Palaeontology
The Palaeontological Association
www.palass.org

[Palaeontology, Vol. 56, Part 1, 2013, pp. 29–48]

LIFE MODE OF *IN SITU CONULARIA* IN A MIDDLE DEVONIAN EPIBOLE

by HEYO VAN ITEN[1*], VICTOR P. TOLLERTON JR[2], CHARLES A. VER STRAETEN[3], JULIANA DE MORAES LEME[4], MARCELLO GUIMARAES SIMÕES[5] *and* SABRINA COELHO RODRIGUES[6]

[1]Department of Geology, Hanover College, Hanover, IN 47243, USA *and* Department of Invertebrate Paleontology, Research Associate, Cincinnati Museum Center, 1301 Western Avenue, Cincinnati, OH 45203, USA; e-mail: vaniten@hanover.edu
[2]Research Associate in Paleontology, New York State Museum, 1908 Sunset Avenue, Utica, NY 13502, USA; e-mail: vmtollerton@verizon.net
[3]New York State Museum/Geological Survey, 3140 Cultural Education Center, Albany, NY 12230, USA; e-mail: cverstra@nysed.gov
[4]Departamento de Geologia Sedimentar e Ambiental, Instituto de Geosciências, Universidade de Paulista, Rua do Lago-562 Cd. Universitária-São Paulo, SP, Brazil 05508-080; e-mail: leme@usp.br
[5]Departamento do Zoologia, Universidade Estadual de São Paulo, IB, UNESP, CP 510, Rubião Júnior, 18618-000, Botucatu, SP, Brazil; e-mail: btsimoes@ibb.unesp.br
[6]Faculadade de Ciências Integradas do Pontal – FACIP, Universidade Federal de Uberlândia, Ciências Biológicas, Av. José João Dib, 2545, Progresso – 38302-000 – Ituiutaba, MG, Brazil; e-mail: scrodrigues@pontal.ufu.br
*Corresponding author.

Typescript received 4 February 2011; accepted in revised form 26 December 2011

Abstract: Exceptionally abundant specimens of *Conularia* aff. *desiderata* Hall occur in multiple marine obrution deposits, in a single sixth-order parasequence composed of argillaceous and silty very fine sandstone, in the Otsego Member of the Mount Marion Formation (Middle Devonian, Givetian) in eastern New York State, USA. Associated fossils consist mostly of rhynchonelliform brachiopods but also include bivalve molluscs, orthoconic nautiloids, linguliform brachiopods and gastropods. Many of the brachiopods, bivalve molluscs and conulariids have been buried *in situ*. Conulariids buried *in situ* are oriented with their aperture facing obliquely upward and with their long axis inclined at up to 87 degree to bedding. Most specimens are solitary, but some occur in V-like pairs or in radial clusters consisting of three specimens, with the component specimens being about equally long or (less frequently) substantially different in length. The compacted apical end of *Conularia* buried *in situ* generally rests upon argillaceous sandstone. With one possible exception, none of the examined specimens terminates in a schott (apical wall), and internal schotts appear to be absent. The apical ends of specimens in V-like pairs and radial clusters show no direct evidence of interconnection of their periderms. The apical, middle or apertural region of some inclined specimens abuts or is in close lateral proximity to a recumbent conulariid or to one or more spiriferid brachiopods, some of which have been buried in their original life orientation. The azimuthal bearings of *Conularia* and nautiloid long axes and the directions in which conulariids open are non-random, with conulariids being preferentially aligned between 350 and 50 degree and with their apertural end facing north-east, and nautiloids being preferentially aligned between 30 and 70 degree. Otsego Member *Conularia* were erect or semi-erect, epifaunal or partially infaunal animals, the apical end of which rested upon very fine bottom sediment. The origin of V-like pairs and radial clusters remains enigmatic, but it is probable that production of schotts was not a regular feature of this animal's life history. Finally, conulariids and associated fauna were occasionally smothered by distal storm deposits, under the influence of relatively weak bottom currents.

Key words: conulariids, life mode, obrution deposits, ecological epibole, Middle Devonian, Mount Marion Formation.

FOSSIL organisms buried *in situ* are potential repositories of critical information bearing on a variety of problems in the interpretation of their respective groups. In addition to preserving delicate anatomical structures susceptible to loss or degradation during transport, such fossils may also preserve their original life orientations and, in large samples, the original patterns of spatial arrangement and age distributions of smothered populations. Conulariids are an extinct (Ediacaran–Upper Triassic) group of marine animals, now generally classified as scyphozoan cnidarians (e.g. Van Iten *et al.* 2006*b*; Leme *et al.* 2008*a*, *b*; 2010; John *et al.* 2010), that have yielded little intrinsic evidence concerning several basic aspects of their growth, life history and mode of life. Substantial progress

doi: 10.1111/j.1475-4983.2012.01146.x

towards resolving some of these issues was made by Simões *et al.* (2000*a*, *b*) and Rodrigues *et al.* (2003, 2006), who reported on the occurrence of *in situ Conularia quichua* Ulrich and *Paraconularia africana* (Clarke) in silty obrution deposits in the Ponta Grossa Formation (Lower Devonian, Pragian–Emsian; Grahn *et al.* 2000, 2002; Gaugris and Grahn 2006) of southernmost Brazil. Solitary and clustered specimens from these rocks preserve some of the most compelling evidence yet documented that steeply pyramidal conulariids were sessile benthic animals that in life were inclined at high angles to the seafloor, with their wide apertural (and presumably oral) end facing upward. More recently, John *et al.* (2010) reported on a sample of exceptionally preserved *Metaconularia manni* Roy from a dolomitic shale lens in the Silurian (Wenlockian) Scotch Grove Formation of east-central Iowa, USA. Of the twenty solitary specimens examined by these authors, seven (35 per cent) were preserved with their longitudinal axis oriented perpendicular to bedding, again with their apertural end facing upward.

Conulariids buried *in situ* also preserve evidence bearing on the nature of monospecific pairs and clusters (e.g. Rodrigues *et al.* 2006; Van Iten and Südkamp 2010), which have been interpreted as clonal colonies or as products of preferential larval settlement (Van Iten and Cox 1992; Brood 1995; McKinney *et al.* 1995), and they have the potential to clarify other problems in conulariid paleobiology as well. One such problem is the nature of the apical wall or schott, which in most cases covers the broken apical end of the periderm; though, in some specimens one or more additional schotts also occur within the peridermal cavity (Van Iten 1991*b*). The schott has variously been interpreted as (1) a cicatrix produced in response to severance of the apical region by bottom currents, (2) a detachment scar associated with assumption of a free-living mode of life or (3) a regular anatomical structure associated with periodic retraction of soft parts towards the oral end of the body. Additional hypotheses, for example, repair of damage inflicted by predators or necrosis, also come to mind. Related to the problem of the nature of the schott is the question of the specific mode of life of conulariids. Although several lines of circumstantial evidence (e.g. Van Iten *et al.* 1996; Van Iten and Südkamp 2010) suggest that relatively small conulariids were epifaunal animals attached at their apical end to hard substrates, to date no one has documented any conulariids preserving direct evidence of attachment. Additionally, other lines of evidence (e.g. Rooke and Carew 1983; John *et al.* 2010) suggest that some conulariids may have stood upon or anchored themselves within bottom sediment, and it has also been proposed (e.g. Babcock and Feldmann 1986) that conulariids were planktonic or pseudoplanktonic or that the largest conulariids were benthic and recumbent (Van Iten and Vyhlasová 2004).

In this study, we document the occurrence of exceptionally abundant conulariids, many of them buried *in situ*, in the Otsego Member of the Mount Marion Formation (Middle Devonian, Givetian) in eastern New York State, USA (Figs 1, 2). The Otsego Member specimens belong to a single relatively large species, here identified as *Conularia* aff. *desiderata* Hall, currently known from Lower and Middle Devonian strata of New York State and Pennsylvania (Babcock and Feldmann 1986). As argued below, the new specimens provide substantial additional evidence bearing on fundamental problems in the interpretation of conulariids in general.

MATERIAL AND METHODS

Conulariids discussed in this study are from a single locality near the village of Middleburgh, Schoharie County, eastern New York State (Fig. 1). (The precise location and ownership of this site may be obtained from the senior author.) A total of 289 specimens were found in place, in sloping to near-vertical rock faces, along a lateral distance of approximately 450 m. Twenty additional specimens were obtained from talus. Of the specimens found in outcrop, 165 were collected. Fifty-four conulariids, nearly all found with their apical end embedded in rock matrix, were collected in oriented blocks or concretions. The stratigraphic level where conulariids occurred in place was measured relative to the base of a rusty-weathering horizon of irregularly shaped, mostly vertically elongate concretions that form a conspicuous marker bed throughout the site (Fig. 2). Owing mainly to variation in the slope of the outcrop, we estimate our stratigraphic level measurement error to be as much as ±0.1 m. The inclination to bedding of the long axis of nearly all conulariid specimens was measured using a Brunton compass. To test for preferential alignment, the azimuthal bearing of the long axis of 180 variably inclined conulariids and 63 orthoconic nautiloid steinkerns was measured, and the direction in which the apertural end of the conulariids faced was also recorded. In part because the long axis of the conulariids does not coincide with a face or corner, we estimate our measurement error for both inclination and azimuth to be as much as ±3 degree. Also, the apical third of a small number of specimens is slightly curved, and in these cases, inclination was measured along the more or less straight middle-apertural region.

Specimens collected with their apical region embedded in rock matrix were prepared mechanically to reveal this region and the rock matrix directly below it. Eighteen specimens (including many of those whose apical end was encased in rock matrix) were also prepared to reveal the peridermal cavity by grinding through one of the four corners using size 600 SiC grit. To check for variation in

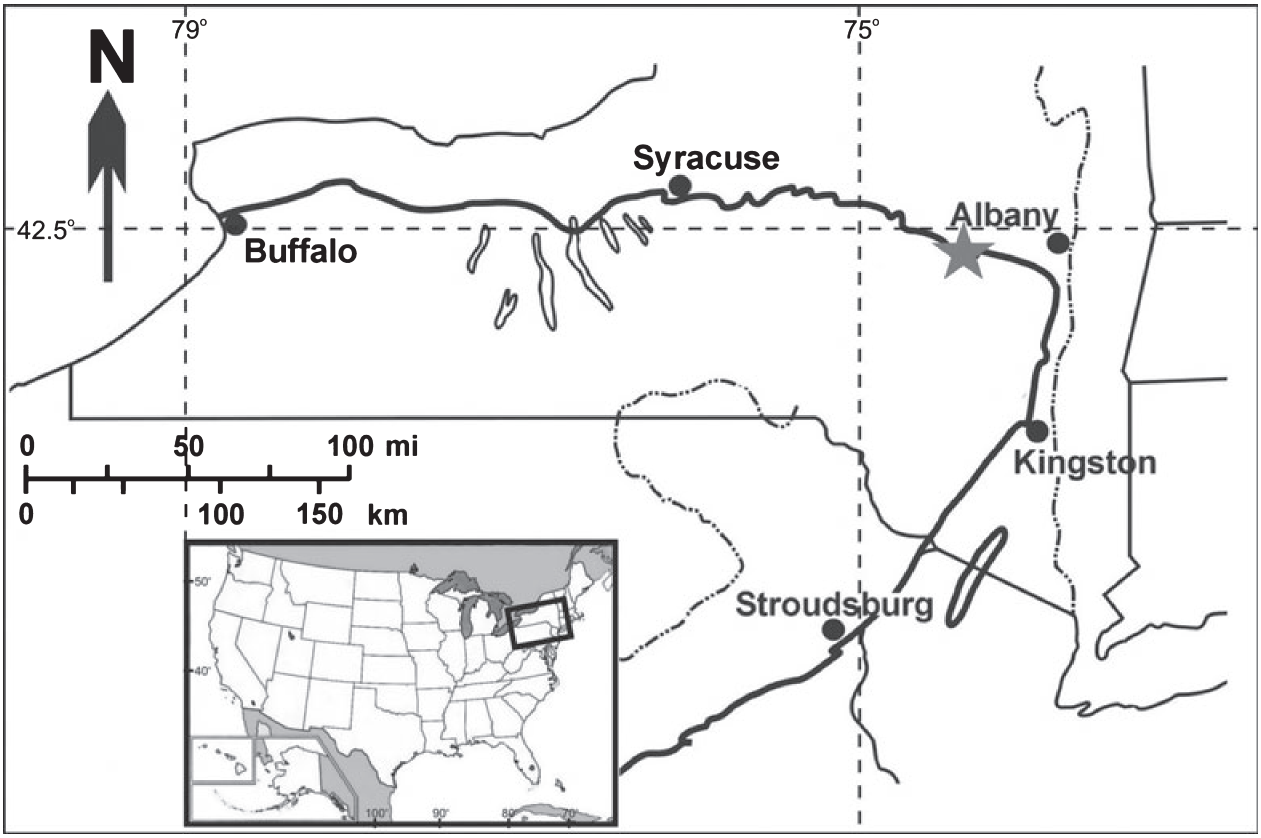


FIG. 1. General location of the study site (star symbol) in eastern New York State. Bold line denotes the northern and eastern limits of the Devonian outcrop belt in this state and adjacent Pennsylvania.

sediment texture, some of the oriented blocks with conulariids were cut perpendicular to bedding and ground on a glass plate using size 600 SiC grit. Additionally, oriented thin sections were prepared from one of the *Conularia*-bearing concretions.

