CONULARIIDS FROM THE SILURIAN (LATE TELYCHIAN) WAUKESHA LAGERSTÄTTE, WISCONSIN

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The Silurian (late Telychian) Brandon Bridge Formation, Wisconsin, USA, **is renowned for hosting the Waukesha Konservat-Lagerstätte, in** which **several rare**, enigmatic constituents have received detailed taxonomic and taphonomic study**. However,** more common species **from this deposit** remain poorly **described**. This study provides the first systematic description of two conulariid species **documented** from the Waukesha Konservat-Lagerstätte—*Conularia niagarensis* and *Metaconularia* cf. *manni*—and assesses their general taphonomy and preservation within this deposit. Specimens were examined using a combination of light microscopy, scanning electron microscopy, and energy dispersive X-ray spectroscopy to assist in taxonomic, taphonomic, and compositional analyses. Conulariid specimens display an array of preservational modes, **primarily** diagenetic phosphatization **and** kerogenization, **with** minor associated pyritization. This **result** suggests a taphonomic **history involving** post-burial demineralization

associated with falling pH conditions, subsequent compression with minimal breakage, and **finally** diagenetic **mineralization** of the compressed **thecae by francolite**.

Keywords: Conulariid, Silurian, taxonomy, taphonomy, Waukesha, Lagerstätte

Introduction

Konservat-Lagerstätten represent sites of exceptional preservation containing fossils with non-biomineralized 'soft' tissues, offering a rare glimpse into ancient ecosystems and their biodiversity (Allison, 1988; Allison & Briggs, 1993; Schiffbauer & Laflamme, 2012). Such sites exhibit an uneven temporal distribution in conjunction with marked shifts in environmental conditions under which exceptional preservation may occur (Muscente *et al.*, 2017). Among the known Silurian Konservat-Lagerstätten from North America, the Waukesha Lagerstätte of the Brandon Bridge Formation is the most diverse assemblage, including representatives of the leperditicopids (Mikulic *et al.*, 1985a), phyllocarids (Jones *et al.*, 2015), synziphosurines (Moore *et al.*, 2005, 2011), thylacocephalans (Haug *et al.*, 2014), trilobites (Mikulic *et al.*, 1985a; Wendruff *et al.*, **2020a**), putative myriapods (Wendruff *et al.*, **2020a**), and a superficially scorpion-like arthropod (Wendruff *et al.*, 2020a, b, but see Anderson *et al.* 2021a). Other fossil groups that have not received formal taxonomic assessment include several annelids (polychaetes), brachiopods, mollusks, echinoderms, conulariids (Mikulic *et al.*, 1985a, b; **Van Iten, 1999;** Wendruff *et al.*, **2020a**), euconodontophylea (Smith *et al.*, 1987), graptolites (Kluessendorf, 1994), and nonbiomineralizing algae (LoDuca *et al.*, 2003). With the limelight **focused** on the exceptional soft-bodied taxa, the less remarkable biomineralizing taxa have been overlooked for systematic study and are often only briefly mentioned as a biotic component.

Preservational pathways observed in the Waukesha Lagerstätte assist in the description and characterization of organisms not usually seen in contemporaneous deposits. Initially it was thought that this site **might** be similar to Burgess Shale-type (BST) deposits**, in which fossils are typically preserved** as **two-dimensional** carbonaceous compressions with secondary pyritization, aluminosilicificaiton, and minor, often anatomically restricted phosphatization (Mikulic *et al.*, 1985a, Orr *et al.*, 1998; Gaines, 2014). **While also compressed, the** Waukesha Biota, however, are primarily preserved via phosphatization and kerogenization**, though some are also expressed as carbonaceous compressions** (Wendruff *et al.*, **2020a)**—at least **in** the case **of** the soft-bodied components (Mikulic *et al.*, 1985a, b; Kluessendorf & Mikulic, 1996; Moore *et al.*, 2005; Jones *et al.,* 2015; Wendruff *et al.*, **2020a**). However, like their taxonomy, **the preservational details of** the biomineralizing organisms at this site have received little focus, and further investigation into their taphonomic pathways is undoubtedly warranted. In part, taphonomic studies of the shelly constituents of the Waukesha **Biota** have been limited by their scarcity, as organisms typical of normal marine conditions (corals, bryozoans, brachiopods, mollusks, and echinoderms, among others) are rare or absent **within** the **deposit** (Wendruff *et al.*, **2020a**). When **present**, many benthic calcareous taxa in the Waukesha **Lagerstätte** show evidence of pervasive decalcification (e.g**.,** Mikulic *et al.*, 1985a), but the processes involved in demineralization of shelly taxa and (re)mineralization of both shelly and soft**-bodied** taxa in this deposit remain poorly documented.

Conulariids are a rare exception to the general trend observed in the biomineralized constituent of the Waukesha Biota in that they are relatively abundant within the assemblage, possess an originally phosphatic theca, and are predominantly sessile. Here, we provide the first formal systematic **treatment** of the two known species, *Conularia niagarensis* Hall, 1852 and *Metaconularia* cf. *manni* (Roy, 1935), in conjunction with a thorough investigation of the taphonomic features of these two taxa. The results of combined light microscopy, scanning electron microscopy, and energy dispersive X-ray spectroscopy**,** in combination with our assessment of biostratinomic processes, provide a framework to develop a taphonomic model specific to this taxonomic group in the context of the Waukesha **Lagerstätte**.

Material and methods

Material

This present study is based on examination of 39 crack-out conulariid specimens **housed in the invertebrate paleontology collection of** the University of Wisconsin-Madison Geology Museum (**specimen prefix UWGM). Of the specimens examined, only three represent part and counter-part pairs. UWGM 3042 and 4265 have respective pairs registered under the same catalogue number and are herein distinguished by stating 'CP' for the counter-part specimen after the catalog number. However, UWGM 3130 and 3172 represent a part and counterpart pair, respectively, and their numbers are retained for curatorial posterity. In instances where there is more than one specimen on a sample, a lower-case letter is used to distinguish between them and is included after the catalog number.** Specimens were photographed using **both a Nikon D600 camera attached to a Nikon SMZ1500 binocular microscope for photomicrographs and** a GIGAmacro Magnify2 Robotic Imaging System with Canon EOS Rebel T6i DSLR and Nikon T1 **1x** and **3x** objectives to acquire gigapixel resolution photomosaics. **Photomicrographs were processed with open-source software digiCamControl v. 2.1 (István, 2018) and images** were **prepared** and traced using Affinity Photo and Affinity Designer software (Serif Ltd., v.1.6.1.104).

Locality and geologic setting

The Silurian (Llandovery Series; late Telychian Stage) Waukesha Lagerstätte is found within the basal Brandon Bridge Formation of southeast Wisconsin, USA. In the Milwaukee area, the unit regionally wedges out overlying the southward-facing paleoslope of the Manistique Formation, below the predominantly dolomitized Waukesha Formation (Fig. 1A–C) (Mikulic, 1977; Mikulic *et al.*, 1985a, b; Kluessendorf, 1990; Kluessendorf & Mikulic, 1996; Kleffner et al., 2018). Exposures of the Lagerstätte-hosting unit are limited, with sampling having been constrained to two active quarries including the Waukesha Lime & Stone Co, quarry (43.03° N, 88.21° W) and the Franklin Aggregate Inc. Quarry (42.91° N, 87.99° W). However, since the fossiliferous units now sit either ~30 meters above the present-day quarry floor (former locality) or beneath overgrown rubble (latter locality), collection of new material is no longer possible (Pulsipher *et al.,* in press).

Karstification of the underlying Manistique Formation during periods of subaerial exposure created localized troughs and scallops on a paleoscarp surface along the intracratonic carbonate platform on the western edge of the Michigan Basin (Kluessendorf & Mikulic, 1996; Grathoff & Moore, 2002). Deposition of the Brandon Bridge Formation occurred within a peritidal setting during a subsequent transgression (Kluessendorf, 1990; Kluessendorf & Mikulic, 1996). The irregular karstified surface created anoxic sediment traps wherein organisms derived from the shallow shelf were deposited and preserved (Mikulic *et al.*, 1985a, b; Grathoff & Moore, 2002).

Fossil specimens described herein are mostly derived from a 12 cm-thick layer of thinly bedded, planar, light green to pink argillaceous dolomudstone, characteristic of the Brandon Bridge Formation, located approximately 2 m above the disconformity surface at the Waukesha Lime & Stone Co. quarry (Fig. 1C) (Mikulic *et al.*, 1985a, b; Smith *et al.*, 1987; Grathoff & Moore, 2002; Moore *et al.*, 2005; Haug *et al.*, 2014; Jones *et al.*, 2015; Wendruff *et al.*, **2020a**).

[Insert Fig. 1 here]

SEM and EDS analysis

Selected conulariid specimens (**UWGM 2754**, 2787ab, & 2825a) exhibiting a range of preservational modes were analyzed using scanning electron microscopy (SEM) and energy dispersive X-ray spectrometry (EDS) at the University of Missouri X-ray Microanalysis Core facility. SEM imaging was conducted using a Zeiss Sigma 500 VP scanning electron microscope with a beam accelerating voltage of 20 keV and current of 40 nA, an aperture size of 60 µm, and at a chamber vacuum of 20 Pa (chamber atmosphere = 99.999% nitrogen). Specimens were secured to the sample stage with copper foil tape, grounding the surface electrical charge to minimize charging during electron imaging (e.g., Orr *et al.*, 2002, 2009). Working distance varied because of sample thickness and topographic variation but was generally maintained at 16 mm ± 1 mm for all samples. All EDS analyses were conducted with dual Bruker energy dispersive x-ray spectrometers at operating conditions identical to **those for** SEM imaging, but with an aperture size of 120 µm to improve x-ray count rate (~150 kilocounts per second with both EDS detectors used in tandem). Large composite SEM imaging, using both backscattered (BSE; high-definition

5-segment backscatter detector) and secondary (SE; cascade current low-vacuum secondary detector) electron detection, was conducted using the ATLAS workflow (Fibics Inc.).

