-shaped branching into 2 sharply diverging, equal distal limbs" Jenkins, 1970a, p. 267).

Ancyrochitina aff. _Anc. corniculans_ Jenkins, 1969
Figure 5.23–5.25

Occurrence. From sample MY-722.6 ft (220.2 m; Point Pleasant Formation) to MY-253.1 ft (77.1 m; Grant Lake Limestone), MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is conical. The conical chamber is separated from the subcylindrical or flaring neck by a marked flexure without shoulders. Flanks straight to concave. Lip fimbriated. At the rounded margin, 8 thick processes (4 on the visible face) that may have simple or bifurcating tips were counted. The vesicle can be smooth but, in most specimens, some ornamentation is present on the chamber and neck, particularly intense in the flexure area, in the form of simple and two-legged spines (Fig. 5.25) and/or granules of different sizes (Fig. 5.23, 5.24). Apical structures were not observed, only tenuous concentric rings at the center of the base (Fig. 5.24).

Materials. N = 115 specimens.

Dimensions. L: 74–107–131 µm; D: 64–74–91 µm; Da: 33–41–50 µm; Lch: 44–71–93 µm; Ln: 23–36–60 µm; L processes: 17–30–45 µm; L/D: 1.03–1.46–1.79; D/Da: 1.51–1.83–2.2 µm (n = 20).

Remarks. Among all *Ancyrochitina* species, this material resembles *Ancyrochitina corniculans* Jenkins, 1969, from the Viola Limestone (*Pa. manitoulinensis* GBz, Oklahoma, USA), based on the following features: dimensions and ratios, presence of thick processes that may bifurcate, and some specimens in this population have gentle ornamentation on the vesicle. However, it differs from this species by not having the range of ornamentation present in the type population (simple, λ, and π spines) and most specimens of our population have more processes than originally described and figured. This morphotype also clearly differs from other Katian, gently ornamented *Ancyrochitina* species. *Ancyrochitina barbescens* Martin, 1975, from the Utica Formation (SW Quebec Province, Canada), has an inflated chamber/convex flanks, with a greater number of cylindrical and narrow processes (10–27). *Ancyrochitina merga* Jenkins, 1970a, from the Sylvan Shale (*Paraorthograptus manitoulinensis* and *Dic. complanatus* GBz, Oklahoma, USA) has thinner and commonly more (8–24) processes at the margin, which can have several orders of bifurcation.

Genus **_Clathrochitina_** Eisenack, 1959

Type species. *Clathrochitina clathrata* Eisenack, 1959; holotype in Eisenack, 1959, p. 15, pl. 1, fig. 3, from Dalhem canal, *Pentamerus gotlandicus* beds from southeast Slite Marls, late Sheinwoodian, Silurian, Gotland, Sweden.

Clathrochitina mangle new species
Figures 8, 14.4, 14.5

1976 *Trochochitina multiramosa* Miller, p. 172–176, pl. 16, figs. 1, 2, 4–7, text-fig. 20.
1980 *Trochochitina multiramosa*; Knabe, p. 111–112, pl. 6, figs. 16, 18.
2016 *Clathrochitina multiramosa*; Velleman, p. 69–70, pl. 5, figs. 16, 17, 21–23.

Holotype. Figure 8.19 (RBINS collection number b 10050); dimensions: L: 142 µm; D: 98 µm; Da: 56 µm; Lch: 88 µm; Ln: 54 µm; L processes: 22 µm; L/D: 1.45; D/Da: 1.74; sample MY-477.0 ft (145.4 m), Kope Formation (Maysville, Kentucky, USA).

Diagnosis. A *Clathrochitina* species with a dense crown of uncountable processes on the margin. The processes are multi-rooted, fine, and solid. The sets of numerous processes anastomose in a mangrove-like aspect and join distally in a simple tip or a partial ring.

Occurrence. In this work, from sample MY-477.0 ft (145.4 m; Kope Formation) to MY-282.0 ft (86.0 m; Grant Lake Limestone), MY-14-01 core, Kentucky, USA. In several other sections of Kentucky and Cincinnati, Ohio, *Cl. mangle* n. sp. was identified in the upper part of the Clays Ferry Formation, the upper part of the Kope Formation, the Fairview Formation, and the lower part of the Grant Lake Limestone (Miller, 1976; Knabe, 1980).

Description. Vesicle's overall shape is conical. When a flexure is conspicuous (i.e., chamber and neck are well differentiated), the chamber is conical and the neck is subcylindrical (e.g., Fig. 8.1). In most specimens, the chamber flanks are straight to convex, but specimens with slightly concave flanks (Fig. 8.4) are also found. When present, the flexure is usually gentle, but it can be sigmoidal and have discrete shoulders (Fig. 8.8, 8.12). In most specimens, the length of the neck is almost half of the total length of the vesicle; however, the neck can also be short (Fig. 8.15) or inconspicuous (Fig. 8.7, 8.14). The lip is gently fimbriated. A prosome has been observed inside the neck (Fig. 8.6). On the margin, there are numerous fine and solid processes, densely packed, resulting in a thick crown. We estimate that the number of processes should be between many dozens and fewer than 200. However, the processes are so numerous and are distributed in such a complex and compact way that their exact number is uncountable. Sets of processes come together in simple tips (Fig. 8.20) and/or partial rings (Fig. 8.14, 8.16), at a maximum distance from the margin of 38 µm. Even when vesicles were intensely eroded, the many spines and granules (resulting from the broken processes) and the complex roots on the margin allowed the identification of this species. Gentle ornamentation can be present on the vesicle, in the form of discontinuous crests on the lower part of the chamber, connected to the sets of processes on the margin (e.g., Fig. 8.6, 8.16, 8.20), and granules randomly distributed on the chamber and neck (Fig. 8.1). At the base, concentric rings and a pit with a mucron have been observed (Fig. 8.5, 8.18).