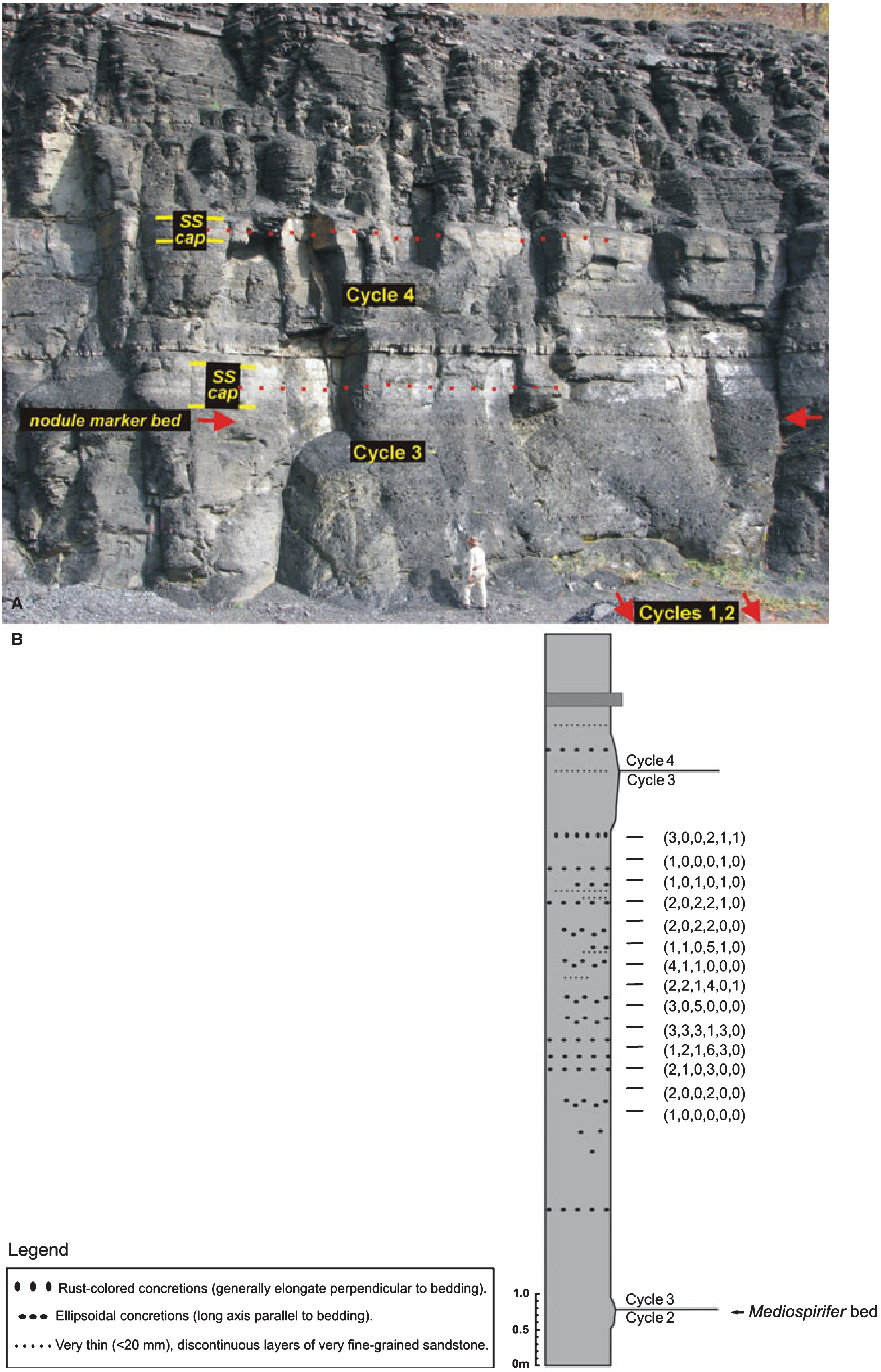
To interpret the original depositional environment and taphonomy of the conulariids, approximately 700 associated fossils were identified and counted, and relevant aspects of their morphology (e.g. size) and preservation (e.g. articulation and orientation) were noted. The specimens were found in blocks that were split repeatedly along natural fractures and then examined with a hand lens, to minimize the chances of biasing the sample against small specimens (see Van Iten *et al.* 2006*c*).

Collected conulariids are reposited in the palaeontological collections of the Cincinnati (Ohio) Museum Center, Department of Invertebrate Paleontology, under specimen numbers CMC IP62785-62916 and CMC IP66118-66122.

STRATIGRAPHY

The Mount Marion Formation occurs in the lower part (Marcellus subgroup) of the Middle Devonian (Givetian) Hamilton Group, which occurs in the lower part of the Devonian Catskill clastic wedge (Ver Straeten and Brett 1995; Brett and Baird 1996; Ver Straeten and Brett 2006; Ver Straeten 2010). In eastern New York State, the Mount Marion Formation is up to 375 m thick and is subdivided (in ascending order) into the Hurley, Cherry Valley, East Berne and Otsego members, and undifferentiated upper beds. The rocks here studied occur in the upper part of the Otsego Member and represent small-scale cycles within the early part of a fourth-order falling stage systems tract (FSST). They were deposited from below to perhaps just above storm wave base during the early stages of a tectonically active to quiescent phase of the Acadian Orogeny (Ettensohn 1985; Ver Straeten 2010).

The conulariid-rich interval comprises the third of four small-scale ('sixth-order') cycles (Cycles 1–4) in the lower part of the study site (Fig. 2). The cycles, which range from 4.2 to 7.5 m thick, are characterized by relatively similar, homogenous, argillaceous and silty very fine-grained sandstone that appears medium dark grey to dark grey where freshly exposed. The degree of burrowing to bioturbation varies between cycles, as does the occurrence, density and diversity of shelly macrofauna. The cycles may be analogous to thinner, metre-scale cycles


SS cap
Cycle 4
SS cap
nodule marker bed
Cycle 3
A
Cycles 1,2
B
Cycle 4
Cycle 3
(3,0,0,2,1,1)
(1,0,0,0,1,0)
(1,0,1,0,1,0)
(2,0,2,2,1,0)
(2,0,2,2,0,0)
(1,1,0,5,1,0)
(4,1,1,0,0,0)
(2,2,1,4,0,1)
(3,0,5,0,0,0)
(3,3,3,1,3,0)
(1,2,1,6,3,0)
(2,1,0,3,0,0)
(2,0,0,2,0,0)
(1,0,0,0,0,0)
Legend
Rust-colored concretions (generally elongate perpendicular to bedding).
Ellipsoidal concretions (long axis parallel to bedding).
Very thin (<20 mm), discontinuous layers of very fine-grained sandstone.
1.0
0.5
0m
Cycle 3
Cycle 2
Mediospirifer bed

(i.e. PACS of Anderson and Goodwin 1990) developed in Lower Devonian carbonates in the region and as such may represent Milankovich-scale precessional cycles on the order of 21 000 or 41 000 years in duration in modern times (they would have been of shorter duration during the Devonian). The distinctly thicker character of the cycles at the study site reflects elevated sedimentation rates of synorogenic siliciclastics transported from the rising Acadian orogenic belt to the present-day east, in western New England (Ver Straeten 2010).

The conulariid-rich zone (Cycle 3) is 7.5 m thick and exhibits highly burrowed to bioturbated textures. Scattered nodule horizons occur through much of the cycle, and a few less than or equal to cm-scale laminated sandstone beds, interrupted laterally by burrowing, are present above the middle of the cycle. A relatively abundant and diverse fauna of small to large invertebrate fossils occurs throughout most of Cycle 3. The interval bounding Cycles 3–4 consists of a relatively resistant capping sandstone (approximately 1.1 m thick) that overlies the above-noted marker bed of bulbous rusty-weathering nodules. In the lower part of this sandstone, a *Zoophycus*-pinstriped, highly bioturbated interval, with three subintervals of scattered medium to large brachiopods, appears to mark shallowest water conditions.

In contrast to Cycle 3, Cycles 1, 2 and 4 feature predominantly laminated to burrow-mottled textures and rare to uncommon fossils, except in the shallow-water cycle caps. Like Cycle 3, Cycle 4 is capped by a distinct sandstone bed containing scattered brachiopods. Overall, the lithology and faunas of Cycles 1–4 indicate upward shallowing and increasing oxygen availability, with the maximum of each occurring in Cycle 3, the conulariid-rich interval.

Finally, the beds described above strike approximately north-east–south-west and dip very gently (<2 degree) to the south-east. They are cross-cut by two dominant sets of joint planes, with one set striking approximately 320 degree and dipping approximately S87W, and the other set striking approximately 40 degree and dipping approximately N80W. The study interval also contains a single bed-parallel thrust fault, within Cycle 2. The lateral displacement along it is not known, but there seems to be no notable change in lithology across the fault. Therefore, lateral movement along the fault probably has not resulted in any significant structurally induced juxtaposition of different palaeohabitats.

RESULTS

Associated fossils

Cycle 3 contains body fossils of at least 45 invertebrate species other than conulariids, predominantly rhynchonelliform and linguliform brachiopods (13 species), bivalve molluscs (15 species), at least one orthoconic nautiloid and gastropods (three species; Table 1; Fig. 3). By far, the most abundant species are the brachiopods *Eumetabolatoechia multicostatum* and *Mediospirifer audaculus*, both of which occur throughout the interval. Among the bivalve molluscs, the three most abundant species are *Paracyclas rugosa*, *Nuculoidea opima* and *Nuculites oblongatus*. Also present but extremely rare are bryozoans (one species), coiled cephalopods (two species), an indeterminate crinoid, hyolithid and monoplacophoran molluscs (one species each), ostracode and phyllocarid arthropods (one species each), cnidarians (*Sphenothallus* sp. and *Plumulina plumaria*), an indeterminate placoderm and woody terrestrial plant stems. Corals and trilobites were not observed.

Fossils are matrix-supported and unabraded, although many (especially spiriferid brachiopods) have been crushed and broken owing to sediment compaction. Large shell chambers generally are filled with mudstone. Brachiopods preserve calcitic or phosphatic shell material, while molluscs (originally aragonitic; Cherns and Wright 2000) are preserved as moulds and casts. Fossils vary widely in size and shape, ranging from <5 mm (e.g. ostracodes and small bivalve molluscs) to >130 mm (conulariids and orthoconic nautiloids) long. Brachiopods generally are closed articulated. Among bivalve molluscs, approximately 70 per cent consist of a single valve, while the rest are either closed articulated (approximately 20 per cent) or splayed (approximately 10 per cent). All three observed grammysioids, by far the largest bivalves in Cycle 3, are closed articulated. Most specimens consisting of a single valve are oriented with their commissural plane parallel to bedding, with approximately 5 per cent of specimens being inclined. The proportions of valves oriented convex up versus convex down are about equal.