Systematic palaeontology

Terminology of conulariid characters principally follows that established by Sinclair (1952), Moore and Harrington (1956), and Van Iten *et al.* (1996). Attempts have been made to clarify the terminology used in the definition of conulariid features (Babcock & Feldmann, 1986ab; Brood, 1995; Van Iten *et al.*, 1996**);** however, some ambiguity remains and has changed to reflect the revised taxonomic placement of these organisms. **We** refer to the entire conulariid shell (mineralized and organic portions) as the *theca* and **distinguish between phosphatic and** organic **microlamellae when appropriate**. Terminology pertaining to ornamentation has been particularly convoluted in prior literature. Herein, we refer to **(i)** *nodes* (Babcock & Feldmann, 1986b; Babcock *et al.*, 1987; Brood, 1995; Van Iten *et al.*, 1996, **2006a, b**, 2008, 2013, 2014, 2016, 2018; Simões *et al.*, 2003; Van Iten & Südkamp, 2010; Lucas, 2012; Robson & Young, 2013; Ford *et al.*, 2016, Bruthansová & Van Iten, 2020) over 'papillae' (John *et al.*, 2010) or 'tubercles' (Slater, 1907; Fletcher, 1938; Hughes *et al.*, 2000; Mergl *et al.*, 2016); **(ii)** ***interspace ridges*** **and** ***interspace furrows*** **(Thomas, 1969; Van Iten** ***et al.*****, 1996, 2005, 2006a, 2013; Simões** ***et al.*****, 2003; Robson & Young, 2013; Ford** ***et al.*****, 2016; Mergl** ***et al.*****, 2016) over '**longitudinal **striae'** (Billings, 1866; McKee, 1935; Fletcher, 1938; Van Iten *et al.*, 1996, **2006a),** 'spines' (Babcock & Feldmann, 1986b; Babcock *et al.*, **1987b**; Ivantsov & Fedonkin, 2002; Van Iten *et al.*, 2008; Robson & Young, 2013; Mergl *et al.*, 2016**),** 'ridges' (Simões *et al.*, 2003; Van Iten *et al.*, 1996, 2005, **2006a**, 2008, 2013, 2014; Van Iten & Südkamp, 2010; Robson & Young, 2013**) or '**interridge' (Babcock & Feldmann, 1986b; Babcock *et al.*, **1987b**); and **(iii)** *transverse ribs*

(Thomas, 1969; Van Iten *et al.*, 1996, 2005, **2006a**, 2008, 2013, 2016; Simões *et al.*, 2003; Leme *et al.*, 2008; John *et al.*, 2010; Sendino *et al.*, 2011; Robson & Young, 2013; Ford *et al.*, 2016; Mergl *et al.*, 2016) over 'transverse rods' (Babcock & Feldmann, 1986b; Babcock *et al.*, **1987b**). In the case of the genus *Metaconularia* Foerste, 1928*,* ornamentation is arranged in regular transverse and vertical rows of nodes (John *et al.,* 2010). Paired midline lineations mark the position of two vertical internal septa. For additional details of the characters used herein refer to Mergl *et al.* 2016 fig. 2 and Simões *et al.* 2003 fig. 3. Note, in the systematic paleontology section below where original taxonomic diagnoses use **antiquated** or alternative terminology, we have provided the equivalent **but updated** term in brackets thereafter.

Phylum **Cnidaria** Hatschek, 1888
Subphylum **Medusozoa** Peterson, 1979
Class **Scyphozoa** Götte, 1887
Order **Conulariida** Miller and Gurley, 1896
Family **Conulariidae** Walcott, 1886

Genus ***Conularia*** Miller, *in* Sowerby 1821

Type species. *Conularia quadrisulcata* Miller in Sowerby, 1821 (TAB. CCLX, fig. 4)

Remarks: The genus *Conularia* was erected by Miller (*in* Sowerby, 1821) and originally included two new species: *Conularia quadrisulcata* (figs. 3–6) and *Conularia teres* (figs. 1–2). Sowerby designated *C. quadrisulcata* the genotype of *Conularia*, and *C. teres* was later redescribed as an orthocone nautiloid (Barrande, 1867).

Since the erection of the genus, the taxonomic history, specifically as it concerns the attribution of the genotype, has become a topic of much confusion and subject to several attempts of clarification (see Fletcher, 1938; Sinclair, 1940; Sendino & Darrel, 2009). In sum, the type specimen of the genus (Sowerby, 1821, pl. 260, fig. 4) was lost according to Sinclair (1940), though one of the remaining specimens from Sowerby's original publication figured as a syntype (Sowerby, 1821, pl. 260, fig. 3) remains in the collections of the British Natural History Museum (NHM 43843). This specimen, refigured by Sendino & Darrel (2009, fig. 3), had been previously reassigned to *Conularia subtilis* Salter (*in* Sedgwick & McCoy, 1855). Consequently, no physical specimen of the genotype remains and hence a lectotype needs to be assigned. Systematic revision of the genotype is **also** desperately needed, but outside the scope of the discussion here.

In lieu of the missing holotype, *Conularia niagarensis* Hall, 1852 has been suggested as representing a North American reference taxon as it is purported to bear close similarity to the original type species (Sinclair, 1940; Babcock & Feldmann, 1986b).

Conularia niagarensis Hall, 1852

(**Figures** 2**, 4–11**)

1843 *Conularia quadrisulcata* Hall: 110, pl. 40, fig. 2.

1852 *Conularia niagarensis* Hall: 294, pl. 65, fig. 1a–h.

1889 *Conularia niagarensis* **Hall;** Foerste: 286, pl. 5, fig. 16.

1890 *Conularia quichua* Ulrich *in* Steinmann & Doderlein: 343, figs. 395d–e.

1892 *Conularia quichua* Ulrich; Ulrich: 34-36, pl. 3, figs. 7a–b.

1893 *Conularia niagarensis* Foerste: 547, pl. 30, fig. 16.

1895 *Conularia quichua* Ulrich; Bernard: fig. 265C.

1897 *Conularia quichua* Ulrich?; Kayser: 288, pl. 11, figs. 1–2.

1901a *Conularia niagarensis* **Hall;** Grabau: 214, fig. 145.

1901b *Conularia niagarensis* **Hall;** Grabau: 214, fig. 145.

1904 *Conularia quichua* Ulrich; Reed: 248, pl. 30, figs. 10–10a.

1904 *Conularia* cf. *undulata* Conrad; sensu Reed:248–249, pl. 31, figs. 1-1a.

1905 *Conularia quichua* Ulrich; Thomas: 254–255, pl. 12, fig. 19.

1913 *Conularia quichua* Ulrich; Clarke: 163.

1920 *Conularia quichua* Ulrich; Douglas: 37-38, pl. 1, fig. 3.

1923 *Conularia niagarensis* **Hall;** Schwartz: 494, figs. 26 & 27.

1923 *Conularia quichua* Ulrich; Kozlowski: 69-70, pl. 7, fig. 6.

1925 *Conularia quichua* Ulrich; Reed:107.

1929 *Conularia quichua* Ulrich *in* Steinmann: figs. 21D-E.

1937 *Conularia quichua* Ulrich; Kiderlen: fig.10.

1939 *Conularia (Mesoconularia) quichua* Ulrich; Bouček: fig. 2e.

1948 *Mesoconularia quichua* Ulrich; Sinclair: 119.

1960 *Conularia quichua* Ahlfeld & Braniša: pl. 4, figs. 4, 10-10a.

1960 *Conularia* cf. *quichua* Ulrich; Ahlfeld & Braniša: pl. 4, fig. 9.

1962 *Conularia quichua* Ulrich; Hansman et al.: 21.

1962 *Conularia* cf. *undulata* Conrad; Hansman et al.: 21-22.

1965 *Conularia quichua* var. nov. Braniša: pl. 43, fig. 2.

1965 *Conularia* sp. B Braniša: pl. 43, fig. 5.

1965 *Conularia* sp. C Braniša: pl. 43, fig. 6.

1965 *Conularia quichua* Ulrich; Braniša: pl. 43, figs. 1, 3–4, pl. 45, figs. 2–4, 6–12.

1987a *Conularia quichua* Ulrich; Babcock et al: figs. 4E–M, 7A, table 1.

1987b *Conularia niagarensis* **Hall;** Babcock *et al.*: 219, fig. 5.

2003 *Conularia quichua* Ulrich; Simões *et al.*: figs 5–6.

2020 *Conularia niagarensis* **Hall;** Wendruff *et al.*: 7, fig. 6a.

Type specimens. *Conularia niagarensis* Hall, 1852 (AMNH 31625, lectotype), from an undefined **s**hale member, likely equivalent to the Rochester Shale (Silurian) in Lockport, Rochester, and Wolcott County; and "lower part of the limestone at **Rochester"** (Hall, 1852), Niagara County; New York, USA.

Original diagnosis. "Broad, pyramidal, tapering abruptly; angles with deep abrupt channels; center of each side with a shallow scarcely defined depression, which produces a more abrupt bending of the striae; transverse striae fine and closely arranged, directed from the angles obliquely to the center, where they are more abruptly bent in crossing the slight depression; striae papillose granulate, intermediate spaces marked by longitudinal striae, and grooves which alternate with the points upon the transverse striae." (Hall, 1852, p. 294).