Etymology. The specific epithet relates to the red mangrove (*Rhizophora mangle*, described by Linnaeus) as the arrangement of the processes on the margin of this chitinozoan species resembles the numerous roots of mangrove trees.

Materials. N = 728 specimens.

Dimensions. L: 89–144–238 µm; D: 76–102–143 µm; Da: 35–52–65 µm; Lch: 63–101–150 µm; Ln: 11–43–88 µm; L processes: 11–20–38 µm; L/D: 0.89–1.41–2.30; D/Dc: 1.51–1.97–2.58 (n = 55).

Remarks. This species was first described from the Maysville area as *Trochochitina multiramosa*, but never formally defined (Miller, 1976). *Trochochitina* is a nomen nudum and was not retained by Paris et al. (1999). The taxon's conical chamber and the crown of compact, anastomosing processes on the margin justify its attribution to the genus *Clathrochitina.* We could not retain the original species name either given that the species *Ancyrochitina multiramosa* Taugourdeau and de Jekhowsky, 1960, was later reassigned to the genus *Clathrochitina* (Taugourdeau, 1967) and has nomenclature priority. Therefore, a new species name was selected for our population.

Two line drawings to clearly show the diagnostic features and variability in the ornamentation of this new species can be found in Fig. 14.4, 14.5. *Clathrochitina mangle* n. sp. is the fourth and youngest element of morphological lineage 1, composed of (older to younger; Fig. 14): *Hercochitina edingerae* n. sp., *Hercochitina krafftae* n. sp., *Hercochitina tharpae* n. sp., and *Cl. mangle* n. sp. *Hercochitina tharpae* n. sp. can be distinguished from *Cl. mangle* n. sp. by always having continuous crests on the chamber and well-differentiated sets of spines that do not connect laterally (i.e., never forming a continuous crown of anastomosing processes). The complexity and density of processes on the margin of the studied specimens are unique within the genus *Clathrochitina.* Species originally attributed to the genus *Clathrochitina* from Middle Ordovician strata have been reassigned to *Sagenachitina* (e.g., Jenkins, 1970a). After the reassignment of *Cl. concinna* Achab 1978b, and *Cl. sylvanica* Jenkins, 1970a, to the genus *Plectochitina*, only one species in open nomenclature, *Clathrochitina* sp. 1 Achab and Asselin in Achab et al., 2013, has been reported from the Upper Ordovician (Hirnantian, Anticosti Island). *Clathrochitina* sp. 1 can be differentiated by its diagnostic small granules randomly distributed throughout the entire vesicle, and its processes on the margin being shorter, less numerous, and more sporadically distributed than those of *Cl. mangle.* n. sp. To date, *Cl. mangle* n. sp. appears to be the oldest reported species of the genus *Clathrochitina.*

Genus ***Plectochitina*** Cramer, 1964

Type species. Plectochitina carminae Cramer, 1964; lost holotype in Cramer, 1964, p. 346–347, pl. 20, fig. 21, from the La Vid de Gordón section, upper San Pedro Formation, Přídolí, Silurian, NW Spain; neotype in Priewalder, 1997, p. 77, pl. 2, fig. 1, pl. 4, figs. 1, 7, 8, from type stratum.

Plectochitina spongiosa (Achab, 1977b)
Figure 5.26–5.28

- **1977b** *Ancyrochitina spongiosa* Achab, p. 2195–2197, pl. 1, figs. 1–9, 12.
- **1978a** *Ancyrochitina spongiosa*; Achab, p. 299–300, pl. I, figs. 1–3.
- **1978b** *Ancyrochitina spongiosa*; Achab, pl. I, figs.11, 12 (non pl. III, figs. 15–17).
- ?**1985** *Plectochitina spongiosa*; Molyneux and Paris, pl. 5, figs. 8, 9.
- **1987** *Ancyrochitina spongiosa*; Achab, p. 1214–1216, pl. I, figs. 1–3.
- ?**2000a** *Plectochitina spongiosa*; Soufiane and Achab, pl. II, fig. 3.
- non **2007** *Plectochitina spongiosa*; Ghavidel-Syooki and Vecoli, p. 181, pl. I, fig. 1.
- ?**2010** *Plectochitina spongiosa*; Loydell et al., fig. 12h.
- ?**2017** *Plectochitina spongiosa*; Al-Shawareb et al., pl. 9, fig. 3 (non pl. 9, fig. 4).

Holotype. GSC49055, core sample 1500 ft (457 m), Vauréal Formation, NACP core, Anticosti Island, Canada (Achab, 1977b, p. 2195–2197, pl. 1, fig. 6).

Occurrence. From sample MY-722.6 ft (220.2 m; Point Pleasant Formation) to MY-253.1 ft (77.1 m; Grant Lake Limestone), MY-14-01 core, Kentucky, USA. Also from the Utica and Lorraine groups, SW Quebec Province (Achab, 1987), and the Vauréal and Ellis Bay formations, Anticosti Island (Achab, 1977b, 1978a, b; Achab et al., 2013), Canada.

Materials. $N = 28$ specimens.

Dimensions. L: 62–92–112 μm; D: 62–73–80 μm; Da: 29–40–47 μm; Lch: 41–59–73 μm; Ln: 18–33–70 μm; L processes: 18–27–31 μm; L/D: 0.83–1.26–1.46; D/Da: 1.59–1.84–2.21 ($n = 13$).

Remarks. This species was originally assigned to the genus *Ancyrochitina* (Achab, 1977b). However, in the type assemblage of this species, a crown of cell-like processes can be observed, which justifies its reattribution to the genus *Plectochitina.* Some authors (e.g., Priewalder, 1997) have questioned if this species could be a junior synonym of *Plectochitina sylvanica* (Jenkins, 1970a). Many characteristics overlap: vesicle shape, size range, organization of the processes, and type assemblages originate from units of similar age. However, a few differences exist between these species: *Pl. spongiosa* has no more than 10 processes, which can be shorter (< 50 μm) than those of *Pl. sylvanica* (< 90 μm), and they seem thicker. We have not reviewed the type material of these species and we are not studying samples from their type strata, so we keep these species separate.