Many of the brachiopods and some bivalve molluscs have been buried in their original life orientations (Fig. 3). Thus, 20 of the 23 '*Lingula*' found in place were oriented with their commissural plane perpendicular to

FIG. 2. Otsego Member of the Mount Marion Formation (Middle Devonian, Givetian) at the study site. A, Photograph of a portion of the exposure, showing Cycles 3 and 4. Man standing in the foreground is approximately 1.7 m tall. B, Measured stratigraphic column for Cycle 3, showing the numbers of observed *Conularia* aff. *desiderata* Hall specimens (total of 96) in six inclination angle bins at 14 different levels spaced approximately 0.3 m apart. First number in each set (parentheses) is the number of specimens inclined at <15 degree to bedding and includes specimens with the aperture facing obliquely upward or downward. All other bins are for specimens facing obliquely upward only, in the following inclination angle ranges (left to right): 15–29, 30–44, 45–59, 60–74, 75–90 degrees.

TABLE 1. Invertebrate species associated with *Conularia* aff. *desiderata* Hall and represented by body fossils.

Species	Relative abundance (per cent)
Brachiopods (13 species)	
Eumetabolatoechia multicostatum	33.7
Mediospirifer audaculus	24.2
Spinocyrtia granulosa	6.0
Mucrospirifer mucronatus	3.7
Athyris spiriferoides	3.4
'*Lingula*' *spatulata*	2.3
Ambocoelia umbonata	<1
'*L.*' *paliformis*	<1
'*Orbiculoidea*' sp.	<1
Productella sp.	<1
Protoleptostrophia sp.	<1
Rhipodomella penelope	<1
Strophodonta sp.	<1
Molluscs–Bivalves (15 species)	
Paracyclas rugosa	4.2
Nuculoidea opima	3.0
Nuculites oblongatus	3.0
Cornulites flabella	<1
Cypricardella bellistriata	<1
Goniophora sp.	<1
Gosseletia triquetra	<1
Grammysia bisulcata	<1
Grammysioidea arcuata	<1
Modiomorpha sp.	<1
Nuculites triqueter	<1
Nyassa arguta	<1
Palaeoneilo sp.	<1
Pterinopectin sp.	<1
Solemya sp.	<1
Molluscs–Cephalopods (4 species)	
Indeterminate orthocone nautiloid	4.1
Indeterminate goniatite (?)	<1
Nephriticeras sp.	<1
Spyroceras sp.	<1
Molluscs–Gastropods (3 species)	
Euryzone itys	1.7
Bembexia sulcomarginata	<1
Palaeozygopleura hamiltoniae	<1
Molluscs–Other (2 species)	
Cyrtonella sp. (monoplacophoran)	<1
Indeterminate tentaculitid	<1
Arthropods—Ostracodes (1 species)	
?Leperditia sp.	<1
Arthropods–Phyllocarids (1 species)	
Paraechinocaris punctata	<1
Bryozoa (1 species)	
Indeterminate ramose branching form	<1
Incerta sedis (2 species)	
Indeterminate hyolithid	<1
Reptaria sp.	<1
Cnidaria (2 species)	
Plumulina sp.	<1
Sphenothallus sp.	<1
Echinoderms (1 species)	
Indeterminate crinoid	<1

Total sample size = 710 specimens.

bedding and with their anterior end facing upward (see Zonneveld and Greene 2010 for *in situ* lingulids). These specimens occurred at multiple levels extending from about 0.5 m above the lowest observed occurrence of *Conularia* to about 0.3 m below its highest occurrence. Among the 240 counted spiriferids, approximately 22 per cent were oriented umbo down, the probable life orientation of these brachiopods (e.g. Alexander 1986). Nearly all of the remaining specimens were oriented with their commissural plane approximately parallel to bedding. Approximately 5 per cent of spiriferid specimens visible on outcrop faces occur in discrete clusters, with some or all of the component specimens being oriented with their umbo facing downward (Fig. 3B). Among closed-articulated bivalve molluscs that originally were infaunal or semi-infaunal, approximately 50 per cent of specimens, including all three observed grammysioids (Fig. 3A), were oriented with their commissural plane approximately perpendicular to bedding and with their hinge line on top and inclined slightly anteriorward. Collectively, these fossils ranged from about the lowest occurrence of *Conularia* to about 1 m below its highest occurrence.

Forty-one (91.1 per cent) of the 45 invertebrate species associated with *Conularia* aff. *desiderata* were benthic, and over half of these, including all of the brachiopods as well as many of the bivalve molluscs, were sessile filter feeders that were epifaunal (rhynchonelliform brachiopods), semi-infaunal (e.g. grammysioid bivalves; Bambach 1971; Marsh 1984) or fully infaunal (e.g. '*Lingula*'). The gastropods were epifaunal deposit feeders. Some bivalves, including *Paracyclas* sp., *Nyassa* sp. and the two nuculoids, were shallow infaunal deposit feeders (Stanley 1972; Brett 1991; Brett and Allison 1998). It should be noted here that Devonian species of *Paracyclas* must be reappraised, as the family Paracyclidae contains some species with lucinid characters (Taylor and Glover 2006). In extant lucinids, sulphide-oxidizing symbiosis probably is obligate, and the same may also have been true of *Paracyclas*. Similarly, extant nuculoids tolerate low oxygen levels, and their Devonian relatives may have shared this characteristic.

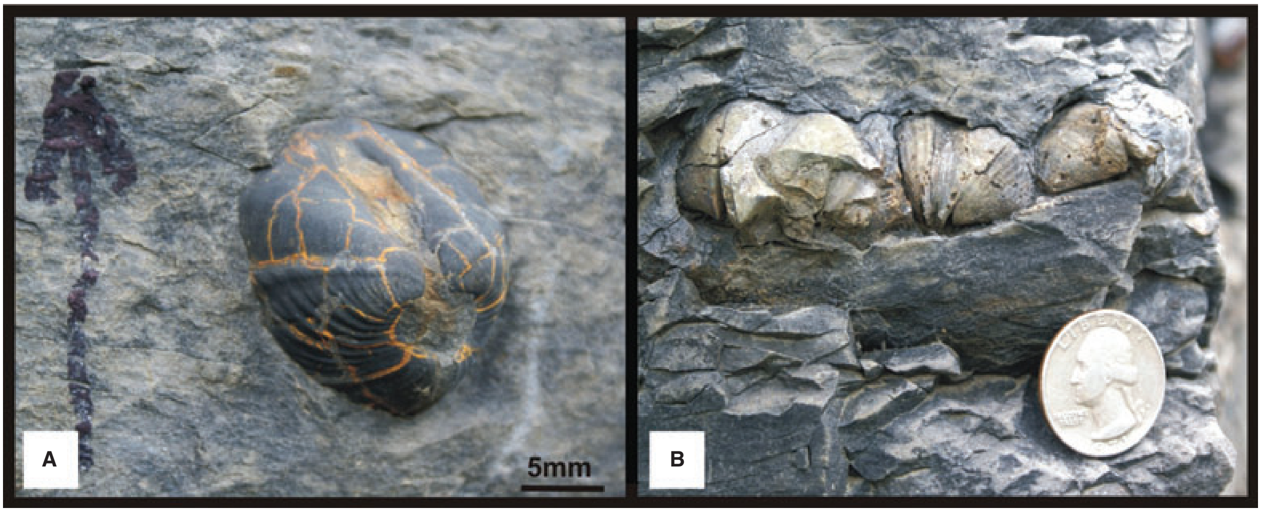


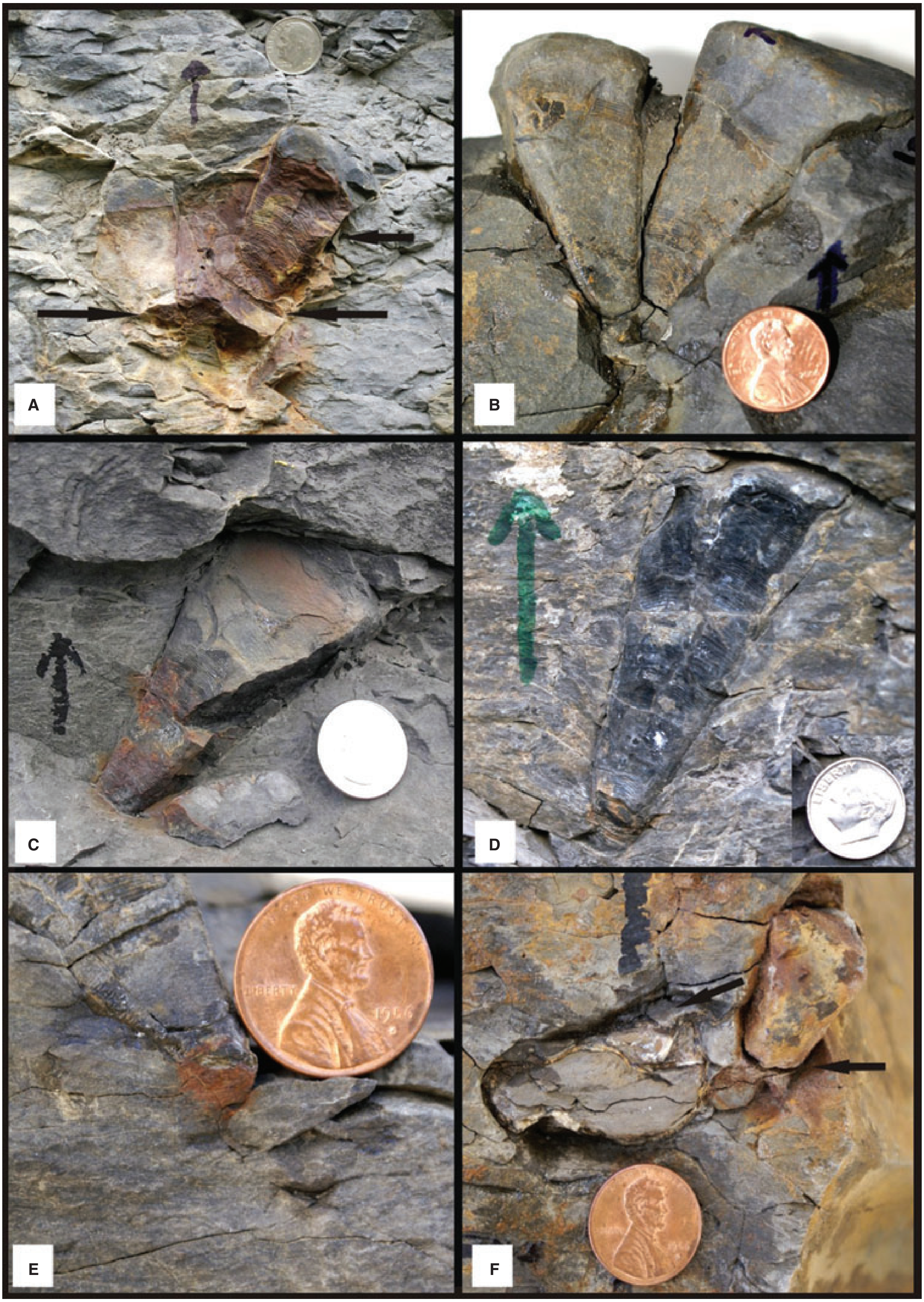
FIG. 3. Outcrop photographs of bivalved fossils associated with Otsego Member *Conularia* aff. *desiderata* Hall in Cycle 3 of the study section. A, *Grammysia bisulcata*. Single closed-articulated specimen preserved with its commissural plane oriented approximately perpendicular to bedding and its hinge line up. B, *Mediospirifer audaculus*. Cluster of three specimens preserved with their umbos facing more or less straight downward and resting on argillaceous and silty very fine-grained sandstone. The cluster occurs at about the same stratigraphic level as a number of conulariids, including the triplet radial cluster in Figure 4A. Diameter of coin scale represents 24 mm.

Conulariids

Preservation. Observed *Conularia* preserve finely ornamented phosphatic periderm and occur either in argillaceous and silty, very fine-grained sandstone or (less frequently) in fine-grained concretions (Figs 4, 5). In the former case, however, the apertural region of the conulariid may be encased within an ellipsoidal or mushroom-cap-like concretion. Some specimens show localized or pervasive Fe staining of peridermal material and adjacent rock matrix, and the sediment filling the peridermal cavity may be darker (with less silt to very fine sand) than the external rock matrix and is generally free of other fossils including trace fossils. As indicated by field inspection and examination of polished slabs, no specimens intersect or abut recognizable lithologic boundaries or very thin resistant sandstone layers. Nearly complete specimens preserve one or more short apertural lappets, the margins of which are gently arcuate. Such specimens range from approximately 36 to 130 mm long (average length about 60 mm), with the largest specimens originally measuring approximately 150 mm long, and are either straight or gently curved in their apical third. Apertural lappets are folded centripetally, partially covering the apertural opening.

