



Palaeobiogeography, palaeoecology and evolution of Lower Ordovician conulariids and *Sphenothallus* (Medusozoa, Cnidaria), with emphasis on the Fezouata Shale of southeastern Morocco



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ABSTRACT

The fossil record of conulariids (Cnidaria, Scyphozoa) extends downward into the topmost part of the Ediacaran System, but the first appearance of diverse, widespread conulariids is in siliciclastic rock units of Early Ordovician age, which collectively host at least six conulariid genera. Some of these same units also contain *Sphenothallus*, a probable medusozoan that frequently co-occurs with conulariids in Ordovician and younger deposits. Lower Ordovician conulariid localities are distributed among five (originally) Southern Hemisphere terranes, namely Core Gondwana (*Archaeoconularia*, *Eoconularia* and *Teresconularia*), Armorica (*Conularia azaisi*), Avalonia (*Archaeoconularia*, *Eoconularia* and *Exoconularia*), Perunica (*Archaeoconularia*, *Conularia* and *Conulariella*) and South China (*Conulariella*). *C. azaisi*, currently known from the Southern Montagne Noire (France), probably represents a new genus. *Sphenothallus* occurs in South China, North China (Korea), Armorica (Southern Montagne Noire) and Core Gondwana (Morocco). In southeastern Morocco, Burgess Shale-type Konservat-Lagerstätten in the Fezouata Shale (Tremadocian–Floian) yield *Archaeoconularia* sp., *Eoconularia* sp. and at least one species of *Sphenothallus*. This low-diversity conulariid assemblage is most similar to the Tremadocian assemblage of Wales (Avalonia), which likewise consists of a single species each of *Archaeoconularia* and *Eoconularia*. In the Fezouata Shale, *Archaeoconularia* sp. and *Eoconularia* sp. frequently occur in monospecific mass associations. Such associations probably represent an original clumped distribution on the seafloor. Additionally, some *Eoconularia* sp. occur in V-like pairs or radial clusters, and also some specimens were attached at the apical end to a phosphatic brachiopod or to a corner sulcus of a larger specimen of *Eoconularia* sp. Similar conulariid/brachiopod associations, consisting of *Conularia trentonensis* and *Onniella* sp., occur in the Upper Ordovician (Katian) Collingwood Shale of southern Ontario, Canada.

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1. Introduction

Conulariids (order Conulariida Miller and Gurley, 1896) and *Sphenothallus* Hall, 1847, two extinct groups of medusozoan cnidarians that produced a finely lamellar, organo-phosphatic periderm (Van Iten et al., 1992, 2006a), first appear in the uppermost Ediacaran and lower

Cambrian systems, respectively (e.g. Zhu et al., 2000; Li et al., 2004; Van Iten et al., 2014a). *Sphenothallus* has been reported widely from the Cambrian System (see for example Fatka and Kraft, 2013; Muscente and Xiao, 2015), but thus far Cambrian conulariids are represented solely by *Baccaconularia* Hughes et al., 2000 from the Furongian Saint Lawrence Formation (Upper Mississippi Valley, USA), though conulariids may occur in Cambrian Stage 1 (see Van Iten et al., 2010 and references cited therein), and *Paraconularia* sp. has been found in the latest Ediacaran Tamengo Formation of Brazil (Van Iten et al., 2014a). The last occurrence is particularly intriguing as recent cladistic analyses (Leme et al., 2008; Van Iten et al., 2014b) posit that *Paraconularia* Sinclair, 1940 was a relatively apical branch on the conulariid tree. In a number of Ordovician and younger rock units,

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conulariids and *Sphenothallus* occur in close association with each other, in some cases in relatively restricted facies in which normal marine benthos such as corals, crinoids and rhynchonelliform brachiopods are rare or absent (e.g. Van Iten et al., 1996, 2012). Thus, in addition to possibly being closely related to each other phylogenetically, conulariids and *Sphenothallus* may have shared similar palaeoenvironmental preferences.