Attribution of the specimens of Molyneux and Paris (1985, pl. 5, figs. 8, 9) to *Pl. spongiosa* is questioned since their processes seem thinner and more complex than the ones of the type assemblage, resembling the features of *Pl. concinna* (Achab, 1978b). We are also uncertain if the specimen of Soufiane and Achab (2000a, pl. II, fig. 3) could be *Pl. spongiosa* since it only preserves one set of two processes joined at the tip and has abundant granules on the vesicle, a characteristic not observed in the type material or described by Achab (1977b). The specimen attributed to this species by Loydell et al. (2010, fig. 12h), has a neck length greater than half of the total length of the vesicle, an ornamentation of abundant small granules, and only two preserved processes with uneven thickenings, features inconsistent with the diagnosis of *Pl. spongiosa* and that resemble the characteristics of *Pl. nodifera* (Nestor, 1980). One of the specimens of Al-Shawareb et al. (2017, pl. 9, fig. 3) identified as *Pl. spongiosa* has fewer and longer (> 50 μm) processes than expected for this species.

Other specimens in the literature may have been erroneously identified as *Pl. spongiosa.* Three of the specimens figured by Achab (1978b, pl. III, figs. 15–17) have an ovoid and elongated chamber, fewer and thinner processes, without evidence of joining at the tip, contrasting with the type material of this species (Achab, 1977b). The specimen pictured by Ghavidel-Syooki and Vecoli (2007, pl. I, fig. 1) has processes bifurcating at the tip, a feature incompatible with the diagnosis of *Pl. spongiosa* and, in our opinion, more similar to those of *Ancyrochitina merga* Jenkins, 1970a. The specimen of Al-Shawareb et al. (2017, pl. 9, fig. 4) only has one preserved process that is longer than 100 μm, inconsistent with the dimensions of the type population of *Pl. spongiosa* (Achab, 1977b).

In Quebec, *Pl. spongiosa* is the nominal species of a biozone defined by Achab (1989), occurring in levels that yielded graptolites of the basal

G. pygmaeus GBz (Riva, 1969; Achab, 1987), correlated with the lower part of the *Pleurograptus linearis* GBz (Maletz, 2021[2023]).

Plectochitina* cf. *Pl. sylvanica (Jenkins, 1970a)
Figure 4.10–4.16

Occurrence. From samples MY-770.3 ft (234.8 m; Point Pleasant Formation) to MY-487.0 ft (148.4 m; Kope Formation), MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is conical. The well-developed flexure, without shoulders, separates the conical chamber from the neck, subcylindrical or flaring towards the aperture. Usually, small and discrete granules are randomly distributed on the neck and lip (Fig. 4.10, 4.11). A maximum of 20 process roots were observed on the margin. The processes have a cell-like structure (i.e., internally, the processes have partitions/divisions, which cause their irregular outline and thickness variation) and anastomose: sets of 2–9 anastomosed processes have been observed; they may unite and split again, making a complex net (Fig. 4.14–4.16). Distally from the vesicle, the processes commonly finish in a simple tip (Fig. 4.12), or they can rarely unite in a ring-like structure (Fig. 4.13). When the base of the vesicle is exposed, discrete concentric rings are sometimes observed (Fig. 4.14). No apical structures were observed.

Materials. N = 846 specimens.

Dimensions. L: 59–100–131 μm; D: 56–76–91 μm; Da: 26–38–53 μm; Lch: 37–64–86 μm; Ln: 21–36–69 μm; L processes: 19–33–50 μm; L/D: 0.84–1.32–1.89; D/Da: 1.38–2.05–2.94 (n = 23).

Remarks. Our material is conspecific with the material described as *Trochochitina radiata* Miller, 1976, nomen nudum (Miller, 1976) from the upper Kope Formation at Maysville, Kentucky. However, all these specimens have a conical chamber and cell-like processes on the margin, suggesting their attribution to the genus *Plectochitina*. All of the specimens strongly resemble *Plectochitina sylvanica* (Jenkins, 1970a) (Sylvan Shale, *Pa. manitoulinensis* and *Dic. complanatus* GBzs, Oklahoma, USA, Goldman and Bergström, 1997), *Plectochitina spongiosa* (Achab, 1977b) (Utica Group to Ellis Bay Formation, *G. pygmaeus* to *Metabolograptus persculptus* GBzs, Canada; Achab, 1978b; Melchin, 2008) and *Plectochitina concinna* (Achab, 1978b) (upper Vauréal to Ellis Bay Formation, *Pa. prominens* to *M. persculptus* GBzs, Anticosti Island; Melchin, 2008; Achab et al., 2011) by having the characteristic long and complex processes, a similar outline and dimensions. In our abundant, well-preserved specimens, we observe a large variability, with all the intermediate forms, surpassing the type populations of both species. For example, unlike *Pl. concinna*, the necks in our specimens can be longer than the chamber, reaching up to two-thirds of the total length of the vesicle; and the anastomosing processes can be longer than 30 μm (Fig. 4.16). The length of the processes of our specimens falls within the range of those of *Pl. sylvanica* and they are longer, thinner, and more numerous than type specimens of *Pl. spongiosa*. However, our specimens can have even more processes than type specimens of *Pl. sylvanica* and rarely have a continuous ring connecting their distal ends, which is common within that species. Also, *Pl. sylvanica*, *Pl. spongiosa*, and *Pl. concinna* were never described as having granules on the neck and the resolution of the images of their type material does not provide that degree of detail. Given this degree of complexity, our specimens are described in open nomenclature.

Subfamily **Angochitininae** Paris, 1981
Genus ***Angochitina*** Eisenack, 1931

Type species. Angochitina echinata Eisenack, 1931; lost holotype in Eisenack, 1931, p. 82, pl. 1, fig. 7, from erratic *Beyrichia* limestones ('Beyrichia-kalk'); neotype in Eisenack, 1964, p. 319, pl. 29, fig. 10, from the topmost part of the Hemse beds, early Ludfordian, Silurian, Gotland, Sweden (Paris et al., 1999).