As discussed in detail below, many of the conulariids are inclined at moderate or high angles (30–87 degree) to bedding, with their aperture facing obliquely upward. Other specimens are subhorizontal and commonly have their aperture facing either obliquely upward or (less frequently) downward. Subhorizontal specimens generally are compressed perpendicular to their long axis, but show little or no distortion of the periderm parallel to this axis. Where preserved close to the apex, the apical end tapers to a facial width of 2.5 mm or less. By contrast, specimens inclined at moderate or high angles to bedding are inflated, with their transverse cross section being rectangular or slightly rhombic, and may show slight compaction parallel to their long axis. Additionally, the apertural end of many inclined specimens has been truncated obliquely, along a plane parallel to bedding (Figs 4D, 5A). Because such truncation occurs in specimens whose apertural end is still encased in rock matrix, it is not an artefact of breakage sustained during collection or through mass wasting. In moderately and steeply inclined specimens whose apical end was embedded in rock matrix at the time of collection, the apical end is not pointed, as in some subhorizontal specimens, but secondarily rounded (Figs 4B, D–E, 5), with the four faces bent centripetally or (less frequently) telescoped. Such distortion probably resulted from compaction of the host sediment, as indicated by the presence on or near some conulariids of clay-rich slickensides and/or mudstone laminae deflected around the specimens' apical and apertural ends (Fig. 4D).

Stratigraphic distribution and modes of occurrence. Within Cycle 3, *Conularia* aff. *desiderata* was found at over 30 levels, mostly as solitary specimens (256 of the 289 specimens found in place; Figs 4C–F, 5B) but also in 14 pairs of mutually adjacent specimens or in five compact clusters of three specimens (Figs 4A–B, 5A). Two additional


A
B
C
D
E
F

solitary specimens, both subhorizontal, were found near the top of Cycle 2. Eight of the 14 pairs found in place are V-like (Van Iten and Südkamp 2010; this study, Fig. 4B), and four of the clusters are radial (Van Iten and Cox 1992; this study, Fig. 4A). With one exception, all of the solitary specimens in Cycle 3 were found at levels extending from the top of the rusty-weathering concretion band to approximately 4 m below the base of this marker bed. Clustered and paired specimens were found at multiple levels located between 0.75 and 3.7 m below the base of the marker bed. One additional V-like pair, associated with a third specimen that may have formed a radial cluster with the other two, was found in talus, as was a single nonradial cluster consisting of four specimens. All of these specimens probably came from Cycle 3. Specimens exposed on outcrop faces generally are spaced several metres or more apart; though, between about 2.6 and 2.7 m below the rusty concretion band, we found four specimens, including two subhorizontal specimens forming a V-like pair, along a length of about 2 m. Approximately 3 m below the marker bed, the apertural end of a steeply inclined solitary specimen was found almost directly below the base of the radial cluster shown in Figure 4A, and several other solitary specimens, collected together in blocks, occur within 0.2 m (laterally) of each other, with the apertural end of one specimen situated at about the same level as the apical end of the other specimen.

Orientation. Nearly half (48.8 per cent) of the 289 specimens found in place were oriented with their long axis inclined at moderate or high angles to bedding and with their aperture facing obliquely upward (Figs 4, 5). Of these, 13 specimens (4.5 per cent) were inclined between 75 and 87 degree (inclusive), 37 specimens (12.8 per cent) between 60 and 74 degree, 51 specimens (17.6 per cent) between 45 and 59 degree, and 40 specimens (13.8 per cent) between 30 and 44 degree. Additionally, 33 specimens (11.4 per cent) were inclined between 15 and 29 degree, and 21 specimens (7.3 per cent) were inclined between 5 and 14 degree. Forty-five subhorizontal specimens (15.6 per cent) were inclined at <5 degree to bedding and faced either obliquely upward or (less frequently) downward. The remaining 49 specimens (17.0 per cent) faced obliquely downward and were inclined between 5 and 85 degree, with 40 (13.8 per cent) of these specimens being inclined between 5 and 44 degree. Chi-square tests (Koenker 1981) reveal a strongly significant preference ($p < 0.01$) for orientation with the aperture facing obliquely upward over obliquely downward. Among specimens facing upward, there is a relatively weak preference ($p < 0.10$) for inclination at moderate-to-high angles (30–87 degree) to bedding over inclination at low angles (<30 degree). Finally, there appears to be no relationship between the angle of inclination of the conulariids and their stratigraphic position: specimens inclined at low angles occur at many of the same levels as moderately and steeply inclined specimens (Fig. 2B).

Among specimens found in place and preserving their apical and apertural ends, there is no correlation (correlation coefficient < 0.1) between the angle of inclination and specimen length. Interestingly, 14 of the 18 specimens whose original length was 100 mm or greater were inclined at 30–70 degree, with their aperture facing obliquely upward. Moreover, four of the five largest specimens, each originally measuring about 110–150 mm long, were inclined at 40–60 degree. The fifth specimen, now about 130 mm long, was found in talus; however, this specimen is inflated and occurs in an elongate rusty-weathering concretion that is expanded around the apertural end of the conulariid. Together, these two

FIG. 4. A–F, *Conularia* aff. *desiderata* Hall. Mount Marion Formation, Otsego Member (Middle Devonian, Givetian) near the village of Middleburgh, Schoharie County, eastern New York State. Clustered and solitary conulariid specimens buried *in situ*. All photographs are oriented with the direction of stratigraphic younging towards the top. A, Outcrop photograph of a radial cluster of three moderately or steeply inclined, aperture-up specimens showing extensive Fe staining. Upper left-pointing arrow indicates a nearly complete specimen (CMC IP 62793A) inclined at approximately 70 degree to bedding. Situated immediately in front of this conulariid is the apical region of a second specimen inclined at approximately 65 degree (lower left-pointing arrow; CMC IP 62793B). The third specimen (right-pointing arrow; CMC IP 62793C) is situated immediately to the left of the other two and is inclined at approximately 57 degree, with its apertural end facing into the outcrop. Diameter of coin represents 18 mm. B, Two moderately steeply inclined (both approximately 55 degree), aperture-up specimens forming a V-like pair. Diameter of coin represents 19 mm; CMC IP 62840A, B. C, Outcrop photograph of a single, moderately steeply inclined (approximately 57 degree), aperture-up specimen found with the apical region still embedded in rock matrix. Diameter of coin represents 24 mm; CMC IP 62853. D, Outcrop photograph of a single steeply inclined (approximately 75 degree), aperture-up specimen showing deflection of sediment laminae around the specimen's compacted apical end and over its apertural end, which has been truncated parallel to bedding. Diameter of coin represents 18 mm; CMC IP 62856. E, Detail of the rust-stained apical region of a single steeply inclined (approximately 60 degree), aperture-up specimen showing the compacted but otherwise intact apical end resting on argillaceous and silty very fine-grained sandstone. Diameter of coin represents 19 mm; CMC IP 62854. F, Single steeply inclined (approximately 65 degree), aperture-up specimen (horizontal arrow), the apical half of which (now largely missing) abuts a closed-articulated spiriferid (oblique arrow). Diameter of coin represents 19 mm; CMC IP 62880.

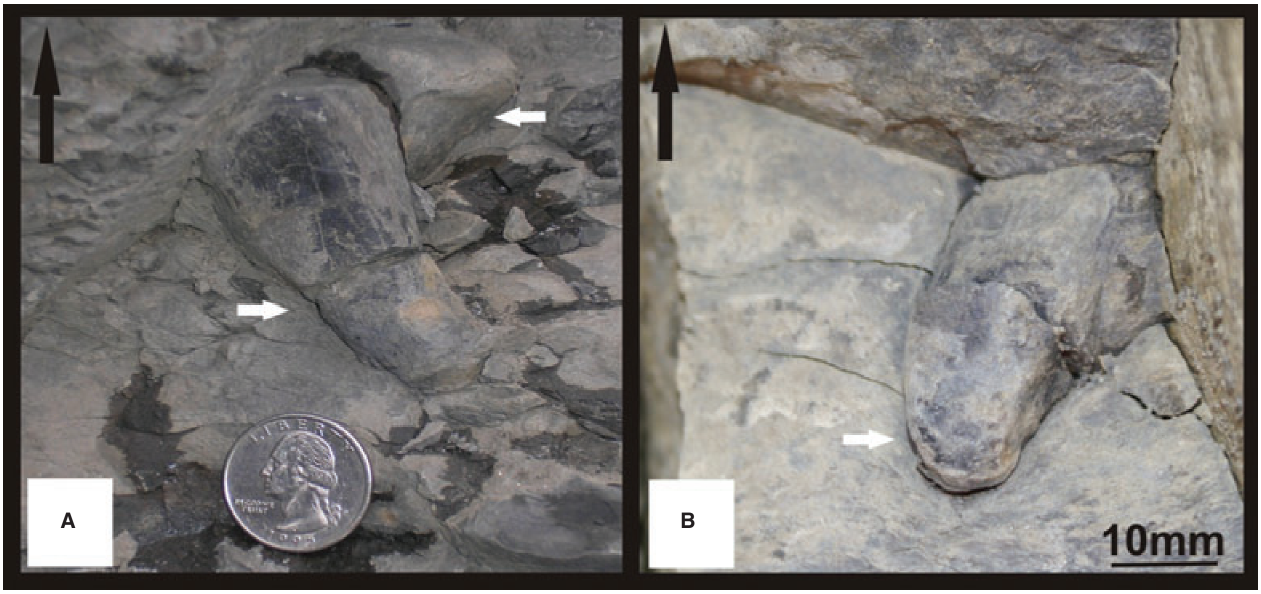


FIG. 5. Outcrop photographs of additional Otsego Member *Conularia* aff. *desiderata* Hall buried *in situ* in Cycle 3 of the study section (black arrow indicates direction of stratigraphic younging). A, Pair of moderately steeply inclined (45 and 55 degree, respectively), aperture-up specimens (horizontal arrows) that cross each other near their obliquely truncated apertural ends. The rounded apical ends of these two specimens rest on argillaceous and silty very fine-grained sandstone. Diameter of coin represents 24 mm; CMC IP 62814A, B. B, Single steeply inclined (60 degree), aperture-up specimen, the rounded apical end (horizontal arrow) of which rests on argillaceous and silty very fine-grained sandstone. CMC IP 66122X.

observations suggest that the specimen came from the rusty-weathering concretion band and originally was oriented with its long axis nearly vertical and its aperture facing upward.

V-like pairs and radial clusters. Thirty-eight of the 309 conulariids examined here, including 33 (11.4 per cent) of the 289 specimens found in outcrop, occur in V-like pairs or in compact radial clusters consisting of three specimens (Fig. 4A–B). The V-like pairs consist of two specimens, the long axes of which converge adapically over all or most of their length, forming an acute angle that ranges from about 20 to 80 degree. In some pairs, the two long axes lie more or less in the same plane and converge on or close to a common point, while in others the two specimens cross each other near their apical ends. In pairs whose angle of convergence is low, the two specimens lie alongside each other, being separated by just a few millimetres of argillaceous sandstone. Among the pairs whose component specimens are inflated and whose long axes are more or less co-planar, the specimens may be arranged in such a way that if rotated through their angle of convergence, they would come together along one of their faces (face-to-face configuration), or the face of one specimen would contact a corner of the other member of the pair (face-to-corner configuration). In all pairs in which the apical region of the component specimens has not been lost, the apical ends of the specimens are situated within 10 mm of each other. And in all pairs whose component specimens are more or less complete, the conulariids are approximately equal in length.

With the exception of three pairs oriented nearly parallel to bedding, all pairs are oriented aperture up and with the long axis of the component specimens generally inclined between 40 and 80 degree to bedding. In one such pair, both specimens are inclined at 80 degree. Another pair, composed of specimens inclined at approximately 40 and 60 degree, respectively, is located immediately adjacent to a single specimen inclined at 65 degree but facing downward. In all pairs in which the component specimens are moderately or steeply inclined, their rounded apical ends lie on or very close to a common horizontal plane.