Emended diagnosis. *Conularia niagarensis* is pyramidal, **tapering toward aperture;** corner **sulcus** deep **and no impression at midline**. Transverse ribs are fine, closely arranged and chevron-like; form obtuse angle pointed apertureward at midlines**;** cross faces without interruption or offset **and are deflected towards aperture at corner grooves**. Ribs marked by round nodes along their length; **interspaces** crossed by **ridges** extending perpendicularly toward apex from nodes. Node and **interspace ridge** pairs are slightly offset from pairs in preceding transverse ribs and interspaces.

Description. Two-dimensionally compressed specimens tapering from aperture to **apical region (Fig. 2A–C). Specimens** measure between 6–40 mm long (n = 39) and individual face widths measure between 3–**15 mm** (n = 39) at aperture. Faces are equal in width with apical angle of 20–29°. Corner **sulcus** defined by deep channels **(Fig. 2F)**; apex **missing, terminating in** blunt **margin due to breakage.** Aperture gently convex outward, often diffuse, **with** short apertural lappets **(Fig. 2A–C).**

Chevron-like transverse ribs form obtuse angles (113–161°) pointed apertureward and cross the faces **at inferred midline and corner sulcus uninterrupted; no bifurcation of ribs apparent (Fig. 2C, D, G, I). Larger specimens may show minor inflection of transverse rib adjacent to corner sulcus.** Angles vary longitudinally with smaller angles (113–130°) closer to the apex, becoming notably obtuse within the top ~10% of the theca (137–161°). Midline diverges **by 1–12%** from geometric longitudinal center of face**.** Ribs number **between 32–51** per **centimeter**, becoming densely spaced closest to the aperture.

Interspaces approximately 2–3 times the width of the transverse ribs**; crossed by prominent bar-like interspace ridges** (Fig. **2E**). Node and **interspace ridges** are offset from pairs in adjacent transverse ribs (Fig. **2E). The center line of the interspace furrows, which are about as wide as the interspace ridges, is marked by a very slender ridge that appears to originate from a node at its apertural end. Relief of the interspace ridges is best-defined in**

the middle to apertural region of the theca (Fig 2A, D, E), and is relatively subdued in the apical portion (Fig. 2G). Nodes are minute (0.03–0.1 mm diameter**, Fig. 2E, G, H) and** closely spaced, **ranging from 5–10** per **mm. Nodes are well-developed across the entire theca and best-**preserved along **the** corner **sulci (Fig. 2F);** often worn on faces (Fig. **2G).**

Studied material. **38** specimens in total**.** Figured and measured **(**UWGM **2655a,** 2754, **2755, 2787b, 2792,** 2825, 3021, 3042a**, b, d, e** [part **and** counterpart], **3054**, 3130 **[part] &** 3172 **[counterpart],** 3174, 3185, 3233, 3626, 3729, **4006**, 4265 [part and counterpart], 4638a**); only measured (UWGM 2655b 2787a, 3042c, f–h [part], 3053, 3804, 3966, 4011, 4638b–d); 26** are complete and 12 are incomplete.

Occurrence. Devonian: Belén, Icla and Sicasica formations of Bolivia (Emsian–?early Eifelian Stage); Bokkeveld Series of South Africa; Talacasto Formation, Argentina (Lochkovian–Pragian Stage); Ponta Grossa Formation, Brazil (Pragian-Emsian Stages); Zorritos Formation, Quebrada Zorritos, Chile; Paraguay and Peru. Early Silurian: Rochester Shale in the vicinity of Lockport (Niagara County), Rochester (Monroe County), and Wolcott (Wayne County), New York; Clinton Group, Todd's Fork in the vicinity of Wilmington, Ohio and "upper shalely courses" in Huffman's Quarry, Dayton, Ohio; Rochester Formation at Rose Hill east of Tonoloway (Calvert County), Maryland; late Llandovery Series (Telychian Stage): Brandon Bridge Formation (Waukesha County Wisconsin**;** this study).

Remarks. Since this taxon was originally erected by Hall (1852), *Conularia niagarensis* has received minimal in-depth systematic analysis in over 100 years. Occurrences of the species have been documented periodically, typically as a minor component or singletons within a more comprehensive faunal assessment of a specific locality (Foerste, 1889; Grabau & Letson, 1901a, b; Wendruff *et al*., **2020a**). Among the more recent contributions documenting *C. niagarensis* are a comprehensive reassessment of North American conulariids from the Devonian and Mississippian provided by Babcock and Feldmann (1986a). Therein, the authors note that *C. niagarensis* had been proposed as a North American reference species, *fide* Sinclair (1940), within the context of the genotype *Conularia quadrisulcata*, though the systematic implication of this statement is never discussed. In a separate revision of Devonian conulariids from Bolivia, Babcock *et al.* (**1987b**) reveal that only four of the five original *C. niagarensis* syntypes illustrated by Hall (1852) are known. In the absence of a designated holotype, the authors chose a new lectotype (AMNH 31625) based on the best-preserved material and imaged the specimen (Babcock *et al.*, **1987b**, fig. 5). The paucity of type material, documentation in the literature, and passage of several decades since its initial description warrant a detailed systematic revision.

The material described herein agrees with the original description of Hall (1852); however, the reporting of **biometric** characteristics such as the apical angle and the distribution of transverse ribs were not commonplace at the time of publication, hence much of our comparison relies on examination of the limited illustrated material (Hall, 1852, pl. 65, fig. 1a–h). The most diagnostic characteristics of *C. niagarensis* are the closely spaced, chevron-like transverse ribs, their nodose ornamentation, and alternating interspace **ridges. All** of these features are observed in the **specimen documented herein. Moreover, the range in apical angle of 22–25° recorded from** the refigured lectotype (Babcock *et al.*, **1987b**, fig. 5**) overlaps with** the Waukesha **Lagerstätte material**. Other occurrences of *C. niagarensis* include a single specimen from the Silurian of Ohio and a single specimen attributed from the Waukesha Lagerstätte of Wisconsin (Foerste, 1889, pl.

5, fig.16; Wendruff *et al.*, **2020a**, fig. 6B). Schwartz (1923) attributes a broken piece of the conulariid **theca** from a Silurian deposit in Maryland, to *C. niagarensis* based on the similarity in ornament (transverse ribs and nodes**);** however**,** the illustration appears only to show the alternation of the nodes and not the **interspace ridges** (Schwartz, 1923, p. 30, figs 26–27). All other accounts of the species in the synonyms above are based on Hall's specimens (incl. Grabau & Letson, 1901a, b), and prior to Babcock *et al.* **1987b** the species had not been illustrated with photographs.

Sinclair (1940) suggested that *C. niagarensis* bears a close resemblance to specimens of *Conularia quadrisulcata* from the Silurian (Wenlock Series) of England and should be considered a North American reference to the genotype. However, nomenclatural issues surrounding the genotype (see Sendino & Bochmann, 2021), **compounded** by the absence of lectotype or syntype specimens make comparison highly problematic. Slater (1907) provides the first documentation of the dimensions of *C. quadrisulcata*, stating specimens vary significantly in size (60–**200 mm** long) and ornamentation. Notably, this far exceeds the average length of the *C. niagarensis* specimens observed in this study (6–40 mm long). *C. quadrisulcata* has equal faces with an apical angle of 14° (compared to *C. niagarensis* with 20–28°) and 16–20 transverse ribs per cm which is far fewer than **the 45 ribs per cm** of *C. niagarensis*. The nodose transverse ribs are another trait that may indicate a close affinity between the two species, though the interarea of *C. quadrisulcata* is notably smooth and devoid of **interspace ridges** (Slater, 1907, pl. 3, figs. 2–6; Fig. 2), unlike that of *C. niagarensis*.

Comparable *Conularia* species which possess the diagnostic transverse ribs oriented in a chevron-like arrangement include ***C.*** *cancellata* Sandberger, 1847; ***C. formosa* Miller and Dyer, 1878;** ***C.*** *milwaukeensis* Cleland, 1911; ***C.*** *porcella* (Robson & Young, 2013); ***C. trentonensis***

Hall, 1847; *C.* *quichua* Ulrich *in* Steinmann and Döderiein, 1890; ***C.*** *rugosa* (Spencer, 1884); and *C. wilkinsi* (Spencer, 1884). **The number of shared traits among some of these species and their tendency to exhibit differential preservational pathways (i.e., compressed and non-compressed specimens) introduces potential for the erection of 'taphotaxa'. For instance, Simões *et al.* (2003) observed the variability of biometric (i.e., apical angle, distribution of transverse ribs and interspace) and morphological traits in *C. quichua* across a range of different taphonomic modes. The authors note that taphonomic artefacts can cause significant discrepancies between specimens of the same species and caution that conulariids should be assessed within the broader context of a taphonomic spectrum. However, this is often complicated by small sample sizes and limited taphonomic variability at any one site.**

Species most reminiscent of *C. niagarensis* are *C. formosa* reported from Middle–Late Ordovician limestones of Indiana, Ohio, Michigan, and Ontario (Richardson & Babcock, 2002), and *C. quichua* from Devonian strata in Bolivia and Brazil (Babcock et al. 1987b; Simões *et al*., 2003). Unfortunately, with the exception of the holotype, specimens of *C. formosa* have been reported from mostly isolated or incomplete specimens. Based on the original description and illustration of *C. formosa* (Miller and Dyer, 1878, fig. 12, 12a), both the Ordovician species and *C. niagraensis* are essentially identical in gross morphology and ornamentation. Notably the description by Miller and Dyer (1878) predates the inclusion of biometric data such as apical angle and distribution of transverse ribs and interspaces. Acid residues originally reported by Clark *et al.* (1999) contain exoskeleton fragments attributed to *C. formosa* that possess 5–7 transverse ribs per cm, and one interspace ridge and node per mm (Richardson & Babcock, 2002). Though these fall outside the range observed in the Waukesaha specimens, we would caution against comparing features based on exoskeleton

fragments alone. One compressed specimen from the Whitewater Formation (Upper Ordovician), Ohio (Richardson & Babcock, 2002, fig. 1.4), does retain morphological detail of the broader theca, with an apical angle of ~11° and obtuse angles between 120–127° for the transverse ribs. Given the broad overlap in characteristics, we consider *C. formosa* as closely related to *C. niagarensis*. We are cautious to assign synonymy, however, given the limited material from which to make an informed assessment.