Angochitina bascomae new species
Figure 6.12–6.17

Holotype. Illustrated in Fig. 6.14, 6.17 (RBINS collection number b 10051); dimensions: L: 129 μm; D: 83 μm; Da: 47 μm; Lch: 94 μm; Ln: 35 μm; H spines: 6 μm; L/D: 1.55; D/Da: 1.77; sample MY-603.5 ft (183.9 m), Kope Formation (Maysville, Kentucky, USA).

Diagnosis. Ovoid to pear-shaped *Angochitina* species with thick spines of different morphologies coexisting in the same specimens: bases can be simple, two-legged, or thorn-like; tips can be simple, pointed, or broad, or they can bifurcate.

Occurrence. Sample MY603.5 ft (183.9 m), Kope Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicle small, subconical to pear-shaped. Chamber ovoid to subconical, with the convex flanks tapering towards the gentle flexure. Maximum width at the lower half of the chamber. Shoulders absent. Neck subcylindrical to gently flaring. A tubular prosome has been observed partially ejected from the vesicle (Fig. 6.13). Lip fimbriated. Ornamentation of randomly distributed, thick spines: simple, two-legged, and/or thorn-like. At the tip, the spines can be simple or bifurcated (few per specimen but easy to spot; indicated with arrows in Fig. 6.17). The spines get shorter, finer, and scarcer towards the aperture and can be replaced by granules close to the lip. The same decrease of ornamental complexity occurs towards the center of the base, where no apical structures were observed.

Etymology. Named after Florence Bascom, an educator and the first woman geologist hired by the U.S. Geological Survey (1896).

Materials. N = 153 specimens.

Dimensions. L: 78–114–190 μm; D: 75–83–101 μm; Da: 29–46–70 μm; Lch: 58–81–110 μm; H spines: 4–7–11 μm; L/D: 0.94–1.37–1.88; D/Da: 1.45–1.87–2.81 (n = 20).

Remarks. Angochitina dicranum Jenkins, 1967 (*Onnia* beds, correlated with the *Dicellograptus morrisi* Subzone of the *Dicranograptus clingani* Biozone, lower Katian, UK; Zalasiewicz et al., 1995) is the only other Upper Ordovician *Angochitina* species that is known to have bifurcating spines. However, the ornamentation in that species is more spaced, the spines are longer, and the vesicle is more elongated than our material.

Angochitina oklahomensis Taugourdeau, 1965
Figure 12.7, 12.8, 12.11, 12.12

1965 *Angochitina*? *oklahomensis* n. sp.; Taugourdeau, p. 466, pl. I, fig. 6.
?**1967** *Angochitina oklahomensis*; Rauscher and Doubinger, p. 315, pl. 1, fig. 9.

Holotype. N°32 J, from the Viola Limestone (= Viola Springs Formation), *P. manitoulinensis* GBz (Goldman and Bergström, 1997), Katian, Criner Hills, Carter County, Oklahoma, USA (Taugourdeau, 1965, p. 466, pl. I, fig. 6).

Occurrence. Upper Ordovician of: US Midwest, Viola Limestone (= Viola Springs Formation) of Oklahoma; in this work, from sample MY-319.0 (Grant Lake Limestone) to sample MY-075.0 (Bull Fork Formation), MY-14-01 core, Kentucky, USA.

Materials. N = 337 specimens.

Dimensions. L: 98–138–172 μm; D: 65–80–88 μm; Da: 35–45–56 μm; Lch: 68–101–127 μm; H spines: 2–3–4 μm; L/D: 1.37–1.73–2.09; D/Da: 1.51–1.78–2.17 (n = 24).

Remarks. This species was originally assigned with doubt to the genus *Angochitina* (Taugourdeau, 1965). In the following years, authors confirmed this assignment (e.g., Rauscher and Doubinger, 1967) and we agree with that decision. While this species has been rarely imaged and only succinctly described, it has diagnostic characteristics that differentiate it from other *Angochitina* species: short, wide, and subcylindrical neck; cylindro-ovoid chamber; and a vesicle densely ornamented with small, simple, pointed spines (Fig. 12.12) We cannot confidently agree that the specimen of Rauscher and Doubinger (1967, pl. 1, fig. 9) belongs to the species *Ang. oklahomensis*: while the shape of the neck and chamber is compatible with the features of this species, the image was obtained with transmitted light microscopy and does not have the necessary resolution to confirm the size and organization of the spines.

Angochitina* cf. *Ang. capillata Eisenack, 1938
Figures 9.15–9.18, 12.13–5.17

Occurrence. From sample MY-457.3 (Kope Formation) to sample MY-075.0 (Bull Fork Formation), MY-14-01 core, Kentucky, USA.

Description. Overall shape of the vesicle is conical. Flexure well developed. Chamber ovoid to subconical with convex flanks. Maximum width situated at the half-length or within the lower half of the chamber. Neck subcylindrical to flaring. Lip fimbriated (Fig. 12.14) and can have small perforations (Fig. 12.16). Vesicle densely ornamented with fine spines, less than or equal to 8 μm in length, always with pointed tips and broad and elongated bases, typically two-legged and aligned with the long axis of the vesicle (e.g., Fig. 9.15, 9.18). The spines are longer in the middle area of the vesicle and decrease both aperturalwards and antiaperturalwards. A pit without a mucron has been observed at the center of the base (Fig. 12.17).

Materials. N = 1348 specimens.

Dimensions. L: 93–128–179 μm; D: 65–76–91 μm; Da: 36–44–56 μm; Lch: 65–94–141 μm; Ln: 17–35–55 μm; H spines: 3–5–8 μm; L/D: 1.26–1.70–2.17; D/Da: 1.48–1.73–1.97 (n = 20).