Three additional pairs, although not V-like, consist of a single moderately or steeply inclined specimen (aperture up), the middle or apical region of which abuts or is located immediately adjacent to a specimen that is subhorizontal. Finally, the members of two pairs overlap each other close to their apertural ends to form an X-like configuration (Fig. 5A), although again with their apical ends (originally) situated on or close to a common horizontal plane.

The radial clusters consist of three specimens, the long axes of which converge adapically or are arranged in a more or less radial pattern. Two of the component specimens lie alongside each other, forming (in effect) a V-like pair in which the angle of divergence of the two long axes is very low. In all clusters save one, all or two of the component specimens are inclined at moderate or high angles to bedding and with their apertural end facing obliquely upward. In one cluster, one of the component specimens is subhorizontal while the other two form a moderately inclined V-like pair, and all three specimens are aligned nearly parallel to each other and with their apertural ends facing in the same direction. Finally, members of a given cluster may be approximately equal in length, or the largest and smallest specimens may differ in length by a factor of approximately two.

Azimuthal trend. The azimuthal trends of conulariid and orthoconic nautiloid long axes in Cycle 3 are summarized in Figure 6. As indicated by chi-square tests, the azimuthal trends of the 63 measured orthocone internal moulds (Fig. 6A) show very strong preferred alignment ($p \ll 0.01$) between 30 and 70 degree. Additionally, there is a secondary (less significant) alignment of orthocone long axes between 330 and 290 degree, or approximately perpendicular to the dominant trend. Because most of the measured specimens were short fragments, the direction in which their apertural end faced could not be determined. The rose diagram for all 180 measured conulariids (Fig. 6C), distributed throughout the conulariid-rich interval and nearly all inclined at low or moderate angles to bedding (with the aperture facing obliquely upward), shows strong preferred alignment ($p \ll 0.01$) of long axes between 345 and 60 degree and with the apertural end facing north-eastward. A secondary alignment, trending north-west-south-east and congruent with the secondary alignment of the bimodal nautiloid plot, is also apparent; though, in this case there is no preferred facing direction. Also, the dominant alignment of the conulariids differs by about 30 degree from the dominant trend of the nautiloids. A similar pattern is displayed by 77 conulariids inclined at <15 degree to bedding and distributed throughout the conulariid-rich interval (Fig. 6B). These specimens again show strong preferred alignment ($p \ll 0.01$) of long axes between 345 and 60 degree, with their apertural end facing predominantly north-eastward, and a secondary north-west–south-east trend.

As noted above, the rocks at the study site exhibit two dominant sets of nearly vertical joints, with one set striking approximately 320 degree and the other set approximately 40 degree. Although many conulariids and orthoconic nautiloids have been exposed on joint planes, in most cases their long axes are inclined to these planes. Thus, the azimuthal trend data here reported are not merely artefacts of preferential exposure of specimens aligned parallel to joint surfaces.

Apical end. Fifty-one of the conulariids actually collected from Cycle 3 and oriented aperture up were found with their narrow apical end partially or fully embedded in rock matrix (Figs 4, 5). Twelve of these specimens occur in V-like pairs or radial clusters. Twenty-one specimens

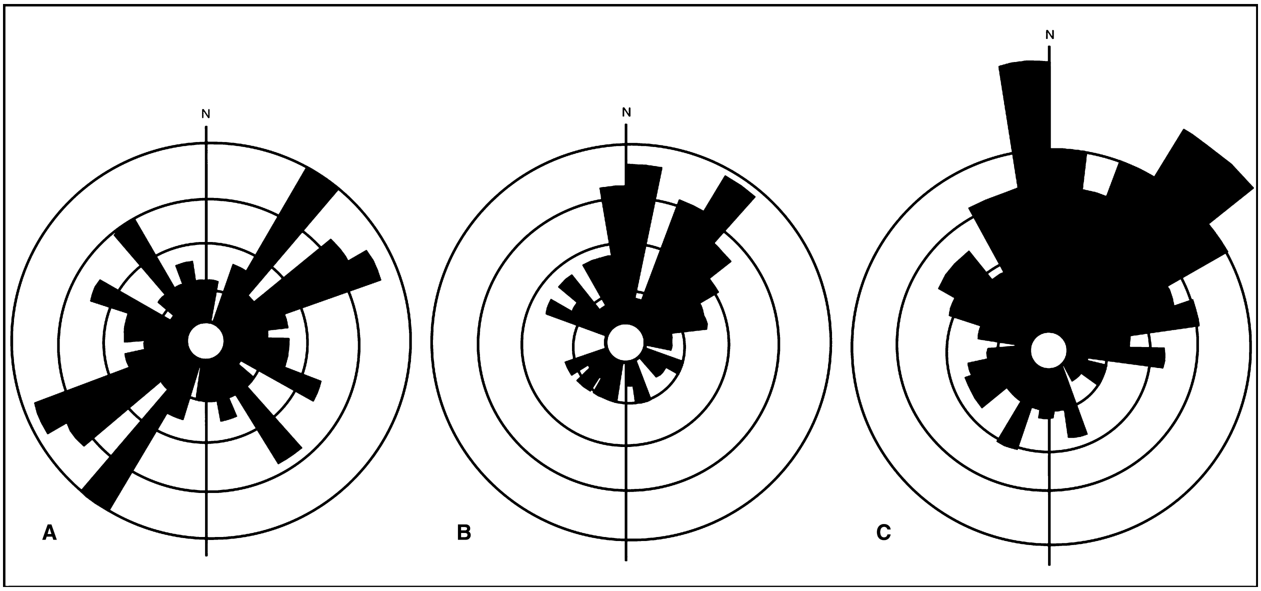


FIG. 6. Rose diagrams showing the azimuthal trends of Otsego Member *Conularia* aff. *desiderata* Hall and associated orthoconic nautiloids in Cycle 3 of the study section. Triangles for the conulariid diagrams expand in the direction in which the aperture faces. A, Rose diagram for the 63 measured orthoconic nautiloids. B, Rose diagram for the 77 conulariid specimens inclined at 15 degree or less to bedding. C, Rose diagram for all 180 measured conulariid specimens, nearly all inclined at low (<30 degree) or moderate (30–44 degree) angles to bedding.

were inclined between 60 and 87 degree, 17 between 45 and 59 degree, and seven between 30 and 44 degree. (The remaining four were inclined at <5, <10 and <25 degree, respectively.) In the single horizontal specimen, the apical end is pointed, tapering to a single face width of approximately 2.5 mm. In all other specimens, the apical end tapers to a single face width of approximately 4–10 mm, at which level the faces bend towards the centre of the peridermal cavity.

With one exception, a specimen directly underlain by an articulate brachiopod, the apical end of all 51 specimens, including all of the specimens occurring in radial clusters or V-like pairs, rests upon argillaceous and silty very fine-grained sandstone (Figs 4B, D–E, 5). In most cases, there is no evidence of macroscopic shell material or any other hard or firm biological substrate within an interval extending at least 10 mm below the conulariid. Additionally, the apical ends of specimens in V-like pairs or radial clusters show no evidence of mutual interconnection. Although situated very close together, the apical ends are separated from each other by argillaceous sandstone.

The apical, middle or apertural third of some of these and other moderately or steeply inclined *Conularia* abuts or is in close lateral proximity to one or more spiriferid brachiopods (mostly *Mediospirifer*), some of which are both closed articulated and oriented with their umbo facing downward, the probable original life orientation of these brachiopods. Other moderately or steeply inclined *Conularia*, some still in outcrop, are located within a few decimetres (laterally) of an umbo-down spiriferid. The incomplete solitary specimen shown in Figure 4F abuts a large spiriferid that is closed articulated, with its commissural plane gently inclined to bedding. Although the apical region of the conulariid is now largely missing, extension of this specimen's corners to their point of intersection indicates that the bottom of the brachiopod is situated about 10 mm above the level at which the apex of the conulariid was formerly located.

Schotts. With the possible exception of a single specimen found in talus, none of the 185 collected *Conularia* specimens exhibits a terminal schott. The 18 specimens that were prepared to reveal the peridermal cavity range from about 36 to 130 mm long and include four of the six largest (and possibly oldest) specimens found. With two exceptions, all of these specimens taper adapically to a single face width of 4–8 mm, beyond which the apical region is either missing (two specimens) or bent inward, producing a rounded end superficially resembling a terminal schott. Three of the specimens, broken apically at single face widths of 5, 6 and 8 mm, respectively, were found in talus. However, one of these specimens is partially encased in a pillar-like ferruginous concretion that expands about the conulariid's apertural end, and as discussed above, it probably stood upright and with its aperture facing upward. A second specimen forms part of a V-like pair that probably was inclined at high angles to bedding (as indicated by the presence of a mushroom-cap-like concretion at the apertural end of the other member of the pair). The third specimen probably was prone when buried. The remaining 15 specimens are nearly complete and were oriented aperture up and inclined at moderate or high angles to bedding.

None of these specimens exhibits internal schotts, even at levels (distances above the former apex) where a terminal schott has been found in conspecific or closely related specimens of similar or smaller sizes from other localities (see discussion below).

INTERPRETATIONS

Depositional environment

Together with lithologic evidence, the taxonomic composition, ecological affinities and preservation of fossils associated with *Conularia* aff. *desiderata* indicate that Cycle 3 contains multiple marine obrution deposits that have been extensively homogenized by burrowing/bioturbation. Discrete obrution deposits, characterized in part by high frequencies of closed-articulated bivalved fossils and multi-element skeletons that are fully articulated and (in some cases) preserved in their original life orientations, have been documented in the middle and upper parts of the Hamilton Group (e.g. Speyer and Brett 1988; Brett 1995; Brett and Baird 1996; Brett and Allison 1998). Additionally, Brett (1995) argued that Hamilton Group mudrocks, representing more offshore facies relative to the strata here examined, consist of obrution deposits that have been obscured by low fossil densities and homogenization by burrowing. In the present case, rapid smothering of live (or recently deceased) bottom fauna, in an environment normally characterized by relatively low levels of physical energy, is indicated by an argillaceous, very fine sandy lithology lacking sedimentary structures indicative of deposition above storm wave base, and by the common occurrence of closed-articulated epifauna (mostly *Mediospirifer* and *Spinocyrtia*) preserved in their original life orientations, at multiple stratigraphic levels. The organisms affected by these events were buried by clouds of muddy sand that settled out of subwave base waters of decreasing physical energy, likely during the waning stages of storms. Individuals of some of the infaunal species (e.g. '*Lingula*' and infaunal bivalve molluscs) may have died between obrution events, but others probably were trapped within their burrow or immediately after they rose from their burrow onto the sediment surface (closed-articulated bivalve molluscs oriented with their commissural plane parallel to bedding; see Anelli *et al.* 1998; Brett 2003).

While sedimentary structures indicative of traction current flow were not detected, the observation that conulariid and nautiloid long axes exhibit nonrandom alignments (Fig. 6) suggests that bottom currents strong enough to bring about such alignments may have been present. The alignment of the conulariids, with specimens preferentially facing in a north-easterly direction, is consistent with the hypothesis of burial under the influence of unidirectional current flow (see Holz and Simões 2002, fig. 37B), but it may also reflect the general trend of background currents during the conulariids' lifetimes. The alignment of the nautiloids, which were free-living and thus less likely to undergo alignment in life than sessile conulariids, may actually reflect alignment by the final sediment-laden current immediately preceding a drop in energy and burial. The apparent absence of erosional scour features suggests that bottom currents were never or seldom strong enough to scour and sculpt the sediment surface to any appreciable extent (see however discussion below).

Between obrution events, background sedimentation occurred at sufficiently low rates, over sufficiently long periods of time (as in the 'episodic starvation' model of Dattilo *et al.* 2008), to allow successful colonization of the seafloor by epifaunal and shallow infaunal filter feeders and herbivores, which most likely required at least moderate levels of dissolved oxygen. Periods of relatively low-to-moderate rates of sedimentation followed by abrupt burial are also indicated by the common presence of disarticulated bivalve molluscs and splayed bivalves. Apparently similar conditions characterized portions of the Devonian Ponta Grossa Formation containing conulariids (Simões *et al.* 2000*a*, *b*; Rodrigues *et al.* 2003, 2006) and clusters of *Australospirifer* buried *in situ* (Simões *et al.* 1998).