***Conularia quichua* from the Middle Devonian has previously been noted to share several traits with *C. niagarensis.* Babcock *et al.* (1987b) provided a thorough synthesis of the similarities between the two species based on material derived from the early Devonian Icla, Belén, and Sicasica formations in Bolivia. The Waukesha Lagerstätte specimens support these observations. *Conularia quichua* is a larger species, up to 290 mm in length, as opposed to the maximum of ~40 mm in *C. niagarensis* from the Waukesha Lagerstätte. The Bolivian species exhibits a smaller apical angle (between ~11–24°) and looser packing of transverse ribs (21–32 per cm) compared to the North American species (20–28° and 32–51 ribs per cm, respectively), though this could be due to taphonomic processes. The most obvious similarity is the ornament, with both taxa displaying chevron-like transverse ribs that are more bell-shaped towards the apical and adapertural portions of the theca respectively (Babcock *et al.*, 1987b, fig. 4a–e; Fig. 2). It has been suggested that these two taxa were closely related (Babcock *et al.*, 1987b), though the Waukesha Lagerstätte material exhibits a greater degree of variation as seen by the distribution of the ribs and nodes. Simões *et al.* (2003) document *C. quichua* from the Devonian (Pragian-Emsian Stages) Ponta Grossa Formation in Brazil and suggest that *C. niagarensis* represents a taphomorph of the former species. Akin to the Bolivian material, there is little to distinguish the specimens documented herein from the**

Brazilian species besides the apical angle (as noted by Babcock *et al.*, 1987b), which has likely been altered due to compressional flattening. Considering the close resemblance between these species, the most parsimonious approach would be to assign these as synonyms, with priority given to the senior North American species, *C. niagarensis*.

Conularia cancellata was erected by Sandberger, 1847 to distinguish specimens described from the Silurian (Wenlock Series) of England from others attributed to *C. quadrisulcata* from the Carboniferous. However, as noted by Sendino & Bochmann (2021), who attempted to resolve the problematic taxonomy of the genotype, *C. cancellata* species has been attributed to several conulariid forms, principally those with **interspace ridges** possessing a cancellate grid-like pattern, despite variations in other characteristic features. The tumultuous history of the taxonomic literature surrounding this species (and possible synonymies with the genotype) are summarized therein (Sendino & Bochmann, 2021; see fig. 9) and emphasize the need for revision of these cancellate forms.

Limited comparison is afforded with *C. niagarensis* by a specimen attributed to *C.* aff. *cancellata* from the Upper Ordovician Macrourus Limestone in northeast Germany. This specimen is closely comparable with *C. niagarensis*, based on the overlap in size, asymmetry in the position of the midline, and most notably the shared chevron transverse ribs ornamented with nodes connected by **interspace ridges** (Sendino & Bochmann, 2021, figs 6, 7). However, *C.* aff. *cancellata* exhibits an apical angle (12–16) below the range of *C. niagarensis*. and the midline is also offset to a greater extent in the former (one third of the face width). Moreover, there is only minimal discrepancy in the angle and spacing of transverse ribs between the middle and apertural portion in *C.* aff. *cancellata* (Sendino & Bochmann, 2021, fig 6b), with more obtuse angles in the midsection. This is distinct from *C. niagarensis* where the adapertural portion possesses ribs with more obtuse angles, and are **additionally** very closely spaced, to the point it can be difficult to distinguish them.

Conularia milwaukeensis from the Lindwurm Member of the Middle Devonian (Givetian Stage) Milwaukee Formation of southeastern Wisconsin exhibits characteristic chevron-like ribs close to the apex (within ~10mm). However, this ornament is not consistent across the specimen, instead forming low asymmetrical curves across much of the faces (Van Iten *et al*., **2006a**, fig. 1.1). In addition, the transverse ribs are more closely spaced in *C. milwaukeensis* (80–90 ribs per cm) as opposed to the **Silurian** specimens (on average 45 ribs per cm). As for *Conularia porcella* from the Upper Ordovician (middle Katian Stage) Cat Head Member of the Red River Formation, Canada, this species can be distinguished by a significantly narrower (12–17º) and distinctly pointed terminal apex (Robson & Young, 2013, figs 2.1–2.2) compared to the broader (20–28°) blunt apex of *C. niagarensis*. Furthermore, *C. porcella* has far fewer transverse ribs (17–27 per cm) and nodes (4 per mm) compared to *C. niagarensis*.

Conularia trentonensis **from the Trenton limestone at Middleville, Jacksonburgh, Trenton Falls, and other locations were documented to share some similarities with *C. formosa* (Miller and Dyer, 1878). The main difference was the presence of nodes along the surface of the transverse ribs, even in samples showing minimal taphonomic alteration. Notably, *C. trentonensis* is also reported to have an impressed midline that is absent in *C. niagarensis*. However, this latter feature not evident from the specimen illustrated by Van Iten *et al.* (1996, pl. 1, fig. 2, pl. 3, fig. 1) which lacks such a depression. Based on *C. trentonensis* specimens from the upper Ordovician, Maquoketa Formation (Elgin Member), several features are comparable with *C. niagarensis*. For instance, in both species, transverse ribs are deflected aperturally before the corner sulci and are confluent across the corners.**

Only minor differences in biometric features are observed, with *C. trentonensis* recording an apical angle of 15–25°, 20–50 ribs per cm, and 4–9 nodes per mm. This partially overlaps with the range of features observed in *C. niagarensis*: apical angle of 20–29°, 32–51 ribs per cm, and 5–10 nodes per mm. Though these species share a close overlap in biometric features, they can be distinguished by shape of their transverse ribs. On the one hand, *C. trentonensis* specimens exhibit a distinct angle at the midline (145–162°) with transverse ribs roughly straight up until the slight deflection at the corner sulci. On the other hand, specimens of *C. niagarensis* documented herein exhibit a gentle curvature in the transverse ribs (Fig. 2A–C) and the angle at the midline (113–161°) is not as pronounced. Nevertheless, these two species appear to be closely related.

Spencer (1884) reported several Silurian *Conularia* species derived from the Niagara Limestone, in the vicinity of Hamilton, Ontario. Among these, ***C.** magnifica* (Spencer, 1879; see Spencer, 1884) was distinguished from *C. niagarensis* based on the following traits: the significant difference in size (240 mm length compared to 6–40 mm in *C. niagarensis*); the closer spacing of the transverse ribs and **interspace ridges**; the lack of the chevron-like ornamentation; deeper corner **sulcus**; and some distinction between the depth of the space between the **interspace ridges** (Spencer, 1884, pl. 9, fig. 1 & figs. 1a–b; Fig. 2). Each of these observations justified the separation between *C. magnifica* and *C. niagarensis* and conforms with our analysis that the Waukesha **Lagerstätte** material belongs to the latter species. In the same report, Spencer (1884) described one incomplete specimen of ***C.** rugosa* from an internal cast from the same stratigraphic interval as *C. magnifica.* The fragment is 130 mm long and 50 mm wide, and hence notably larger than *C. niagarensis*. In addition, this species has far fewer transverse ribs per cm than the **Silurian** specimens (10 ribs per cm as opposed to 45 ribs per cm). Based on the illustration provided, however, *C. rugosa* bears chevron-like transverse ribs comparable to those of *C. niagarensis* (Spencer, 1884, pl. 8–9, fig. 2; Fig. 2) in conjunction with alternating **interspace ridges** (Spencer, 1884, pl. 8–9, fig. 2a). The last species from this locality is ***C.** wilkinsi*, measuring 20–30 mm long with 30–40 transverse ribs per cm, which is comparable to *C. niagarensis*. Unfortunately, *C. wilkinsi* was erected based on one incomplete specimen (Spencer, 1884, pl. 9, fig. 3), and has not been documented since. Given the similarities between these taxa, it is likely that they may be synonymous. However, without direct observation of the specimen and additional material we cannot make any conclusions regarding the relation of *C. wilkinsi* to *C. niagarensis*.

[Insert Fig. 2 here]

Genus ***Metaconularia*** Foerste, 1928

Type species. *Conularia aspersa* Lindström, 1884 from the Silurian (Wenlock Series), Vattenfallet, Visby, Gotland.

Diagnosis. "Midlines flanked by paired internal septae, often expressed as paired ridges or lineations flanking midline on the external surface. Periderm pliable, generally less than 0.1 mm thick, and covered in rows and columns of small (<0.25 mm diameter), rounded, equant papillae." (John *et al.*, 2010**, p. 9**)

Metaconularia* cf. *manni (Roy, 1935)

(Figure 3A–C)

Description. Single incomplete, two-dimensionally compressed specimen missing apical region and aperture (Fig. 3A). Specimen large for the Waukesha **Lagerstätte, measuring 24 mm in** length and 17 mm **wide across the** two **exposed** faces**.** Estimated complete length and width measure 40 mm long from apex to aperture and 25 mm wide at aperture, with individual faces approximately 12 mm wide. Faces equal in width with an estimated apical angle of 16–21° (range given due to uncertainty). Pronounced paired midline lineations expressed as shallow rounded **depressions** (Fig. 3B). Rows of nodes arch evenly from corner to corner and continue across the midline **and corner sulcus** without interruption (Fig. 3C). Fine (0.03–0.07 mm diameter) rounded nodes organized in a grid-like pattern with 13–15 rows per mm and 11–16 columns per mm (Fig. 3C).