Remarks. The type material of *Ang. capillata* Eisenack, 1938 (erratic block, Upper Ordovician, Baltica) appears to display thicker and longer spines (dimensions not provided and the original images are too low resolution to recalculate some measurements of this material), described as thorn-shaped and not as two-legged or lambda spines. However, the original vesicle dimensions and its outline are similar to the characteristics of our material. Given the uncertainties, it is appropriate to apply open nomenclature.

Order **Operculatifera** Eisenack, 1931
Family **Desmochitinidae** Eisenack, 1931, emend. Paris, 1981
Subfamily **Desmochitininae** Paris, 1981
Genus ***Desmochitina*** Eisenack, 1931

Type species. Desmochitina nodosa Eisenack, 1931; lost holotype in Eisenack, 1931, p. 92, pl. 3, fig. 1, from erratic Ordovician calcareous sandy siltstone; neotype in Laufeld, 1967, p. 330–332, fig. 26, from the 'Skagen' Formation, Baltoscandian Keila Stage, ca. Sandbian–Katian boundary, Upper Ordovician, Fjäka section, Dalarna, Sweden.

Desmochitina* cf. *D. holosphaerica Eisenack, 1968
Figure 4.19

Occurrence. From samples MY-741.1 ft and MY-701.6 ft (225.9–213.8 m), Point Pleasant Formation, MY-14-01 core, Kentucky, USA.

Description. Overall shape of the vesicle subspherical. Greatest width at the upper half of the vesicle. Very wide aperture (Da = 67% of Dp). Short, straight collarette. The operculum is thick and not ornamented. Vesicle wall smooth. The operculum of the preceding specimen is still attached to the base of the following vesicle (Fig. 4.19).

Materials. N = 4 specimens.

Dimensions. L: 71–71–72 μm; D: 64–69–72 μm; Da: 43–46–48 μm; L collarette: 5–6–7 μm; L/D: 0.99–1.04–1.13; D/Da: 1.48–1.49–1.50 (n = 3).

Remarks. Of all the *Desmochitina* species known to have an operculum of the preceding specimen still attached to the base of the following vesicle, our material presents many similarities with *D. holosphaerica* from glacial erratics of the Baltic region, which Eisenack (1968) considered Caradocian in age (Sandbian–lower Katian), in having a subspherical vesicle, a very short collarette, and a wide aperture. In the type material of *D. holosphaerica*, the short collarette flares gently while in our material the collarette is approximately straight. Also, no structure that could resemble a copula between the base of the vesicle and the operculum of the preceding specimen, as described by Eisenack (1968), was observed in our specimens: the way the vesicle was folded could be hiding this structure or it might not be present at all. These differences, the low abundance of specimens of this morphotype in our samples, and the lack of published images of *D. holosphaerica* after its definition favor the use of open nomenclature. *Desmochitina holosphaerica* has been reported but not figured from the Baltoscandian Uhaku to Keila stages (e.g., Nõlvak, 2008; Goldman et al., 2015).

Subfamily **Eisenackitininae** Paris, 1981
Genus ***Eisenackitina*** Jansonius, 1964, restrict. Paris, 1981

Type species. Eisenackitina castor Jansonius, 1964; holotype in Jansonius, 1964, p. 912–913, pl. 2, fig. 16, core sample from 253 m (758 ft), Hume Formation, Givetian, Devonian, northern Canada.

Eisenackitina* cf. *E. ripae Soufiane and Achab, 2000b
Figure 13.8–13.13

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Occurrence. Samples MY-065.4 ft and MY-055.0 ft (19.9–16.8 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicles can be elongated and subcylindrical (Fig. 13.8) to short (Fig. 13.11), subconical, and stout (Fig. 13.9). Flexure commonly inconspicuous (Fig. 13.8, 13.10). When recognizable, the gentle flexure separates the conical chamber from the mildly flaring, short neck (Fig. 13.9). Lip moderately (Fig. 13.9, 13.13) to intensely fimbriated, sometimes also displaying perforations (Fig. 13.10). Maximum width at the rounded margin or slightly above. Vesicle densely and homogeneously ornamented with granules. The outer half of the base is similarly ornamented, but the ornamentation decreases towards the center of the base, where a pit with a mucron and concentric rings can be observed (Fig. 13.12), when the base is not invaginated (Fig. 13.9–13.11).

Materials. *N* = 289 specimens.

Dimensions. L: 120–189–277 µm; D: 84–104–122 µm; Da: 64–77–93 µm; L/D: 1.25–1.81–2.40; D/Da: 1.16–1.36–1.51 (*n* = 26).

Remarks. *Eisenackitina ripae* type material (*Paraorthograptus pacificus* and *Metabolograptus extraordinarius* GBzs, from central Nevada and Arctic Canada; Finney et al., 1999; Štorch et al., 2011; Maletz, 2021[2023]) and our material have important features in common: vesicle shape and dimensions, and dense, small ornamentation. Yet, in contrast to the *E. ripae* type material, our population is ornamented with granules (tubercles or cones absent), and the presence and size of the ornamentation appear uniform throughout the entire vesicle. These differences favor the use of open nomenclature.

Within the Family Desmochitinidae, the genus *Bursachitina* is characterized by its glabrous and conical chamber, while specimens of the genus *Eisenackitina* have an ovoid chamber with randomly distributed spines (Paris et al., 1999). The holotype and paratypes of *E. ripae* display a conical chamber and this species is described as having tubercles and cones without indicating dimensions, and spines were not mentioned or observed. These features seem more compatible with the genus *Bursachitina.* However, given the doubt that our material even is conspecific with this species, we only mention the possibility of reassigning the mentioned species to the genus *Bursachitina* without making a formal suggestion.

***Eisenackitina* sp. 1**
Figure 6.18–6.21

Occurrence. Sample MY-603.5 ft (183.9 m), Kope Formation, MY-14-01 core, Kentucky, USA.