The argillaceous sandy bottom sediment was sufficiently stable to support the weight of moderately large spiriferid brachiopods resting on their posterior end. Pore water within the sediment was sufficiently aerated, at least to shallow depths, to allow infaunal organisms, most likely soft-bodied worms and some burrowing bivalve molluscs, to mix and churn the sediment thoroughly, largely destroying the original stratification.

Finally, the contrast in conulariid abundance between Cycle 3 and adjacent Cycles 1, 2 and 4, with the latter rocks being largely devoid of these fossils, is striking. Possible explanations of this difference include taphonomic bias and variation in the ecological suitability of bottom conditions for conulariids. At this point, we see no evidence that conulariids were substantially more likely to be preserved in the environment of Cycle 3 than in the environments represented by Cycles 1, 2 and 4. Physical processes of sediment deposition appear to have varied but little over this interval, and we see no reason why phosphatic conulariids should have been any more susceptible to diagenetic alteration/loss in sediments of Cycles 1, 2 and 4 than they (presumably) were in deposits of Cycle 3. The possibility of exceptionally favourable environmental conditions for conulariids remains open, and thus Cycle 3 may represent an ecological epibole (Brett and Baird 1997; see also discussion below).

Life orientation of Otsego Member Conularia

The *Conularia*-rich Otsego Member beds of Cycle 3 are unusual both in the exceptional abundance of their conulariids and in the fact that many of these specimens are inclined at moderate or high angles to bedding, generally with their aperture facing obliquely upward and with their periderm inflated. Many other North American rock units, for example, the Elgin Member of the Upper Ordovician Maquoketa Formation (Van Iten *et al.* 1996), also contain conulariids. However, in none of these units is the proportion of conulariids to other fossils as high as that here observed, and well over 90 per cent of specimens in these rocks have been flattened and are oriented with their long axis more or less parallel to bedding.

At this point, it appears that the only known conulariid-bearing rock unit comparable to the beds here described is the Ponta Grossa Formation of Brazil (Simões *et al.* 2000*a*, *b*; Rodrigues *et al.* 2003, 2006). Unfortunately, the Lower Silurian shale lens that yielded *in situ Metaconularia manni* has been largely destroyed (N. C. Hughes, pers. comm. 2010). Approximately 24 per cent of the 111 Ponta Grossa conulariids measured by Rodrigues *et al.* (2003) were oriented aperture up and with their long axis inclined between 70 and 90 degree to bedding. The remaining Ponta Grossa specimens were inclined between 20 and 60 degree (27 per cent) or were parallel to bedding or slightly inclined (between 1 and 19 degree; 49 per cent) to it. Approximately 19 per cent of the moderately or steeply inclined Ponta Grossa specimens occurred in V-like pairs or in radial clusters of three specimens. As noted above, approximately 11 per cent of the Otsego Member *Conularia* specimens found in outcrop are paired or occur in radial clusters. However, the actual percentage of paired or clustered specimens may have been higher than this, as some now-single specimens originally may have occurred in pairs or clusters that were disaggregated by mass wasting of the outcrop face.

The steeply inclined Ponta Grossa conulariids were interpreted as sessile benthic animals that were buried *in situ*, in their original life orientations or close thereto

(Simões *et al.* 2000*a*, *b*; Rodrigues *et al.* 2003, 2006). These authors also suggested that the conulariids were either epibenthic or slightly infaunal, with the apical-most part of the periderm embedded in silty sediment (see Rodrigues *et al.* 2006, fig. 4). Specimens inclined at low or moderate angles to bedding were interpreted as transported remains or as specimens that were reoriented during or after burial. Rodrigues *et al.* (2006) argued further that steeply inclined specimens lived in relatively deep waters below storm wave base, while many specimens now oriented at low angles to bedding originally lived in shallower shelf environments between storm wave base and fair-weather wave base.

The conulariid-rich interval here investigated spans a more limited depth and time range than that spanned by the Ponta Grossa conulariids. In addition to extending over a narrower stratigraphic range (approximately 4 m versus approximately 19 m for the Ponta Grossa sample), Otsego Member *Conularia* show no evidence of a correlation between their angle of inclination and their level in the section (Fig. 2B), and the change in sediment texture through Cycle 3 is relatively slight. Of course, our interpretations of the depositional environment of these rocks, taken alone, do not rule out the hypothesis that Otsego Member *Conularia* originally lived above the seafloor, either as free-living animals or attached to erect, floating or mobile substrates. It is also possible that the present high frequency of moderately to steeply inclined, aperture-up conulariids is an artefact of reorientation. Conulariids living in the water column might have alighted on the bottom while still alive, or they may have settled onto the seafloor accidentally or after death. Alighting of live, free-living *Conularia* seems a highly improbable explanation of the present attitude of most specimens, which presumably would have alighted with the head (apertural) end down or on one of their faces. Similarly, the hypothesis of passive settling, presumably with the apex pointing downward (the hydrodynamically stable orientation for a conical or steeply pyramidal object of uniform mass distribution; Munson *et al.* 1994), requires that settling speeds were high enough to cause the conulariids to be injected into sandy sediment, to depths great enough to allow the preservation of high inclination angles. This scenario, although plausible perhaps for isolated specimens, seems to collapse in the face of multiple occurrences of V-like pairs and radial clusters. More specifically, the settling hypothesis seems to require far too many instances of (presumably) coincidental proximity of individuals in space and time, not to mention favourable spatial orientation and direction and depth of apical insertion, to account for the occurrence of semi-erect specimens preserved side-by-side and converging adapically, and moreover with their apical ends occurring at the same level. Likewise, it is difficult to imagine how planktonic clusters, which presumably would have been epiplanktonic or attached (apically) to a floatation structure, could have come to rest on the seafloor in the attitudes now exhibited by specimens in nearly erect V-like pairs and radial clusters. Then, too, why would so many more conulariids have lived in the water column at this time versus the times represented by Cycles 1–2 and 4, in which conulariid fossils are absent or extremely rare? Finally, while it is also possible that the present high frequency of moderately or steeply inclined, aperture-up specimens is an artefact of reorientation owing to bioturbation, this hypothesis, although plausible perhaps for certain isolated specimens, does not seem likely in the case of V-like pairs or radial clusters. More specifically, it seems highly improbable that members of observed pairs or clusters were all reoriented in such a manner as to preserve original, adapical convergence or to bring about such alignments secondarily.

In short, then, there seems to be no plausible explanation of the observed high frequency of steeply inclined, aperture-up Otsego Member conulariids other than the hypothesis that they were benthic animals that were buried *in situ*, in their original life orientations or close thereto. Some of these conulariids lived in pairs or clusters, and in cases where two or more conulariids lived side-by-side, their long axes converged adapically, to about the same level on or within the bottom sediment.

Mode of life of Otsego Member Conularia

The life orientation argued for above is consistent with both an epifaunal or a fully or partially infaunal mode of life. Previous investigators have documented circumstantial evidence of an epibenthic mode of life involving apical attachment for relatively small conulariids (<10 cm long), rare specimens of which are embedded within or arrayed along lithistid sponges (Finks 1955, 1960; Van Iten 1991*a*), nautiloid casts or phragmocones (Van Iten 1991*b*; Van Iten *et al.* 1996), hyolithid shells (Babcock *et al.* 1987), *Sphenothallus* tubes (Van Iten *et al.* 1996), crinoid stems (Sabattini and Hlebszevitsch 2004) or other organisms (Van Iten and Südkamp 2010). If attachment to hard, macroscopic biological substrates such as these was a more general mode of life for conulariids, and included species such as *Conularia desiderata*, then specimens of these taxa preserved *in situ*, with no post-mortem transport or significant postburial displacement, should be preserved with their apical end in direct contact with or in very close proximity to their substrate, and this substrate should be fairly large (provided it has been preserved).

Throughout the *Conularia*-rich interval in the Otsego Member, potential skeletal substrates, mostly calcitic spiriferids but also (dissolved) mollusc shells, are well preserved or at least clearly discernable, and thus it seems unlikely that an original substrate/attacher relationship between them and conulariids buried *in situ* would not itself be preserved. As discussed above, however, the apical end of nearly all observed moderately or steeply inclined, aperture-up *Conularia* rests upon argillaceous sandstone. Again, some of these specimens occur in radial clusters or V-like pairs, and thus, it is unlikely that the absence of underlying shell material is an artefact of transport. Although many of the specimens are in close *lateral* proximity to one or more rhynchonelliform brachiopods, almost none of them are situated with their apical end directly underlain by a brachiopod or other shell. Of course, it is possible that originally epifaunal *Conularia* were attached to nonmineralized plant stems or to other organic matter, for example, resistant biomats (see Seilacher and Hagadorn 2010), but if this was the case then the organic substrate has been not preserved. It is also possible that the present inclined, aperture-up attitude of at least some of the *Conularia* showing it is a taphonomic artefact, but as argued above, this probably is not the case for specimens forming V-like pairs or radial clusters, which almost certainly were buried *in situ*.

In addition to attaching to macroscopic hard substrates, other strategies for inhabiting fine-grained bottom sediments include (1) sediment sticking, (2) stable reclining, (3) rooting, (4) implantation by current scour and (5) 'resurrection' (Seilacher 2005). Implantation by current scour (4) and resurrection (5) seem out of the question in the present case as both require the action of scouring bottom currents, and the organisms that employ(ed) these strategies generally are single-shell-bearing recliners or bivalved. Similarly, stable reclining (2) does not apply to conulariids that were steeply inclined to the seafloor, but it may apply to specimens that are now subhorizontal. Although rooting structures (3) have not been documented in large conulariids (see however Kozlowski 1968 for illustrations of possible rhizoid structures near the apex of minute conulariid specimens), and were not observed in this study, it has been proposed (Van Iten 1992) that the conulariid periderm possessed a nonmineralized outer layer, and such a layer could conceivably have produced rooting structures that are not generally preserved.

This leaves the strategy of sediment sticking (1), which implies that semi-erect *Conularia* were infaunal. As summarized by Seilacher (2005, p. 261), the general idea is that the organism begins its sessile benthic existence on 'a dead starter substrate in concert with slow accumulation of sediment, and thereby become(s) progressively anchored (within sediment)'. Stable anchoring can be enhanced by passive implantation (Thayer 1975), which in the case of conical organisms is commonly brought about by differential growth and weighting of the apical end (see also Serezhnikova 2010).

Homogenization of Cycle 3 by burrowing organisms has made it all but impossible to determine the position of the original sediment–water interface along the periderm of semi-erect *Conularia*, as has been accomplished for other fossils such as partially infaunal bivalve molluscs (e.g. Bambach 1971, fig. 11). Nevertheless, at least three lines of evidence suggest that Otsego Member *Conularia* were not deeply embedded mud stickers, but rather epifaunal or partially infaunal organisms whose apical part alone may have been covered by sediment (e.g. Simões *et al.* 2000*b*, fig. 5; Fig. 7A). First, the apical region of the periderm is very thin (<0.5 mm) and shows no evidence of differential weighting through preferential deposition of shell material. Second, and as noted above, three of the observed V-like pairs are recumbent or nearly so, and assuming that they were originally V-like and semi-erect, it seems unlikely that they could have preserved their V-like configuration had they been fully infaunal and subjected to bottom currents strong enough to scour away the sediment originally surrounding them. Rather, it seems more likely that they were epifaunal or partially infaunal specimens that were toppled over. Third, the apical region of some of the semi-erect *Conularia* abuts or is situated immediately adjacent (laterally) to a horizontal conulariid or to one or more articulated spiriferids (Fig. 7), some of which are oriented umbo down and may have been smothered. Although one can conceive of various ways of bringing spiriferids or recumbent conulariids and the apical region of semi-erect *Conularia* into lateral juxtaposition, we think that the simplest and most likely hypothesis is that the horizontal conulariids and spiriferids were resting on top of sediment that originally covered the apical region of the adjacent semi-erect *Conularia*. In other words, the middle and apertural regions of these *Conularia* stuck out above the sediment-water interface. As noted above, the bottom sediment was stable enough to prevent sinking of moderately large spiriferids below this surface, and thus, it is at least plausible that the sediment could also bear the weight of semi-erect conulariids. To be sure, the presence of laterally adjacent brachiopods or recumbent *Conularia* at levels closer to the aperture suggests that at least some semi-erect *Conularia* were buried up to their middle or apertural region prior to complete and final burial (Fig. 7B–C). Such occurrences may have affected specimens already dead as well as living specimens. Occurrences of semi-erect conulariids having their apical end situated more or less directly above the apertural end of other such specimens suggest that the original thickness of at least some obrution deposits was on the order of several tens of millimetres. We suspect that final burial of many conulariids now oriented at high angles to bedding occurred in life,