Material. One incomplete specimen; UWGM 2755 (Fig. 3A–C).

Occurrence. Lower Silurian, late Llandovery Series (Telychian Stage): Brandon Bridge Formation, Wisconsin.

Remarks. A single specimen (UWGM 2755) of this taxon was present within the material examined in this study. Previously, Wendruff *et al.* (2020, fig. 6a) reported and figured the counterpart of this specimen (UWGM 2448) and attributed it to *Metaconularia* cf. *manni*, though no systematic discussion accompanied this placement and hence is provided herein. Though specimen UWGM 2755 is incomplete and exhibits primarily moldic preservation it is possible to assess several taxonomic features. For instance, **this** sample **does share** traits with the Silurian species *Metaconularia manni* (Roy, 1935**), originally** described from the Early Upper Silurian (Gorstian Stage) Lockport Formation (Lechthaylus shale) Blue Island, IL, and Lower Silurian (Wenlock Series), Scotch Grove Formation, Shaffton Quarry, IA (John *et al.,* 2010). A key similarity is the apically convex **crosshatch** rows and columns composed of closely spaced nodes (John *et al*., 2010, fig. 23.3; Fig. 3C). In our specimen, the nodes and lineations are expressed as depressions and hence, less conspicuous (Fig. 3C). Our specimen has 13–15 rows per mm, 11–16 columns per mm, and nodes measure 0.03–0.06 mm in diameter. This is comparable to *M. manni* which measures 9–11 rows per mm, 13–15 columns per mm, and a node diameter of 0.03–0.07 mm. Given the incomplete nature of our material, ornamentation serves as the most diagnostic feature for identification. The apical angle of *Metaconularia* cf. *manni*, based on **part and counterpart** is **between 16–21**° (Wendruff *et al*., **2020a**, fig. 6a**); however, this** does not fall within the known range of *Metaconularia manni* between 35–42° (Roy, 1935; John *et al*., 2010). **Hence** our attribution of the specimen documented here remains tentative.

Other possible affinities for the specimen include *Metaconularia perglabra* (Ruedemann, 1925), an Upper Silurian species from North Buffalo, NY. This species has similarly been described based on a poorly preserved specimen (John *et al*., 2010), though it bears some resemblance to *M.* cf. *manni*. *Metaconularia perglabra* measures 35–50 mm in length with an apical angle of 15°, comparable to the Waukesha **Lagerstätte** specimen, which measures approximately 40 mm long with an estimated apical angle of 16–21°. The paired midline lineations of *M. perglabra* also bear some similarly to those of *M.* cf. *manni* (John *et al*., 2010, fig. 20.1; Fig. 3A). However, most of the ornamentation of *M. perglabra* has been lost due to the poor preservation of the specimen, which **hinders** further comparison. Given the limited sample size and poor preservation of *M. perglabra* we cannot make any additional conclusions regarding the relationship between this species and the material **herein**.

Metaconularia multipuncta (Ringueberg, 1886), a Lower Silurian species from the Niagara Shale of Rockport, NY, is also worthy of comparison given several shared features with the specimen documented herein. *M. multipuncta* is small (17–18 mm long and 10 mm wide) with an apical angle of 30° and closely spaced nodes that arch across each face convex toward the apex. Ornamentation of the Rockport species is characterized by a nodose **crosshatch** pattern, with the range of columns per mm overlapping that of the Waukesha **Lagerstätte** specimen, though the concentration of rows is not as closely spaced (only 8 per mm). Both species also share a pair of ridges flanking the midline of each face (John *et al.*, 2010, fig. 29 1–3; Fig. 3A). However, the Rockport species is based on a single specimen that is poorly preserved, providing little additional information for proper systematic comparison.

[Insert Fig. 3 here]

Results

Light microscopy

Conulariid specimens exhibit a spectrum along which the quality of preservation progresses observationally from a recrystallized phosphatic **theca** to carbonaceous films and kerogen patches. Many specimens also exhibit moldic impressions of the external ornament in the marl matrix of the host rock (**Figs 3;** 4A–C**; 5A–C**). Approximately 30% of the conulariid specimens exhibit dominant patches of white to blue-white phosphatic material preserved as francolite with little to no secondary mineral overgrowth (**Figs 2A–C;** 4A–**B**). Roughly 20% have visible kerogenization with or without fragments of the phosphatic **theca** overlying or underlying the carbonaceous material (**Figs 4C; 6A–F, I**). Conulariid specimens that are preserved as impressions and exhibit little to no phosphatic material (**Figs 4D; 5; 6G, H**) are prevalent in the Waukesha **Lagerstätte**, comprising ~50% of the observed fossil samples.

[Insert Fig. 4 here]

It is important to note however, that the specimens herein often lack counterparts and that the presence of phosphatic material on any one specimen may relate to the mechanical fracturing of the rock, as observed in other Waukesha **Lagerstätte** samples. That is, whilst one part may preserve patches of phosphate, the opposing counterpart may only exhibit kerogenized films and/or moldic impressions of exterior ornament (compare to Anderson *et al.*, 2021a, fig. 1d–e, f–g). This is evident in select conulariid specimens, where the negative impressions of external ornament preserve phosphatic material in the transverse ribs and nodes (Figs **4C ; 6A, B**). In other specimens however, including those for which both part and counterpart exist (e.g., UWGM **3042 [Fig. 4D] and** UWGM 4265 **[Fig. 6G, H]**), there is evidence that **minimal or** no phosphatic material remained suggesting true taphonomic **or diagenetic processes** could have occurred (i.e., dissolution).

Fidelity of the external ornamentation across the face surfaces, including transverse ribs and nodes, is retained across most of the specimens. Some specimens preserve clearly discernible features with topographic relief characteristic of the phosphatic **theca** (e.g., **Figs 2C**; 4A**, B**), while others lacking a mineralized **theca** preserve ornament as external molds (**Figs 3A; 4D, E; 5**). There is evidence in some specimens that the conulariid theca was partially infilled with sediment prior to compaction, as demonstrated by specimens where part of the infill has been removed displaying the external mold from the opposing faces of the theca **(e.g. Fig. 2A)**. In specimens that lack a phosphatic **theca** and show little to no evidence of sediment infilling, the transverse ribs often appear to overlay those of the opposing side of the conulariid (**Fig. 5A, B**). Compressional offset is also observed along transverse ribs and corner **sulci** between two flattened faces, wherein the overlying corner **sulcus** expressed as negative topographic relief can be distinguished from the underlying **sulcus, which shows** positive relief (**Fig. 5A, C).**

[Insert Fig. 5 here]

Optically, kerogenization of the conulariid specimens is easily differentiated from the surrounding matrix due to the areas of darker coloration (Fig. **6A**–F). In rare cases, kerogenized patches and thin films appear outside the confines of the **theca** (Fig. **6G, H**). Upon investigation of the sedimentary laminae, the clotted textures appear to occur on a surface above the conulariid specimen, indicating the presence of an overlying microbial film and associated decay halo. The general appearance of the kerogen in these specimens ranges from dark (almost black) solid patches to diffuse light brown patches (**Fig. 6A–G**) and can preserve fine details of the external ornament. Kerogenization replicating the external ornament is typically associated with the topographically raised features of the **theca**, such as transverse ribs, nodes, and marginal corners bracketing the corner **sulcus**, though there is a large degree of variability between and within individual specimens.

[[Insert **Fig. 6** here]

SEM-EDS

Compositional BSE imaging via SEM can further distinguish phosphatic material and carbonaceous films from the host rock (**Figs 7A**–C). The brightest material **corresponds to relatively higher atomic number elements, here representing** the phosphatic **theca** of the conulariid**,** as **contrasted with** the **relatively darker and lower atomic number** material representing carbonaceous films **(Fig. 7B**, C). Residual phosphatic material in well-preserved specimens is often present within the impressions of transverse ribs left in the host clay matrix where much of the **theca** is no longer present (Figs **7B**, C; **8F**). Notably, not all regions of dark staining observed under light microscopy were readily visible in BSE imaging (compare Figs **2A and 7B, C), plausibly resulting from diffuse, interstitial carbonaceous material.**

[Insert Fig. **7** here]

EDS analysis of conulariid samples show that the host rock is composed of high concentrations of Si and Al in addition to K, Mg, Na, and Fe, matching the composition of clay minerals and quartzose silt grains as documented previously (Jones *et al.*, 2015; Anderson *et al.* 2021a; Figs **7F, K; 8B**, D**,** E**; 9D,** F, **G**). The carbonaceous film, indicated by a dark patch on the organism where the **mineralized portion of the theca** is absent, has a similar elemental composition to the matrix with the addition of a carbon signal (Figs **7E**, J; **8C; 9E**). As with BSE imaging, only relatively robust carbonaceous films return a carbon signal with EDS (compare to Lieberman *et al.* 2017; Anderson *et al.,* 2021a).

[Insert Fig. 8 here]

The conulariid **theca** shows enhanced P and Ca signals in conjunction with a weak S signal (Figs **7G,** H, L**,** M; **8B**, F, H**,** I; **9D**, H, J), and correspondingly exhibits spatial lows in Al, K, Si, Mg, Na, and Fe (Figs **7F**, K; **8B**, D**,** E, G; **9D**, F**, G**). Combined BSE and EDS analysis show overlap of localized Fe and S signals in specimens UWGM 2825 (Fig. **8G**, H**) and** UWGM 2787b (Fig. 9I) indicative of disseminated pyrite framboids and crystals. The distribution of pyrite is particularly evident in association with an overlapping specimen of *Parioscorpio venator* Wendruff *et al.*, 2020a (Fig. 9A, I).