Description. Vesicle stout, ovoid to pear-shaped. The pear-shaped vesicles have a gentle flexure separating the ovoid chamber from the neck that tapers towards the aperture (Fig. 6.20, 6.21). Convex flanks. Maximum width mid-chamber or on its lower half. The lip is usually poorly preserved but seems to be gently fimbriated (Fig. 6.18). The sealing structure seems to be an operculum at the aperture of the vesicle (Fig. 6.18). The vesicle is ornamented with randomly distributed, small, pointed, and broad-based spines. Base invaginated in most specimens: ornamentation of granules and discrete concentric rings were observed on the base, but it was impossible to observe the presence of apical structures.

Materials. *N* = 62 specimens.

Dimensions. L: 64–97–117 µm; D: 70–81–95 µm; Da: 29–38–48 µm; H spines: 2–3–5 µm; L/D: 0.92–1.19–1.50; D/Da: 1.65–2.19–2.74 (*n* = 21).

Remarks. *Eisenackitina* sp. 1 can be very similar to some specimens of *Angochitina bascomae* n. sp., present in the same sample. However, *Ang. bascomae* n. sp. typically has longer spines with more variable morphologies coexisting on the same vesicle, commonly with bifurcating tips. Also, specimens of *Ang. bascomae* n. sp. usually are longer. No other *Eisenackitina* species from the Upper Ordovician is known to have such an ovoid vesicle.

Genus ***Nevadachitina*** Soufiane and Achab, 2000b

Type species. *Nevadachitina vininica* Soufiane and Achab, 2000b; holotype in Soufiane and Achab, 2000b, p. 175, pl. I, fig. 2, from the uppermost Vinini Formation, Vinini Creek section, Hirnantian (Upper Ordovician), Roberts Mountains, Nevada, USA.

Remarks. The genus *Nevadachitina* was erected after the revision work of Paris et al. (1999), and therefore was not included there. Since then, this genus has been consistently used by different authors (e.g., Sinha et al., 2011; Paris et al., 2012; Achab et al., 2013). Until now, only three species were attributed to *Nevadachitina*, one of them in open nomenclature (Soufiane and Achab, 2000b). The number of crowns and longitudinal rows, together with spine characteristics, have been considered key features for discerning between species (Soufiane and Achab, 2000b). Before the current study, species belonging to the genus *Nevadachitina* were identified and reported only from central Nevada, within the *Dic. ornatus* (upper Katian), *M. extraordinarius*, and *M. persculptus* (Hirnantian) GBzs (Finney et al., 1999; Soufiane and Achab, 2000b; Maletz, 2021[2023]).

Nevadachitina soufianei new species
Figure 13.14–13.18

Holotype. Illustrated in Figure 13.18 (RBINS collection number b 10052); dimensions: L: 132 µm; D: 74 µm; Da: 54 µm; H spines: 19 µm; L/D: 1.77; D/Da: 1.39; sample MY-065.4 ft (19.9 m), Bull Fork Formation (Maysville, Kentucky, USA).

Diagnosis. *Nevadachitina* species with spaced spines on the whole vesicle, organized in 15–16 crowns and 10–12 longitudinal rows regularly distributed on the visible face. The spines appear to be stiff to slightly flexible, subcylindrical, and long (< 19 µm), their bases are frequently perforated and elongated longitudinally, and their rounded tips sporadically bifurcate.

Occurrences. Sample MY-065.4 ft (19.9 m), Bull Fork Formation, MY-14-01 core, Kentucky, USA.

Description. The overall shape of the vesicle is conical. In a few specimens, the chamber and neck are not differentiated, and the vesicle gets narrower towards the aperture with convex flanks. When separated by a gentle flexure, the chamber is conical to subcylindrical, with convex to straight flanks, and the neck is short and subcylindrical. Lip finely fimbriated. Sealing structures were not observed. Ornamentation consists of spaced spines on the whole vesicle, regularly organized in 15–16 crowns and 10–12 longitudinal rows on the visible face. The spines appear to be stiff to slightly flexible, subcylindrical, widening slightly towards the vesicle wall, and tapering to blunt, rounded tips at their distal end. The bases of the spines are frequently perforated and elongated longitudinally, and distally, the tips may bifurcate—rarely but observable at least once in all the studied specimens of the population (Fig. 13.14, 13.18). The spines are long (< 19 μm) on the margin and the chamber, getting shorter towards the aperture, and evolving to thorns and granules near the lip, where they lose their regular distribution. Rounded margin. Base ornamented with spines in concentric rings around the apical structure: a simple pit (Fig. 13.18), or a pit with a discrete mucron (Fig. 13.16).

Etymology. This species is dedicated to Azzedine Soufiane for his work on Ordovician and Silurian chitinozoans and his heroic behavior during the Québec City mosque attack in 2017.

Materials. $N = 17$ specimens.

Dimensions. L: 95–133–158 μm; D: 71–79–90 μm; Da: 46–50–56 μm; H spines: 9–14–19 μm; L/D: 1.34–1.69–1.97; D/Da: 1.39–1.60–1.88 ($n = 9$).

Remarks. The presence of spines on the whole vesicle regularly organized in crowns and longitudinal rows warrants the inclusion in the genus *Nevadachitina*. The studied material differs from *Nevadachitina praevininica* Soufiane and Achab, 2000b, and *N. vininica* Soufiane and Achab, 2000b, from the Hanson Creek (upper Katian, *Dic. ornatus* GBz) and uppermost Vinini (Hirnantian, *M. extraordinarius* and *M. persculptus* GBz) formations, respectively (Nevada, USA). *Nevadachitina soufianei* n. sp. has a vesicle and/or chamber more conical than ovoid, more crowns and rows of spines, and rare bifurcated spines. The specimens of our population also are usually longer and always wider than the specimens of *N. praevininica* and *N. vininica.* These differences justify erection of a new species. The number of crowns and longitudinal rows of spines of the specimens in our population, as well as their dimensions, partially overlaps with those attributed to *Nevadachitina* sp. Soufiane and Achab, 2000b, from the lower part of the Vinini Formation. However, in the latter, most of the spines seem shorter (no measure provided), the number of crowns and longitudinal rows are mostly inferred by the scars of broken spines, and spines with bifurcated tips were not observed. Those distinct characteristics may be either a result of taphonomical processes or morphological differences between two species. Given this uncertainty, we do not synonymize our material with Soufiane and Achab's (2000b) specimens attributed to *Nevadachitina* sp.