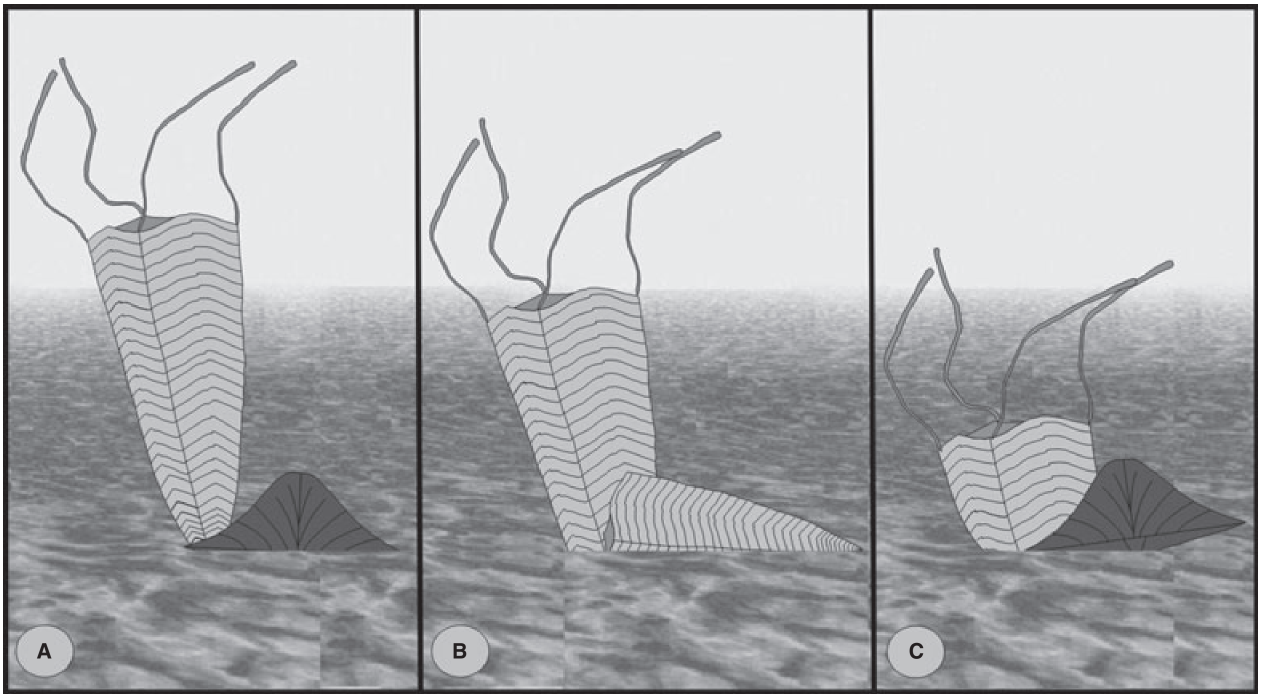


FIG. 7. Interpretive reconstructions of steeply inclined Otsego Member *Conularia* aff. *desiderata* Hall showing varying degrees of burial. Drawings based on observed conulariid-conulariid or conulariid-brachiopod associations. A, Living specimen standing next to a spiriferid brachiopod (in life orientation) and with its apical region partially buried in bottom sediment. B, Specimen situated next to a recumbent conulariid and buried up to its middle region. C, Specimen situated next to a spiriferid brachiopod and buried up to its apertural region.

before their (presumably) delicate apical end had time to decay. This hypothesis may account for the observations that the apertural lappets of semi-erect specimens are folded inward (a possible response to catastrophic burial; Van Iten and Südkamp 2010), and that the apertural region of inclined specimens is often encased in a concretion, the formation of which may have been triggered by decay of conulariid soft parts.

Assuming that Otsego Member *Conularia* were steeply inclined during life and that their middle and apertural regions normally projected up out of the bottom sediment, fossil specimens now inclined at low or moderate angles to bedding can be interpreted as individuals that were tilted or toppled prior to or during final burial, or as individuals that were realigned while buried, presumably as a result of sediment compaction and/or burrowing and bioturbation. As noted above, specimens inclined at low or moderate angles show strong evidence of preferential alignment of their azimuthal trends. This observation suggests that postburial realignment alone cannot account for their present attitudes and thus that tilting and toppling, possibly induced by storm currents, and realignment by currents may have been important factors. Then, too, conulariids may have shown preferential alignments in life, perhaps in response to weak bottom currents between storm events. Tilting or toppling could have occurred either following death or prior to it. In the latter case, toppled individuals may have adopted a recumbent mode of life (provided they could prevent fouling of their oral end by sediment).

The very small percentage of specimens that both are steeply inclined and have their aperture facing downward are a special problem. Here again, though, the explanation may involve toppling, on an originally uneven seafloor, or perhaps local scour and tipping into small scour pits, from small-scale, very brief turbulent bursts within the flow of a burial current.

Depositional Settings: Otsego Member versus Ponta Grossa Formation conulariids

As noted above, portions of the Devonian Ponta Grossa Formation of Brazil also feature abundant *in situ* conulariids (Simões *et al.* 2000*a*, *b*; Rodrigues *et al.* 2003, 2006). The conulariids occur in rocks indicative of low sedimentation rates, punctuated by abrupt burial below storm wave base, under dysaerobic to aerobic seafloor water conditions. Their occurrence has been interpreted to be the result of enhanced taphonomic preservation at the base of parasequences (see Rodrigues *et al.* 2003, p. 383, fig. 2), within the broader transgressive systems tracts of multiple third-order depositional sequences (Simões *et al.* 2000*a*; Rodrigues *et al.* 2003). Optimal preservation of *in situ* conulariids in the Ponta Grossa Formation seems to be linked to rock successions deposited below storm wave base, during the TST, especially in environments of low net sedimentation rates punctuated by abrupt burial.

In contrast to the Ponta Grossa conulariids, those in the Otsego Member occur within a single sixth-order parasequence (Cycle 3). Adjacent parasequences lack conulariids (with the exception of two specimens found at the top of Cycle 2). Moreover, the Otsego Member conulariids occur throughout most of Cycle 3, appearing to be absent only in the lower 2.7 m and topmost 0.8 m of the cycle. While parasequence-scale systems tract boundaries are difficult to delineate within Cycle 3, the conulariids clearly occur through the sixth-order HST and likely through the lower to middle FSST, with or without part of the TST, and are absent through at least part of the TST and the FSST/LST (cycle cap). Furthermore, Cycle 3 falls within the early stage of a fourth-order FSST, and within the FSST of the larger third-order cycle.

In all of these senses, then, the occurrences of *in situ* conulariids in the Otsego Member contrast with their distribution through sequences and systems tracts in the Brazilian Ponta Grossa Formation. Thus, and as suggested above, the conulariid-rich interval in the Otsego Member probably is not a taphonomic epibole (*sensu* Brett 1995), but an ecological epibole, that is an epibole reflecting exceptionally favourable physical, chemical and/or biological conditions for population growth of an otherwise rare faunal element. Nevertheless, like the Ponta Grossa conulariids, the Otsego Member specimens appear to have lived in settings below storm wave base, within the influence of bottom currents, under largely aerobic seafloor conditions, and to have been buried by distal obrution event deposits.

Nature of the conulariid schott

Some specimens of six of the 11 North American Devonian and Mississippian species of *Conularia* terminate in a schott (Babcock and Feldmann 1986; Van Iten *et al.* 2006*a*). Babcock and Feldmann (1986) stated that schotts have not been observed in *Conularia desiderata*. As illustrated by Babcock and Feldmann (1986, figs 10.4, 11.2, 12.3, 14.1 and 15.4) and reported by Van Iten *et al.* (2006*a*), the position of the contact line between the transverse portion of the schott and the inner surface of the periderm proper is variable, ranging from a single face width of 1.5–4 mm in relatively small species (e.g. *C. ulsterensis* and *C. milwaukeensis*; original maximum lengths 30 and 100 mm, respectively) to a single face width of 10–20 mm in larger species (e.g. *C. multicostata* and *C. subcarbonaria*; original maximum lengths 250 and 350 mm, respectively). In *C. undulata*, which is similar in size to *C.* aff. *desiderata*, the contact line of the terminal schott in one specimen (Babcock and Feldmann 1986, fig. 14.1) occurs at a single face width of approximately 12 mm, or several tens of millimetres above the position of the (now missing) apex.

The absence of schotts in the peridermal cavity of 18 relatively large *C.* aff. *desiderata* here examined, 15 of which were buried *in situ*, suggests that schott production was not a regular feature of the ontogeny of this conulariid. To be sure, distortion of the apical end of most of the specimens makes it impossible to assess whether schotts were present at levels still closer to the apex. Nevertheless, if schotts in relatively large conulariids (100 mm long or greater) generally were situated several tens of millimetres above the apex, then the present results can be seen as falsifying the hypothesis that schott production was a regular feature of conulariid ontogeny.

Origin of conulariid pairs and clusters

As noted above, members of V-like pairs and radial clusters here examined show no direct evidence of original continuity of peridermal material at their apical ends. However, the observation that several of the V-like pairs are subhorizontal, apparently as a result of toppling, does suggest some kind of material connection between the component specimens in life. While such a connection does not necessarily indicate a clonal origin for these associations, at present we cannot rule out this hypothesis.

SUMMARY AND FINAL COMMENTS

1. Exceptionally abundant *Conularia* aff. *desiderata* Hall occur in the upper part of the Otsego Member of the Mount Marion Formation (Middle Devonian, Givetian) of eastern New York State, where a brachiopod-mollusc-dominated macrofauna inhabited a relatively low-energy, siliciclastic marine shelf environment in which conulariids and associated invertebrates were sometimes smothered by episodic depositional events.
2. *Conularia* originally measuring up to about 150 mm long were oriented in life with their long axis inclined at high angles (up to almost 90 degree) to the sea floor and with their apertural (oral) end facing upward.
3. *Conularia* did not attach to hard biological substrates. Rather, the erect or semi-erect animals either stood upon or had their apical region partially buried within very fine sediment that was stable.

4. Most *Conularia* were solitary, but some specimens lived in compact pairs or clusters of three or four individuals, some or all of which converged adapically.
5. *Conularia*-forming V-like pairs or radial clusters show no direct evidence of original continuity of peridermal material at their apical ends.
6. Schott formation was not a regular feature of the life history of Otsego Member *Conularia*.
7. The conulariid-rich interval in the Otsego Member appears to constitute an ecological epibole characterized by environmental conditions exceptionally favourable for conulariid life.

Acknowledgements. Permission to access the study site was granted by M. Wright. Many of the *Conularia* specimens examined here were found by M. Burkey, L. Hernick, Z. Lumley, T. and K. Preston, R. J. Van Iten and R. Wright. Photographs of fossil specimens were taken by K. Preston and T. Van Iten. Partial financial support for this research was provided by grants to the senior author from the Hanover College Faculty Development Committee.

Editor. George Sevastopulo

REFERENCES

ALEXANDER, R. 1986. Life orientation and post-mortem reorientation of Chesterian brachiopod shells by paleocurrents. *Palaios*, **1**, 303–311.

ANDERSON, E. J. and GOODWIN, P. W. 1990. The significance of metre-scale allocycles in the quest for a fundamental stratigraphic unit. *Journal of the Geological Society*, **147**, 507–518.

ANELLI, L. E., SIMÕES, M. G. and ROCHA-CAMPOS, A. C. 1998. Life mode of some Brazilian Upper Paleozoic anomalodesmatans. 69–74. *In* JOHNSTON, P. A. and HAGGART, J. W. (orgs). *Bivalves: an eon of evolution. Paleobiological studies honoring Norman D. Newell.* Calgary University Press, Calgary, Saskatchewan, 461 pp.

BABCOCK, L. E. and FELDMANN, R. M. 1986. Devonian and Mississippian conulariids of North America. Part A. General description and *Conularia*. *Annals of Carnegie Museum*, **55**, 349–410.