The first appearance of multiple genera of conulariids, in localities throughout much of the world, is in Lower Ordovician formations, some of which also host *Sphenothallus* (Table 1). Interestingly, all currently known Lower Ordovician conulariids and *Sphenothallus* are from (originally) Southern Hemisphere terranes and localities, predominantly Gondwanan and peri-Gondwanan, which, with the exception of North China, generally were situated at mid- to very high palaeolatitudes (Cocks and Torsvik, 2004). In part this may reflect the fact that the Lower Ordovician rock records of the relatively few low-latitude terranes such as Laurentia are dominated by sparsely fossiliferous dolostones deposited in restricted environments (e.g. Overstreet et al., 2003), suggesting that the lack of conulariids and *Sphenothallus* in these regions may be, at least to some extent, caused by palaeoenvironmental or taphonomic artifacts. The most recent discoveries of Lower Ordovician conulariids are in the Santa Victoria Group of northwestern Argentina (*Teresconularia*; Leme et al., 2003), the Tonggao Formation of Guizhou Province, South China (*Conulariella*; Van Iten et al., 2013), and the Fezouata Shale of southeastern Morocco (Van Roy et al., 2015). In the last two formations, conulariids co-occur with *Sphenothallus*. The Tremadocian–Floian Fezouata Shale contains two exceptionally preserved fossil intervals (EPFs) yielding soft-bodied arthropods and other taxa, some of which were originally described from Burgess Shale-type biotas of early or middle Cambrian age (Van Roy et al., 2010; Martin et al., in press). *Sphenothallus* and two species of conulariids collectively occur in both of these intervals, one of which (60 m thick) occurs in the lower part of the formation and is late Tremadocian in age, and the other of which (15 m thick) occurs in the upper part and is mid Floian in age (Gutiérrez Marco and Martin, 2016–in this issue). Many Burgess Shale-type Cambrian faunas have been sampled intensively, yielding tens of thousands of exceptionally well-preserved fossils ranging from micro-invertebrates to chordates (e.g. Caron and Jackson, 2008; Zhao et al., 2010). *Sphenothallus* sp. is extremely rare in the mid Cambrian Burgess Shale (British Columbia, Canada; Van Iten et al., 2002), but to date neither this nor any other Cambrian Konservat-Lagerstätte has produced even a single conulariid.

The present article addresses key aspects of the distribution, palaeoecology and evolution of Lower Ordovician conulariids and *Sphenothallus*, in the context of a parsimony-based cladistic hypothesis of phylogenetic relationships among conulariid genera (Fig. 1). We pay particular attention to the Fezouata Shale, which at present is the only Ordovician rock unit in Africa known to contain conulariids and *Sphenothallus*. In addition to Burgess Shale-type organisms, the Fezouata Shale has yielded exceptionally preserved conulariids exhibiting evidence of original apical attachment to phosphatic brachiopods and conulariids apparently attached to other conulariid specimens.

2. Material and methods

The present study is based on review of the relevant literature and on direct examination of fossil specimens in collections of the following seven institutions: Department of Earth Sciences, Cadi Ayyad University, Marrakesh, Morocco (sample number prefix AA); Department of Earth Sciences, University of Lyon, France (sample number prefix UCBL-FSL); Department of Earth Sciences, Montpellier University, France (sample number prefix UM); National Museum of Wales (Cardiff, UK); Natural History Museum (London, UK); University of Michigan Museum of Paleontology (Ann Arbor, USA); specimen prefix number UMMP); and Yale University Peabody Museum (New Haven,

Table 1
Distribution of Lower Ordovician conulariids and *Sphenothallus* [in brackets]. An asterisk (*) next to a species name indicates that the occurrence is first reported/document in the present paper.