Morphological lineages

Chitinozoans represent a fossil group with uncertain biological affinities, therefore it is challenging to recognize phylogenetic relationships and evolutionary lineages (Servais et al., 2013). To date, it has been impossible to perform a cladistic analysis for the entire group. The closest attempt was a cladogram of the Family Desmochitinidae by Paris et al. (1999).

In relatively continuous sedimentary sequences and with a high sampling resolution, the detailed study of chitinozoan assemblages may reveal species or morphotype lineages (Jenkins, 1970b; Jansonius and Jenkins, 1978). In such context, evolutionary lineages have been proposed for chitinozoans (e.g., Jenkins, 1969; Melchin and Legault, 1985; Vandenbroucke, 2008b). In other studies, more restricted terms have been used (e.g., the *Spinachitina* lineage of Vandenbroucke et al., 2009b). In essence, these lineages represent a succession of morphological features appearing in stratigraphical order that can be grouped into various species. Therefore, the documentation of these lineages may be a useful tool for constructing high-resolution biostratigraphical schemes such as those of graptolites (e.g., Štorch and Melchin, 2018).

Here, use of the term 'morphological lineages' is preferred, to avoid any implications concerning their paleobiological character. In this study of the chitinozoans of the MY-14-01 core, two morphological lineages are proposed (Fig. 14). Morphological lineage 1 includes four species: *Hercochitina edingerae* n. sp. (Fig. 14.1), *Hercochitina krafftae* n. sp. (Fig. 14.2), *Hercochitina tharpae* n. sp. (Fig. 14.3), and *Clathrochitina mangle* n. sp. (Fig. 14.4, 14.5). In this lineage, there is considerable variation in vesicle shape and ornamentation. The multirooted spines/processes on the margin are always present, but their abundance, length, and lateral distribution vary.

The lowest morphotype in morphological lineage 1 is *H. edingerae* n. sp., a species that usually has an elongated vesicle, ornamented with a few crests that commonly bifurcate towards the aperture, and that are continuous from margin to lip. In some samples stratigraphically above this occurrence (39.4 ft interval, 12 m), a morphotype with intermediate characters was identified as *H. krafftae* n. sp., with a vesicle that is usually more stout, has an inflated chamber, and numerous discontinuous crests and spines on the chamber that become smaller aperturalwards. Similar to those of *H. edingerae* n. sp., the crests commonly bifurcate towards the aperture and multirooted spines are present on the margin, even if shorter and less developed. From sample MY-565.8 ft to MY-506.4 ft (172.5–154.4 m), the highest records of *H. krafftae* n. sp. co-occur with *H. tharpae* n. sp., which displays continuous crests on the chamber and has a wide base. As is the case in the two previously mentioned *Hercochitina* species, the crests may bifurcate towards the aperture. But in contrast to *H. edingerae* n. sp. and *H. krafftae* n. sp., the multirooted spines on the margin of *H. tharpae* n. sp. are extended laterally, almost connecting with the other sets of spines, and they are longer than those in *H. krafftae* n. sp.

Stratigraphically above the highest occurrence of *H. tharpae* n. sp. (MY-487.0, 148.4 m), the lowest occurrence of *Clathrochitina mangle* n. sp. was identified in the sample MY-477.0 (145.4 m). This species has the characteristic features of its genus (conical chamber, crown of anastomosed processes on the margin) and the diagnostic feature of uncountable, mangrove-like processes on the margin. Another unique feature of *Cl. mangle* n. sp. is the diffuse longitudinal ornamentation on the chamber, present in most specimens occurring lower in the Maysville core (samples MY-477.0 ft to MY457.3 ft, 145.4–139.4 m), and gradually becoming less expressive and uncommon in the highest occurrences, where specimens of *Cl. mangle* n. sp. display a completely glabrous vesicle (most specimens of sample MY-447.4, 136.4 m) or randomly distributed granules on the chamber and neck (most specimens of sample MY-350.7, 106.9 m). While it may seem counterintuitive to consider genera of different chitinozoan families within the same lineage, the diffuse, phantom-like crests in the lowest occurrences of *Cl. mangle* n. sp. in this core provide a strong argument to link this species with *H. tharpae* n. sp.

Morphological lineage 2 includes three species: *Hercochitina andresenae* n. sp., *Belonechitina laciniata* n. sp., and *Hercochitina polygonia* n. sp. In this lineage, there are only slight changes in the vesicle shape, the ornamentation is short and discrete, and spines