[Insert Fig. 9 here]

Discussion

Conulariid fossils occur in abundance throughout the Waukesha Lagerstätte**: these occur as flattened theca** with low topographic relief (Fig. **7A) lying** parallel to bedding. Brittle fracture is **rare and occurs mostly** along the corner **sulci** (e.g.**,** Figs **5C; 6I), which may have concentrated compressive stresses.** Preservation of **the theca** is variable, **reflecting differences between the conulariids in** taphonomic pathways**.** Due to the circumstances of **collection (and perhaps also lithology), the material examined typically constitutes a single specimen preserved on individual slabs** with limited surrounding matrix**. Consequently,** most contextual information regarding **spatial** distribution and orientation **across the bedding plane** has been lost. **A single**

sample among the observed material preserves multiple conulariids **(n = 5) on the same slab;** positioned close together **but with apparently** random orientations **and no evidence of clustering** (Fig. 4D**, E). Together, the prone position and truncated apical ends typical of specimens—which in life were attached to** hard **biological substrates (e.g.,** Babcock & Feldmann, **1987b**; Van Iten, **1991a, b, 1996,** 2016**; Vinn *et al.*, 2019)—suggest that the conulariids underwent postmortem** transport**.**

Biostratinomy

Much like other records of the fauna from the Waukesha Lagerstätte (Mikulic *et al.*, 1985b; LoDuca *et al.*, 2003; Jones *et al.*, 2015; Wendruff *et al.*, **2020a, b**), none of the conulariids appear to be preserved *in situ* or attached to any surface. Neither are associated epibionts preserved attached to their conulariid hosts, despite the abundant evidence of their presence from holdfast scars (Fig. **2D**). It is reasonable to assume conulariids were transported to the anoxic sediment traps within the Brandon Bridge Formation from an adjacent environment. **Currents passing over these traps may have created localized eddies that served to capture material transported off the paleo-slope (Kluessendorf, 1994; Moore *et al.*, 2005; Jones *et al.*, 2015; Wendruff *et al.*, 2020a, b). This is consistent with the fact that conulariid specimens may be overlain by other soft-bodied organisms, as is the case in one such example involving *P. venator* (Fig. 9).**

Among the specimens examined herein, there is minimal to no evidence of damage caused by excessive transport (e.g., fragmentation or abrasion), as **indicated** by the preservation of fine ornament, including nodes, of the conulariid **theca. The** limited transportation **that** was involved prior to burial of the conulariids**, however, may** have been sufficient to dislodge attached epibionts, which might explain their pervasive absence in the fossil assemblage.

Preservation of conulariid soft-bodied tissues

Despite the exceptional preservation of numerous soft-bodied organisms within the Waukesha **Biota** (Mikulic *et al.*, 1985a, b; LoDuca *et al.*, 2003; Moore *et al.*, 2005, 2011; Haug *et al.*, 2014; Jones *et al.*, 2015; Wendruff *et al.*, **2020a, b**), features of conulariid soft tissues within the theca are apparently not preserved in any recognizable fashion **at this locality. The absence of such preserved soft tissues is likely** linked to a combination of biological attributes and taphonomic processes.

The **Waukesha Lagerstätte does capture soft tissues in other taxa, however. This differential soft-tissue taphonomy in organisms such as arthropods** and **polychaetes as compared to** the conulariids may be grounded in **histological distinctions between diploblastic and organ-grade, triploblastic organisms** (Van Iten *et al.*, 1996**, 2006b**; Hughes *et al.*, 2000; Ivantsov & Fedonkin, 2002; Van Iten & Südkamp, 2010; John *et al.*, 2010; Sendino *et al.*, 2011; Lucas, 2012; Ford *et al.*, 2016). **For example, in** recent decay experiments**,** Gibson *et al.* (2018) noted rapid and preferential loss of the most labile tissues, such as tentacles, **of diploblastic model organisms (i.e., *Condylactis gigantea*).** Similarly, Hancy and Antcliffe (2020) **concluded** that cnidarian tissues **(i.e., *Actinia equina*) showed substantial** decay relatively rapidly, within the 20-hour duration of the experiment, across a range of oxic, anoxic, and reducing conditions. Moreover, the fidelity of cnidarian preservation, particularly with respect to external features, appears to be closely tied to the timing of epidermis rupture and subsequent lithification, such that early rupturing is closely followed by the decay of the mesenteries and tentacles, as bacterial decay operates faster on external **and exposed** features than autolysis does on internal structures (Hancy & Antcliffe, 2020). Additionally, the rate of decay observed in external features such as the tentacles is impacted by their relative position postmortem. For instance, tentacles retracted within the ectodermal collar **decay at** a **rate** similar to other internal tissues, whereas if extended, they begin to decay very early. Though anoxic conditions slowed decay by approximately two hours compared to oxic conditions, diagnostic features such as the tentacles, hypostome, and mesenteries **became** unrecognizable within 24 hours (Hancy & Antcliffe, 2020).

Altogether, the inferred **biostratinomic and** taphonomic processes in the Waukesha **Lagerstätte** that preceded **final** deposition of the conulariid specimens (e.g., minor transportation) **do** not conform with immediate burial upon the death of the organism. Hence, the taphonomic pathways experienced by the Waukesha **Lagerstätte** conulariids were not conducive to the preservation of cnidarian-grade external soft tissues based on information **obtained** from decay experiments, regardless of purported oxygen levels or **the presence of** microbial entombment (Wendruff *et al*., **2020a**).

It is worth noting that the presence of **relict** conulariid soft **parts** remains highly speculative, with the few reports identifying enigmatic structures. X-rays of pyritized specimens from the Hunsrück Slate were said to exhibit ambiguous internalized structures (Van Iten **& Südkamp, 2010**). Babcock and Feldmann (1986c) identified tubular structures with a 'contracted mass' replaced by iron oxide in the interior portion of up to eight specimens of *Paraconularia subulata* (Hall, 1858). The authors suggested these features may represent internal organs, though these specimens warrant further examination to determine whether these structures are truly representative of original soft tissues or are instead a taphonomic artefact.

While conulariids **of the Waukesha Lagerstätte** do not preserve soft **parts such as circumoral tentacles, they do** exhibit **variation in the location of** kerogenized patches and carbon films within the **outlines** of the **theca**. These kerogenized patches could have been derived from decayed organic material of the conulariid **theca**, internal soft tissues, or microbial films. For the most part, specimens **show** no discernable pattern in the distribution of kerogenized patches, and those that do constitute only a small **percentage of the total** number of **conulariids examined**. For instance, specimen UWGM 3174 (Fig. **6A**) shows a clear patch of mottled carbonaceous material in the **apertural half** of the **theca** separated from a more distinct solid patch in the **apical half**. There are also **a few** specimens that have circular to ovoid **'windows'** of no carbonaceous material close to the corner **sulcus** along the length of the specimens (Fig. **6A**, D–F). **The origin of the 'windows' remains unclear, possibly related to differential soft-tissue preservation within the theca that could undergo kerogenization. Alternatively,** conulariids are known to possess an internalized **septum**-like feature, known as a schott, which manifests as a thin, convex, transverse wall **at** the end of **a truncated theca.** It is possible that such a feature might have restricted degradation to the upper portion of the **theca, serving as a barrier to keep degrading soft tissue or microbes out of the lower portions of the theca. Breakage** of this feature postmortem may have allowed organic material to infiltrate the rest of the conulariid. However, the **lack of preservation** of such a **schott** or any compressional anomalies associated with it in *C. niagarensis* or *M.* cf. *manni* seems to contradict this suggestion.

Outside the 'windows', the origin for the kerogen of carbonaceous materials could vary in source. Adaperturally, amorphous, decayed soft-bodied tissue could contribute to kerogenization, while adapically, the closing angles of the faces, and the closer proximity of the thickened **theca** associated with the corner **sulci** (Van Iten, 1992) would provide greater amounts of organic material in the phosphatized lamellae (Van Iten *et al.*, 1992; Muscente & Xiao, 2015b; Ford *et al.,* 2016) and **theca** for kerogenization. More typically, the internal soft-bodied matter may have spilled into the whole internal cavity of the **theca**, or decayed entirely, preventing the preservation of such **'windows' (Figs 2B, C; 6B,** C, G–I)

EDS analysis corroborates that kerogenized patches are likely to have been sourced from the conulariid itself and not solely from the microbial mats which are pervasive in the deposit. For instance, the weak carbon signal observed in association with the conulariid is likely residual organics from the theca (Figs **7J; 8C**). The comparatively depleted carbon signal in the host rock seems to suggest that microbial activity was limited, and rather than representing a thick mat was instead a thin film (Figs **7E**, J; **8C**). The only instance with strong evidence for the influence of microbial mats on the preservation of carbonaceous material is seen in **part and** counterpart **specimens UWGM 4265, exhibiting** blotchy patches of material just outside the vicinity of the conulariid **theca** (Fig. **6G, H**). Establishing whether this was microbially induced or the result of decayed organic matter escaping during the compression of the organism is difficult to determine through optical and electron microscopy.

We identified two other instances where EDS analysis revealed carbon signals that were not directly associated with the conulariids. One conulariid specimen (UWGM 2787b, Fig. **9**) shows a strong carbon signal on the apical end of the specimen in association with overlapping remains of **the** soft-bodied arthropod, *P. venator*. In this case, the primary source of carbon **was likely the** *P. venator* **individual**, which also served to promote localized pyrite formation (Fig. **9I**, J), likely induced by the activity of sulfate reducing bacteria degrading the soft tissues.