—— —— WILSON, M. T. and SUAREZ-RIGLOS, M. 1987. Devonian conulariids of Bolivia. *National Geographic Research*, **3**, 210–231.

BAMBACH, R. K. 1971. Adaptations in *Grammysia obliqua* (McCoy) (Mollusca: Bivalvia). *Lethaia*, **4**, 169–183.

BRETT, C. E. 1991. Organism-sediment relationships in Silurian marine environments. *Special Papers in Palaeontology*, **44** (1991), 301–344.

—— 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. *Palaios*, **10**, 597–616.

—— 2003. Taphonomy: sedimentological implications of fossil preservation. 723–729. *In* MIDDLETON, G. V. (ed.). *Encyclopedia of sediments and sedimentary rocks*. Kluwer Academic Publishers, Boston, 821 pp.

—— and ALLISON, P. E. 1998. Paleontological approaches to the environmental interpretation of marine mudrocks. 301–349. *In* SCHIEBER, J., ZIMMERLE, W. and SETHI, P. (eds). *Shales and Mudstones I*. E. Schweizerbart'sche Verlagsbuchhandlung (Nagele und Obermiller), Stuttgart, 369 pp.

—— and BAIRD, G. C. 1996. Middle Devonian sedimentary cycles and sequences in the northern Appalachian basin. 213–241. *In* WITZKE, B. J., LUDVIGSON, G. A. and DAY, J. (eds). *Paleozoic sequence stratigraphy: views from the North American craton*. Boulder, Colorado, *Geological Society of America Special Paper*, **306**, 434 pp.

—— —— 1997. Epiboles, outages, and ecological evolutionary bioevents: taphonomic, ecologic, and biogeographic factors. 249–284. *In* BRETT, C. E. and BAIRD, G. C. (eds). *Paleontological events: stratigraphic, ecologic, and evolutionary implications*. Columbia University Press, New York, 604 pp.

BROOD, K. 1995. Morphology, structure, and systematics of the conulariids. *GFF*, **117**, 121–138.

CHERNS, L. and WRIGHT, P. V. 2000. Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea. *Geology*, **28**, 791–794.

DATTILO, B. F., BRETT, C. E., TSUJITA, C. J. and FAIRHURST, R. 2008. Sediment supply versus storm winnowing in the development of muddy and shelly interbeds from the Upper Ordovician of the Cincinnati region, USA. *Canadian Journal of Earth Sciences*, **45**, 243–265.

ETTENSOHN, F. R. 1985. The Catskill Delta complex and the Acadian Orogeny: a model. 39–49. *In* WOODROW, D. L. and SEVON, W. D. (eds). *The Catskill Delta. Geological Society of America Special Paper*, **201**, 246 pp.

FINKS, R. M. 1955. *Conularia* in a sponge from the west Texas Permian. *Journal of Paleontology*, **29**, 831–836.

—— 1960. Late Paleozoic sponge faunas of the Texas region. The siliceous sponges. *Bulletin of the American Museum of Natural History*, **120**, 7–160.

GAUGRIS, K. A. and GRAHN, Y. 2006. New chitinozoan species from the Devonian of the Paraná Basin, south Brazil, and their biostratigraphic significance. *Ameghiniana*, **43**, 293–310.

GRAHN, Y., PEREIRA, E. and BERGAMASCHI, S. 2000. Silurian and Lower Devonian Chitinozoan biostratigraphy of the Paraná Basin in Brazil and Paraguay. *Palynology*, **24**, 147–176.

—— —— —— 2002. Middle and Upper Devonian Chitinozoan biostratigraphy of the Paraná Basin in Brazil and Paraguay. *Palynology*, **26**, 135–165.

HOLZ, M. and SIMÕES, M. G. 2002. *Elementos fundamentais de taphonomia*. Editora da Universidade/UFRGS, Porto Alegre, Brazil, 231 pp.

JOHN, D. L., HUGHES, N. C., GALAVIZ, M. I., GUNDERSON, G. O. and MEYER, R. 2010. Unusually preserved *Metaconularia manni* (Roy, 1935) from the Silurian of Iowa, and the systematics of the genus. *Journal of Paleontology*, **84**, 1–31.

KOENKER, R. H. 1981. *Simplified statistics for students in education and psychology*. Littlefield, Adams and Co., Totowa, New Jersey, 171 pp.

KOZLOWSKI, R. 1968. Nouvelles observations sur les conulaires. *Acta Palaeontologica Polonica*, **13**, 497–535.

LEME, J. M., SIMÕES, M. G., RODRIGUES, S. C., VAN ITEN, H. and MARQUES, A. C. 2008*a*. Major developments in conulariid research: problems of interpretation and future perspectives. *Ameghiniana*, **45**, 407–420.

—— —— —— —— —— 2008*b*. Cladistic analysis of the suborder Conulariina Miller and Gurley 1896 (Cnidaria, Scyphozoa; Vendian-Triassic). *Palaeontology*, **51**, 649–662.

—— —— and VAN ITEN, H. 2010. *Phylogenetic Systematics and Evolution of Conulariids: systematics and evolution of a problematical fossil taxon: the Family Conulariidae (Cnidaria; Ediacaran/Triassic)*. Lambert Academic Publishing, Saarbrücken, 49 pp.

MARSH, L. F. 1984. Mode of life and autecology of Silurian-Devonian Grammysiidae (Bivalvia). *Palaeontology*, **27**, 679–691.

MCKINNEY, F. K., DEVOLVÉ, J. J. and SOBIERAJ, J. 1995. *Conularia* sp. from the Pyrénées: further support for a scyphozoan affinity for conulariids. *Lethaia*, **28**, 229–236.

MUNSON, B. R., YOUNG, D. F. and OKIISHI, T. H. 1994. *Fundamentals of fluid mechanics*, 2nd edn. John Wiley and Sons, New York, 893 pp.

RODRIGUES, S. C., SIMÕES, M. G. and LEME, J. M. 2003. Tafonomia comparada dos Conulatae (Cnidaria), Formação Ponta Grossa, Bacia do Paraná, Estado do Paraná. *Revista Brasileira de Geociências*, **33**, 1–10.

—— LEME, J. M. and SIMÕES, M. G. 2006. Significado paleobiológico de agrupamentos (coloniais/gregários) de *Conularia quichua* Ulrich 1890 (Cnidaria), Formação Ponta Grossa, Devoniano (Pragiano-Emiano), Bacia do Paraná, Brasil. *Ameghiniana*, **43**, 273–284.

ROOKE, H. and CAREW, J. L. 1983. New light on a poorly understood fossil group. *Geological Society of America, Abstracts with Program*, **15**, 53.

SABATTINI, N. and HLEBSZEVITSCH, J. 2004. Nueva evidencia en relación con el modo de vida de los Conulariida. *Ameghiniana*, **41**, 399–404.

SEILACHER, A. 2005. Secondary soft-bottom dwellers: convergent responses to an evolutionary 'mistake'. 257–271. *In* BRIGGS, D. E. K. (ed.). *Evolving form and function: fossils and development*. Yale University Press, New Haven, 288 pp.

—— and HAGADORN, J. W. 2010. Early molluscan evolution: evidence from the trace fossil record. *Palaios*, **25**, 565–575.

SEREZHNIKOVA, A. E. A. 2010. Colonization of substrates: Vendian sedentary benthos. *Paleontological Journal*, **44**, 1560–1569.

SIMÕES, M. G., KOWALEWSKI, M., TORELLO, F. F. and ANELLI, L. E. 1998. Long-term time-averaging despite abrupt burial: Paleozoic obrution deposits from epeiric settings of Paraná Basin, Brazil. *Geological Society of America, Abstracts with Program*, **30**, 384.

—— MELLO, L. H. C., RODRIGUES, S. C., LEME, J. M. and MARQUES, A. C. 2000*a*. Conulariid taphonomy as a tool in paleoenvironmental analysis. *Revista Brasileira de Geociências*, **30**, 757–762.

—— MARQUES, A. C. and COLLINS, A. G. 2000*b*. *In situ* preservation of conulariids from the Ponta Grossa Formation (Devonian of Brazil), with comments on the phylogenetic placement of Conulatae within Cnidaria. *Paleobios*, **20**, 9.

SPEYER, S. E. and BRETT, C. E. 1988. Taphofacies models for epeiric sea environments: middle Paleozoic examples. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **63**, 225–262.

STANLEY, S. M. 1972. Functional morphology and evolution of bysally attached bivalve molluscs. *Journal of Paleontology*, **46**, 165–212.

TAYLOR, J. D. and GLOVER, E. A. 2006. Lucinidae (Bivalvia) – the most diverse group of chemosymbiotic molluscs. *Zoological Journal of the Linnean Society*, **148**, 421–438.

THAYER, C. W. 1975. Morphological adaptations of benthic invertebrates on soft substrata. *Journal of Marine Research*, **33**, 177–189.

VAN ITEN, H. 1991*a*. Repositories of and additional comments on Permian sponge specimens containing molds of *Paraconularia*. *Journal of Paleontology*, **65**, 335–337.

—— 1991*b*. Anatomy, patterns of occurrence, and nature of the conulariid schott. *Palaeontology*, **34**, 939–954.

—— 1992. Microstructure and growth of the conulariid test: implications for conulariid affinities. *Palaeontology*, **35**, 359–372.

—— and COX, R. S. 1992. Evidence of clonal budding in a radial cluster of *Paraconularia crustula* (White) (Pennsylvanian: ?Cnidaria). *Lethaia*, **25**, 421–426.

—— and SÜDKAMP, W. 2010. Exceptionally preserved conulariids and an edrioasteroid from the Hunsrück Slate (Lower Devonian, SW Germany). *Palaeontology*, **53**, 403–414.

—— and VYHLASOVÁ, Z. 2004. Conulariids. 119–123. *In* WEBBY, B. D., PARIS, F., DROSER, M. L. and SMITH, J. A. (eds). *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 484 pp.

—— FITZKE, J. A. and COX, R. S. 1996. Problematical fossil cnidarians from the Upper Ordovician of the North-Central USA. *Palaeontology*, **39**, 1037–1064.

—— LEME, J. M., RODRIGUES, S. C. and SIMÕES, M. G. 2006*a*. New data on the anatomy of *Conularia milwaukeensis* Cleland, 1911 (Middle Devonian, Iowa and Wisconsin). *Journal of Paleontology*, **80**, 393–395.

—— —— SIMÕES, M. G., MARQUES, A. C. and COLLINS, A. G. 2006*b*. Reassessment of the phylogenetic position of conulariids (?Ediacaran-Triassic) within the subphylum Medusozoa (phylum Cnidaria). *Journal of Systematic Palaeontology*, **4**, 109–118.

—— LICHTENWALTER, M., LEME, J. M. and SIMÕES, M. G. 2006*c*. Possible taphonomic bias in the preservation of phosphatic macro-invertebrates in the uppermost Maquoketa Formation (Upper Ordovician) of northeastern Iowa (north-central USA). *Journal of Taphonomy*, **4**, 129–144.

VER STRAETEN, C. A. 2010. Lessons from the foreland basin: Northern Appalachian basin perspectives on the Acadian orogeny. 251–282. *In* TOLLO, R. P., BARTHOLOMEW, M. J., HIBBARB, J. P. and KARABINOS, P. M. (eds). *From Rodinia to Pangea: the lithotectonic record of the Appalachian region. Geological Society of America Memoir*, **206**, 972 pp.

—— and BRETT, C. E. 1995. Lower and Middle Devonian foreland basin fill in the central Catskill front: stratigraphic synthesis, sequence stratigraphy, and the Acadian orogeny. 313–356. *In* GARVER, J. I. and SMITH, J. A. (eds). *Field trips for the 67th annual meeting of the New York State Geological Association, Union College, Schenectady, NY*, 426 pp.

—— —— 2006. Pragian to Eifelian strata (middle lower to lower Middle Devonian), northern Appalachian basin – stratigraphic nomenclatural changes. *Northeastern Geology and Environmental Sciences*, **28**, 80–94.

ZONNEVELD, J. P. and GREENE, S. E. 2010. Lingulid response to severe storms recorded in Middle Triassic strata of northeastern British Columbia. *Palaios*, **25**, 807–817.