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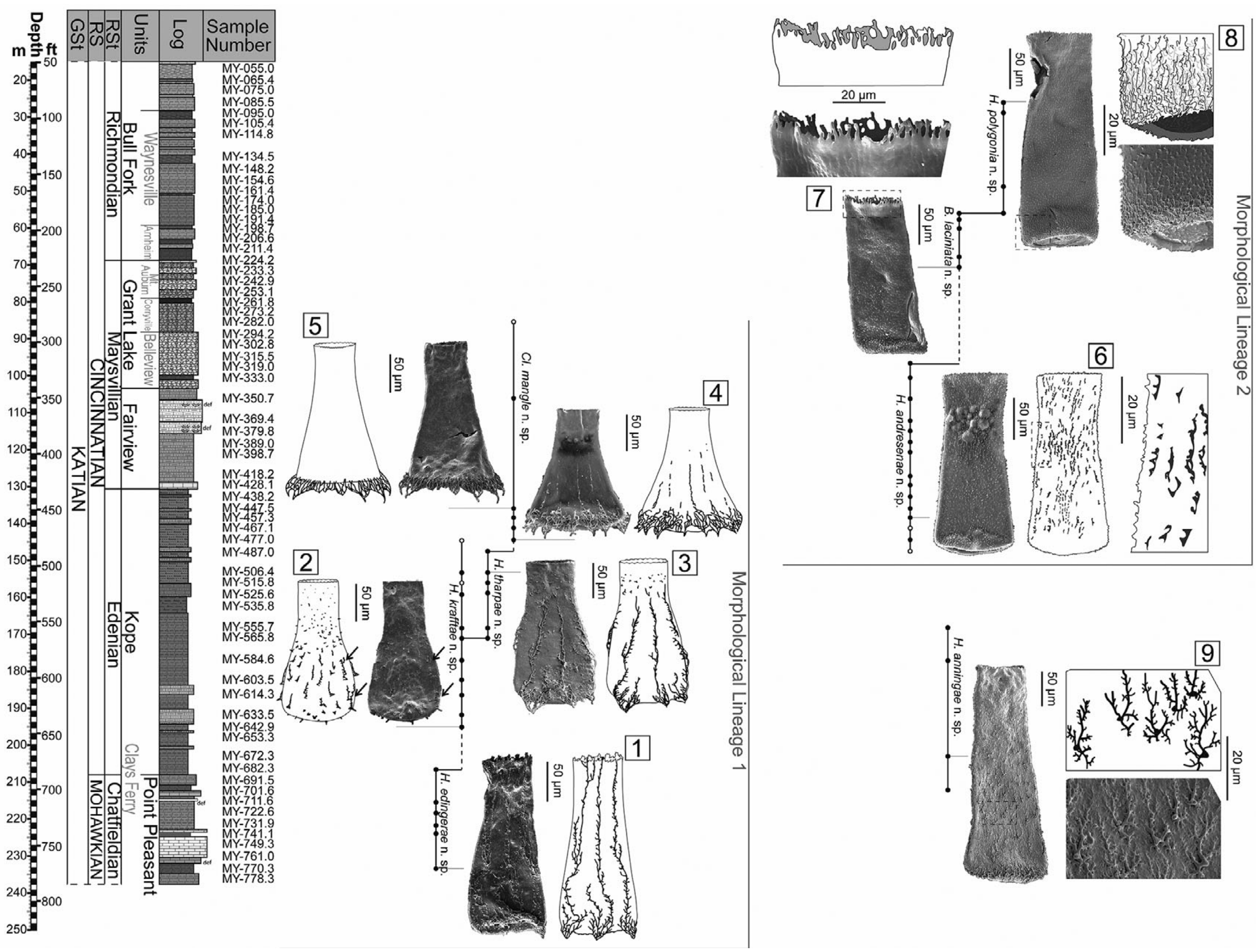

Figure 14. Morphological lineages 1 (**1–5**) and 2 (**6–8**), emphasizing the characteristic ornamentation of each species (original SEM images with the respective illustrations, slightly idealized, to better display the vesicle outlines and ornamentation details), and their stratigraphic ranges in the MY-14-01 core (Kentucky, USA). *Hercochitina anningae* n. sp. (**9**) is the only new *Hercochitina* species not included in one of the morphological lineages; however, it is added as additional information, to better illustrate its diagnostic ornamentation.

are always present, arising from the vesicle of *B. laciniata* n. sp. or from the crests of *H. andresenae* n. sp. and *H. polygonia*. n. sp. From sample MY-477.0 ft to MY-319.0 ft (145.4–97.2 m), the lowest elements of this lineage belong to *H. andresenae* n. sp., characterized by a conspicuous flexure and discontinuous but somewhat long, spiny crests that, when intensely perforated, may resemble lacework. In stratigraphically higher samples, *B. laciniata* n. sp. is first identified in sample MY233.0 ft (71.1 m). This species resembles the previous *Hercochitina* species due to its vesicles of similar size, and the bases of the spines can be elongated and aligned with the long axis of the vesicle, overall resembling the appearance of a species of *Hercochitina.* However, the spines never connect (i.e., crests are not formed), and *B. laciniata* n. sp. can be identified by its inconspicuous flexure and exceptionally ornamented lip. In the sample MY-185.0 ft (56.4 m), the highest occurrence of *B. laciniata* n. sp. is recorded in the sample with the lowest occurrence of *H. polygonia* n. sp. Although these species share similarities in vesicle size and shape and their ornamentation is quite short, *H. polygonia* n. sp. can be distinguished by its small crests connecting the short spines, thorn-like projections, and the polygonal-like mesh on the margin. Although it is not common that the same chitinozoan lineage includes species of different genera, there are similar precedents (e.g., in Jenkins, 1969, and Melchin and Legault, 1985): *Belonechitina robusta–Hercochitina spinetum–Hercochitina normalis.*

Conclusions

Katian chitinozoans are abundant, diverse, and well preserved in the Cincinnati region. Our systematic paleontology study of the chitinozoans in the MY-14-01 core identified 50 species: 12 are new, 17 were previously reported in Katian assemblages, and 21 were left in open nomenclature.

Several key chitinozoan species stand out in the MY-14-01 core in terms of their biostratigraphical potential, some of them used to define biozones in other parts of Laurentia (*Belonechitina duplicitas, Kalochitina multispinata, Sphaerochitina gracqui*? (Fig. 9.19), *Acanthochitina cancellata, Plectochitina spongiosa, Conochitina*? *pygmaea*) and Avalonia (*Acanthochitina latebrosa*). This is a robust starting point for establishing a chitinozoan biostratigraphic framework for the Cincinnati region in following studies; it will be a powerful tool for chronostratigraphic correlations, which are currently difficult due to the marked provincialism of the conodonts and graptolites, and a foundation for subsequent biochemostratigraphical studies. This future framework will also complement the existing Ordovician chitinozoan biozone scheme for North America.

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Competing interests. The authors declare none.

Data availability statement. Chitinozoan counts, measurements, and an alphabetical list of species and reference to their respective figures are available on Zenodo (https://doi.org/10.5281/zenodo.15633214).

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