Preservation of the conulariid theca and phosphate dissolution

SEM-EDS analyses **reveal** the carbonate-rich apatite **of the conulariid theca** (Van Iten, 1992a; Wendruff *et al*., **2020a**), though the presence of a weak sulfur signal across the **theca** indicates these specimens have subsequently been altered to francolite [$(Ca, Mg, Sr, Na)_{10}(PO_4, SO_4, CO_3)_6F_{2–3}$] during diagenesis. Moreover, conulariid specimens exhibit a clear taphonomic continuum, ranging from the preservation of a phosphatic **theca** to kerogenization without phosphatization, to full dissolution of the phosphatic **theca** without appreciable kerogen (Fig. 4A–**E**). The degree to which dissolution of the conulariid **theca** proceeds is controlled by **several interconnected factors, including:** i) the composition, microstructure, and thickness of the **theca;** and ii) the chemistry of **burial environment, including** the pH and **ionic strength of pore fluids and the** saturation levels **of calcium and phosphorus/phosphate (e.g.,** Muscente & Xiao, 2015b).

Theca thickness and microstructure play an important role in the extent of dissolution and quality of preservation observed in the shelly constituent of the Waukesha **Biota. However, due to the limited available material within the collection and inability to resample the original site, consumptive sampling was not permissible on the material examined, precluding certain preparation and analytical techniques.** Though we were unable to observe the microstructure of the Waukesha **Lagerstätte** conulariids **in thin section**, the genus *Conularia* is known to possess relatively thick **theca** by comparison to other genera, including *Metaconularia* (Brood, 1995). In *C. niagarensis*, ornamentation is best preserved at the **shoulders of the** corner **sulci** where the **theca** is thickest due to internalized carinae, thereby making it more resistant to demineralization (Figs **2B**, D, **F; 6C**–F, I) (Van Iten, 1992b; Brood, 1995). Even in specimens that are otherwise pervasively demineralized, the **shoulders of the** corner **sulci** may be topped with slivers of phosphate (Fig. **5C**). Transverse ribs and nodes provide areas of **theca** thickening and are frequently mineralized (Figs **2D–H; 8F**), whereas adjacent **interspaces** seem most prone to dissolution. The single specimen of *M.* cf. *manni* is pervasively demineralized, which thus precludes examination of the phosphatic **theca (Wendruff *et al.* 2020a, fig. 6A; Fig**. 3).

Transverse ornamentation and paired internal carinae are still recognizable via both kerogenization and external molds. Given that this genus is characterized by a thinner **theca** (Brood, 1995), it is plausible that *Metaconularia* specimens would be less likely to preserve the **theca** than *Conularia* specimens in the Waukesha **Lagerstätte**.

Ultrastructual organization of the conulariid **theca** revealed by HCl acid etching experiments in previous studies reveals alternating phosphate-rich and organic-rich lamellae, with the latter estimated to constitute more than 50% of the overall theca (Ford *et al.*, 2016). This predominance of organic material is not evident from EDS analyses of the conulariid **theca** surfaces herein, which reveal a relatively faint carbon signal (Figs **7E**, J; **8C**). Instead, the strongest carbon signal is preserved as kerogenized patches on or below the **theca. Differentiating** between residual carbon derived from the organic matrix of the **theca**, as opposed to the internal soft-bodied tissues**,** is difficult to confirm with confidence**. However**, the strength of the carbon signal **as well as the** distribution **and texture of remnant carbonaceous material** may provide some indication as to which is which. For instance, kerogenization replicating the **theca** ornament as light brown patches **appears** distinct from more randomly distributed mottled and solid darker patches which may represent poorly preserved soft-bodied material **(**e.g**., Fig. 6A**) or microbial films (e.g**.,** Fig. **6G, H**). That the light brown patches may represent residual organic carbon of the theca is corroborated by taphonomic experiments that were conducted on the organophosphatic **test** of *Sphenothallus* fossils from the Lower Cambrian of South China, which used a series of HCl solutions to replicate the process of demineralization (Muscente & Xiao, 2015b). Provided that kerogenization of the organic materials of the **test** preceded the loss of the biomineralized **portion**, removal via HCl treatments or (by analogy) diagenetic demineralization of the test still retained insoluble carbonaceous material (Muscente & Xiao, 2015b). Thicker kerogenized deposits associated with soft-bodied material or microbial mats could also be explained by relatively recalcitrant extracellular polymeric substances (EPS) associated with degrading microbes or the mats, respectively.

Taphonomic model

We propose a taphonomic model including pre- and post-burial processes based on the taphonomic continuum observed in conulariids from the Waukesha **Lagerstätte**. *Conularia niagarensis* was used for this model (Fig. 10A) to show the variations in orientation, demineralization, and kerogenization observed in the **38 conulariid** specimens used in this study.

The timing between the death and deposition of the organism is **challenging** to constrain in the specimens **observed herein**, though the lack of obvious abrasion and fragmentation seems to suggest relatively little transportation. Despite this, given that cnidarian tissues are known to preserve poorly in oxic and anoxic conditions on a timescale of only 24 hours (Hancy & Antcliffe, 2020), the conditions required to preserve non-biomineralized tissue would have to involve very rapid burial. Microbial decay of remaining soft tissues likely ensued soon after transportation and deposition.

Deposition of conulariids within the anoxic troughs of the quiet, restricted paleoscarp surface allowed for the development of microbial films which entombed individual specimens. As decay proceeded, **and while** the films were **still** tenuous, sediments may have partly infilled the theca, forming a relatively thin layer before final burial. In other specimens there is virtually no sediment infilling **(Figs 4C–E; 5),** potentially due to rapid sediment entombment prior to decay, or robust microbial films preventing sediment from entering the aperture. Extended exposure of the theca at the sediment surface likely promoted initial degradation of the organic lamellae of the

theca, thereby weakening the biomineralized portion of the organism. Organic acids produced by microbial films may also have lowered pH (e.g., Sagemann *et al*., 1999; Anderson *et al.*, 2021b). The extent of demineralization during this phase depends on pH conditions as well as phosphate concentration of the ambient water column and top layer of the sediment (Muscente & Xiao, 2015b). Given that most of the other calcified taxa within the Waukesha **Biota** also **experienced** extensive demineralization, we assume conditions were conducive to the dissolution of soluble biominerals such as calcite and phosphate, suggesting a localized reduction in pH (Wendruff *et al*., **2020a**).

Subsequently, during burial the theca collapsed in a rhombic fashion, flattening along two of the faces (Fig. 10B, C**). This style of preservation is comparable to other conulariid specimens exhibiting compressed thecae with articulated faces from the Ordovician Cat Head Member of the Red River Formation in southern Manitoba, Canada (Robson & Young, 2013) and the Silurian Welton Member, Scotch Grove Formation at Shaffton Quarry, Iowa (John *et al.*, 2010).** The flexible nature of the organic-rich microlamellar structure of *Conularia* is supported by the rare occurrence of breakage or fracture in the **theca** (Ford *et al.*, 2016). However, compression of the **theca** was likely influenced by partial demineralization prior to burial, and also very early in the taphonomic process**, during which the conulariids were buried under multiple sub-millimetric lamellae and microbial mats (Fig. 11A).** During this phase there is evidence to suggest protracted periods of sedimentation, as indicated by repeated sub-millimetric-scale laminae bounded by interlaminar partings, at least some of which are likely microbial mats (Fig. 11A). These do not show evidence of draping around a three-dimensional **theca** which collapsed later but appear to be of relatively even thickness. Thus, the **theca** likely collapsed, before it could be deeply buried.

Specimen UWGM 2792, a partially vertically oriented specimen, confirms the readily collapsible nature of the **theca during compaction (John *et al.*, 2010).** It shows vertical compression that is preserved across up to five laminae, with the apical portion transecting at least four laminae and the apertural portion on the uppermost lamina (Fig. 11B). This specimen also possesses a taphonomic gradient from the lower apical region to the apertural region, its phosphatic material gradually decreasing in abundance, presumably due to the prolonged exposure of the **theca** above the sediment water-interface (Fig. 11B).

[Insert Fig. 10-11 here]

Post-compression, the **theca underwent** taphonomic and diagenetic alterations along a continuum. In instances where the **theca** remains, it has been recrystallized to francolite as indicated by EDS analyses and the prevalence of sulfur throughout the **theca**. Though the relative thickness of the **theca** differs across specimens, it also appears to influence the preservation of carbonaceous films. For example, cross-sections of specimens with thicker or **clean** patches of recrystallized phosphate tend to exhibit darker and more robust kerogenous films (Fig. 10D). Such films are typically preserved on the external mold of the specimens (Fig. 10E, F), but in rare cases are found on the intervening sediment infill of the interior **theca** surface (Fig. 10D). Specimens that preserve an extremely thin layer of phosphate and a laminar layer of sediment infill display evidence of kerogenization on the external mold surface (Fig. 10E). These specimens may be linked to earlier dissolution in the pre-burial phase. Finally, in instances where the phosphatic theca is not preserved and sediment infill is lacking, the external mold shows kerogenization reduced to a brown carbonaceous film on the sediment (Fig. 10F). In **some** specimens, this later stage is artificially caused by mechanical breakage along the exterior surface of the preserved theca as seen in specimen UWGM 3130, where the sediment infill has been partly removed (Fig. 10E).