Terrane/locality	Unit	Age	Taxon or Taxa	Lithotype(s), references (–), repositories [–]
Amorica (Montagne Noire, France)	Saint Chinian Formation (upper part)	Late Tremadocian	<i>Conularia azaisi</i> Thoral, 1935	Monotonous dark gray and green claystones and siltstones with fine–medium sandy intercalations and siliceous nodules (<i>C. azaisi</i> occurs in shale or in siliceous nodules) (1) [ULF, MUF]
Amorica (Montagne Noire, France)	La Maurerie Formation (lower part)	Early Floian	<i>Conularia azaisi</i> Thoral, 1935	Alternating dark shales and fine sandstones (2) [ULF]
Amorica (Montagne Noire, France)	Landeyran Formation	Late Floian	<i>Conularia cf. azaisi</i> Thoral, 1935	Silty shale (2) [MUF]
Avalonia (Wales)	Dol–Cyn–Afon Formation	Tremadocian	<i>[Sphenothallus sp.]</i> <i>Archaeoconularia homifrayi</i> (Salter, 1866)	Gray mudstone, silty mudstone and siltstone with rare bioturbated sandstone (3) [NHM, NMW]
Perunica (Czech Republic)	Ogof Hên Formation Bolshaul Member Mlina Formation	Floian Tremadocian	<i>Eoconularia linnaeensis</i> (Holm, 1893) <i>Eoconularia</i> sp. nov. Mortin, 1986	Interbedded mudstone and siltstone (4) [NMW]
North China (Korea)	Klabava Formation	Early–late Floian	<i>Archaeoconularia insignis</i> (Barrande, 1867) <i>Conularia rarcostata</i> Barrande, 1867	Dark shale with chert nodules (5) [NMP]
South China (Guizhou Province)	Myto Member	Tremadocian	<i>Conulariella purkynei</i> (Želízko, 1911) <i>Conulariella robusta</i> (Barrande, 1867)	Clayey shales with subordinate micaceous shales and tuffaceous material and siliceous nodules (all three species of <i>Conulariella</i> occur in siliceous nodules) (5) [NMP]
Core Gondwana	Dumugol Formation Tonggao Formation Santa Victoria Group Fezouata Shale	Early Floian Early Floian Early Tremadocian Late Tremadocian–mid Floian	<i>Conulariella sulca</i> (Želízko, 1921) <i>Sphenothallus</i> sp. <i>Conulariella</i> sp. [<i>Sphenothallus</i> sp.] <i>Teresconularia argentinensis</i> Leme et al., 2003 <i>Archaeoconularia</i> sp.* <i>Eoconularia</i> sp.* [<i>Sphenothallus</i> sp.*]	Lime mudstone and argillaceous lime mudstone (6) Blue–gray shale and yellow–green shale and silty shale (7) [NIGP] Conglomerate (8) [IMI] Green silty mudstone and micaceous sandy siltstones (9) [CAU, ULF, YPM]

Taxonomic and/or lithological references (references dealing with systematic paleontology indicated by a double asterisk): (1) Thoral, 1935; (2) Kröger and Evans, 2011; Vizcaino et al., 2006; (3) Vizcaino et al., 2001; Tortello et al., 2006; (4) Mortin, 1986; (5) Barrande, 1867; (6) Bouček, 1928; (7) Kraft and Kraft, 2003; Van Iten and Vhylasova, 2004; (8) Choi, 1990; (9) Van Iten et al., 2013; (10) Leme et al., 2003; (11) Martin et al., in press; Gutiérrez Marco and Martin, 2016–in this issue. Repositories: CAU—Cadi Ayyad University, Marrakesh, Morocco; IMI—Facultad de Ciencias Naturales, Instituto Miguel Lillo, Tucumán, Argentina; MUF—Montpellier University, France; NHM—Natural History Museum, London; NIGP—Nanjing (China) Institute of Geology and Palaeontology; NMP—National Museum of Wales, Cardiff; ULF—University of Lyon, France; YPM—Yale Peabody Museum, USA.