The observed taphonomic pathways of the Waukesha **Lagerstätte** conulariids may be compared to **those of** the organophosphatic tests of *Sphenothallus* from the lower Cambrian Shuijingtuo and Niutitang formations in the Hubei and Hunan provinces (respectively) of South China (Muscente & Xiao, 2015b). Complete demineralization of the South China *Sphenothallus* material **is manifested** as carbonaceous material with no mineralized test present. In comparison, pervasive demineralization of the conulariid **theca** leaves a carbonaceous impression or mold in the clay matrix (**Figs 3,** 4C–**E; 5A–C**). Partial demineralization of the South China *Sphenothallus* is described as compositionally intermediate between fully shelly and carbonaceous (Muscente & Xiao, 2015b). Most of our material resembles this description, with conulariids that retain some of their phosphatic **theca**, but which are primarily preserved as external molds in the host rock with carbonaceous films (e.g., Fig. **6A**).

Conclusions

Conularia *niagarensis* and ***Metaconularia*** cf. *manni* from the Silurian Waukesha Lagerstätte **(southeastern Wisconsin) underwent** a **complex** taphonomic **history, elements** of **which are shared with conulariids** from **other rock units and localities such as the Silurian Scotch Grove Formation of east-central Iowa. The Waukesha specimens variably exhibit** recrystallization of phosphatic **microlamellae**, kerogenization **of organic microlamellae, and complete** dissolution of the **phosphatic component. Mineralized microlamellae are** composed of carbonate apatite with **trace amounts of** sulfur, suggesting **alteration** to francolite. Prior to

final burial, the conulariids **underwent** limited transport**,** as **indicated** by **their alignment parallel to bedding,** the absence of the **apical attachment disc,** and the **apparent random trend of specimen orientations. Following final burial, the** soft tissues **of the conulariids** decayed rapidly, **unlike the** soft **parts of associated** arthropods and annelids**. This observation lends additional weight to** the **hypothesis** that the **soft parts of conulariids** were **similar in composition and** preservation **potential to those** of **extant cnidarians.**

Based on our findings, we propose a taphonomic model **involving a sequence of processes** similar to that demonstrated **for** other deposits preserving phosphatic shelly faunas (**John *et al.*, 2010; Robson & Young, 2013**; Muscente ***et al.***, **2019**). Following **transport** and deposition of the conulariids in anoxic sediment **traps, the organisms were partially entombed within** microbial films**, initiating bacterial** decay of the soft tissues. The **extent** of dissolution **of the phosphatic microlamellae was** controlled by the composition, microstructure, and thickness of the **theca** as well as **by** the chemistry of the **sediment pore water** and **water column**. Kerogenization may **have occurred concomitantly** with demineralization, leaving carbonaceous material on both the interior and**,** particularly**,** exterior surfaces **of the theca.**

Finally, our investigation adds to a growing body of literature across the geological **time scale documenting** the influence **on paleontology of both "minor" lagerstätten and taxa that have been relegated to relative obscurity for being problematic, or not as "showy" as some better-preserved or character-rich taxa. However, conulariids are one of the most abundant skeletonized components at the Waukesha Lagerstätte, and are common at many other deposits, too. The relative plentitude of conulariids also makes them good investigatory tools as to the taphonomy of organophosphatic skeletal components, as the spectrum of preservation at the Waukesha Lagerstätte demonstrates. It is our hope that**

this work will spark further interest in this group that still has much to contribute to paleobiology.

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Figure 1. Geologic setting of the Waukesha Lagerstätte. **A**. Map showing the approximate location of quarry sites of Waukesha Lagerstätte, WI (green circle). **B**. Uppermost Ordovician and lower Silurian stratigraphic column of southeast Wisconsin (after Wendruff *et al.*, 2020a, Reused from Pulsipher *et al.* in press). C. Idealized stratigraphic column of the Brandon Bridge Formation (after Kluessendorf, 1990, reused from Pulsipher *et al.* in press).

Figure 2. Light photomicrographs of *C. niagarensis* Hall, 1852 from the Silurian (Llandovery, Telychian) Waukesha Lagerstätte, Wisconsin. **A**. **UWGM 2754**. **B. UWGM 4006**. C. **UWGM 3021**. **D**. **Magnification of inset in A**, showing the geometry of several transverse ribs in the vicinity of the midline. **E**. **Magnification of inset in D showing details of external ornament. F**.

Magnification of corner sulcus and ornament (inset shown in B). G. Magnification of **nodes and reduced interspace ridges** in **apical half of the theca (inset shown in B). H. Nodes and** transverse ribs **preserved close to the aperture (inset shown in B). I**. Magnification of **inset** in C showing the geometry of the transverse ribs. White arrow indicates the corner **sulcus, UWGM 3021. H= holdfast scars, IR= interspace ridges;** TR = transverse rib; Nd = node; CG = corner sulcus. Scale bars = 2 mm (A–F); 1 mm (G–I).

Figure 3. *Metaconularia* cf. *manni* (Roy, 1935), UWGM 2755 **from the Silurian (Llandovery, Telychian) Waukesha Lagerstätte, Wisconsin**. White arrows indicate features of note. **A**. View of entire specimen, CG = corner grove. **B**. Magnification of boxed area in A; PML = paired midline lineations. **C**. Magnified view of boxed area in B, Nd = node. Scale bars = 2 mm (A); 1 mm (B); 0.5 mm (C).

Figure 4. Reflected-light images of *C. niagarensis* **demonstrating** key preservation styles. **Inset in A-C gives broader context of specimen in normal light. A. UWGM 2825 showing** a phosphatic **theca** and partial kerogenization. **B**. **UWGM 2655 showing evidence of wrinkling within interspaces on theca. C. UWGM 4638a showing partial** demineralization of the phosphatic **theca** with **kerogenous** material. **D–E**. **UWGM 3042a, b, d, e (part [E] and** counterpart **[D]) showing** multiple demineralized conulariid specimens **with** random orientation. Scale bars = 2 mm (A–C); 5 mm (D–E).

Figure 5. **Reflected-light images of *C. niagarensis* showing evidence of compressional offset. A. UWGM 3042a**. **B**. Magnified image of boxed area in A showing overlapping transverse ribs. Black arrows indicate surficial transverse ribs with positive relief and white arrows indicate underlying ribs with negative relief. **C**. **UWGM 3054** with white arrows showing offset corner **sulci** with opposing relief polarities; black arrow indicates fracture. Scale bars = 2 mm (A**, C); 1** mm (**B**).

Figure 6. Reflected-light images of *C. niagarensis* with varying amounts of kerogenized material preserved. White arrows indicate examples of mottled carbonaceous texture; black arrows with white outline indicate solid carbonaceous textures; **'windows'** are indicated by **areas** within the dotted **lines**. Solid black arrows indicate fractures. **A**. **UWGM 3174**. **B**. **UWGM 3729**. **C**. **UWGM 4006**. **D**. **UWGM 3185**. E–F. **UWGM 3130 part [E] and UWGM 3172** counterpart **[F]. G–H. UWGM 4265 part [G] and counterpart [H]** with decay halo. I. **UWGM 2792 shows evidence of vertical compression**, progressive demineralization from apex to aperture, **and** some breakage **along the corner sulci**. All scale bars = 2 mm.

Figure 7. SEM-EDS images of *C. niagarensis*, **UWGM 2754**. **A**. Mosaic C2D-SEM image. **B**. Mosaic BSE-SEM image. **C**. Mosaic SEM composite image. **D–M**. SEM-EDS elemental maps scanned at 20 keV **from beam voltage locations indicated by boxed areas shown in C. Elemental maps show** carbon **(green),** silicon **(magenta), phosphorus (**orange**),** and calcium (**blue**). Scale bars = 2 mm (A–C); 500 μm (D–M).

Figure 8. EDS analysis of *C. niagarensis*, **UWGM 2825**. **A**. BSE-SEM image. **B**. EDS map composite of aluminum, silicon, phosphorous, and calcium. **C–I**. Individual EDS elemental maps of view B **showing** carbon **(green),** aluminum **(teal),** silicon **(magenta),** phosphorus **(orange),** iron **(red),** sulfur **(yellow),** and calcium **(blue).** All scale bars = 1 mm.

Figure 9. EDS analysis of *C. niagarensis*, **UWGM 2787b** overlapping a specimen of *Parioscorpio venator* Wendruff *et al.*, **2020b**. **A**. Reflected-light image showing inferred boundaries of *P. venator* and the conulariid specimen (solid and dashed white lines). **B**. BSE-SEM composite of A. C–K. Magnified view of boxed area in B. **C**. BSE-SEM image. **D**. EDS map composite of carbon (green), aluminum (teal), iron (red), and phosphorous (orange). **E–K**. EDS elemental maps **of** carbon **(green),** aluminum **(teal),** silicon **(magenta),** phosphorus **(orange),** iron **(red) and sulfur (**yellow**) together**, and calcium **(blue).** Scale bars = 2 mm (A–B); 1 mm (C–K).

Figure 10. Taphonomic model of the preservation of conulariids at the Waukesha Lagerstätte. **A**. Conulariid in life position. **B**. Conulariid after transportation and deposition. C. Conulariid specimen compressed two dimensionally. **D–F**. Cross section views of compressed specimens of *C. niagarensis*. **D. UWGM 3233 showing phosphatic theca with infilled sediment. E. UWGM 3130 showing phosphatic theca with considerable infilled sediment. F. UWGM 3174 with a fully demineralized theca**. White arrows indicate phosphatic material; solid black arrows indicate carbonaceous material; **grey** arrows with white outline indicate sediment infill. All scale bars = 0.5 mm.

Figure 11. Laminae with distinct interlamellar partings preserved in two specimens of *C. niagarensis*. Black arrows indicate individual interlamellar partings. **A**. **UWGM 3626** showing several flat laminae above a conulariid specimen. **B**. **UWGM 2792**, exhibiting a taphonomic gradient **in phosphatic dissolution** from the apical to apertural region as it intersects up to 5 individual interlamellar partings. All scale bars = 1 mm.