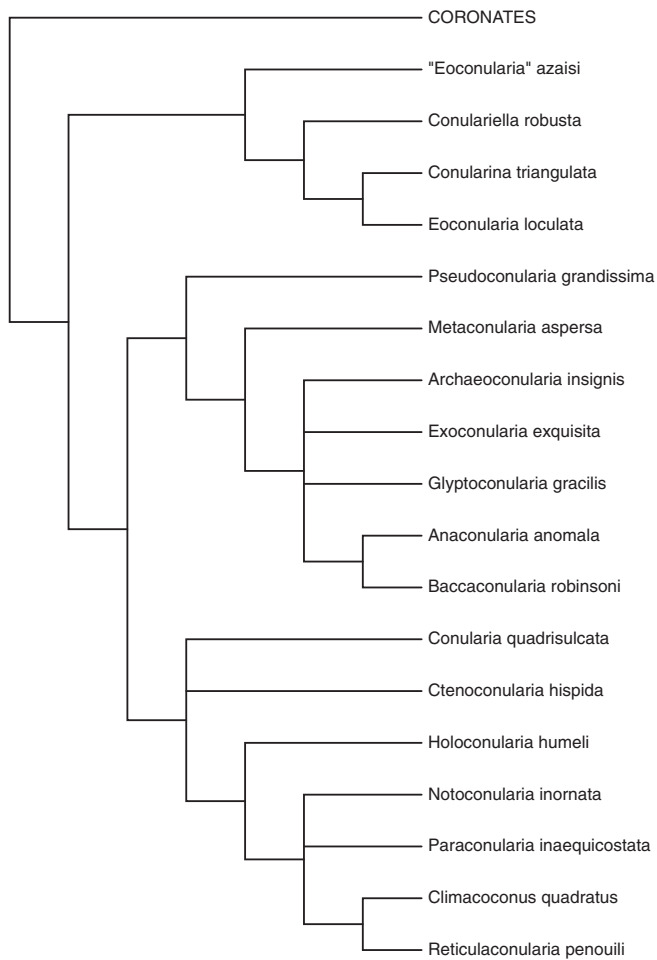


Fig. 1. Most parsimonious cladistic hypothesis of the phylogenetic relationships between 17 conulariid genera (represented by their type species) and *Conularia azaisi* Thoral, 1935 (length = 35, consistency index = 0.514, rescaled consistency index = 0.764). Analysis based on 18 unweighted, binary characters of the periderm polarized using coronate scyphozoans as the outgroup (see Supplemental data).

Connecticut, USA; sample number prefix YPM). The most recent reports of Lower Ordovician conulariids and *Sphenothallus* are authored by one or more of the present investigators, and, with the exception of the *Sphenothallus* reported by Choi (1990), all other reports accepted here as valid were verified by direct examination of reposit specimens. Several of the occurrences tabulated here, namely *Sphenothallus* sp. from the Southern Montagne Noire (France) and this genus as well as two species of conulariids from the Fezouata Shale, are first reported in this article (Table 1). Material from the Fezouata Shale (approximately 500 examined specimens, primarily conulariids) was collected near the town of Zagora (Central Anti-Atlas) by field parties under the direction of B. Lefebvre (University of Lyon) and P. Van Roy (Ghent University (Belgium) and Yale University), during the course of multiple field seasons. Our phylogenetic analysis was conducted using PAUP* 4.0 b10 (Swofford, 2003) and followed the general procedures of Marques and Collins (2004), Collins et al. (2006) and Van Iten et al. (2006a, 2014b). Our character matrix is provided as Supplementary data.

3. Lower Ordovician conulariids and *Sphenothallus*

Together with *Sphenothallus*, Lower Ordovician strata have yielded six genera of conulariids: *Archaeoconularia* Bouček, 1939, *Conularia*

Miller in Sowerby, 1821, *Conulariella* Bouček, 1928, *Eoconularia* Sinclair, 1944, *Exoconularia* Sinclair, 1952 and *Teresconularia* Leme et al., 2003 (Figs. 2–4). *Conularia azaisi* Thoral, 1935 (Fig. 2A), originally described from the Saint Chinian Formation of the Southern Montagne Noire, France, has also been recorded from this region in the La Maurerie and Landeyran formations, and identified either as *Eoconularia azaisi* (La Maurerie Formation) or as *E. cf. azaisi* (Landeyran Formation) (Vizcaino et al., 2001, Fig. 3; this paper, Table 1). This assignment may have been based in part on the presence on the faces of this species of broad, sinusoidal transverse undulations similar to those of *E. loculata* (Wiman, 1895), the type species of the genus (Sinclair, 1944; see also illustrations in Jerre, 1994). However, the Southern Montagne Noire species differs from *Conularia*, *Eoconularia* and all other conulariids in possessing a raised midline crossed by very fine, trochoidal (long.) transverse ribs lacking nodes and interspace ridges (Van Iten, pers. obs.; this paper, Fig. 2A). Therefore, *C. azaisi* probably represents a new genus. Despite these differences, our cladistic analysis (Fig. 1), which revealed three major clades within Conulariida, places *C. azaisi* in the clade that includes *Eoconularia*, *Conularina* and *Conulariella*. This group is united by a single non-homoplastic synapomorphy, namely termination of the transverse ribs on the shoulders of the corner sulcus. The remaining Lower Ordovician conulariids collectively belong in the other two subclades, and thus all three major groups within Conulariida were in existence by early Ordovician times.

Recent chronostratigraphical revisions (e.g. Ebbestad and Högström, 2007) prove that several previous reports of Lower Ordovician conulariids were incorrectly dated. Thus, Sinclair (1948) and Hessland (1949) together listed *Archaeoconularia*, *Conularia* and *Pseudoconularia* as occurring in “Lower Ordovician” strata of Baltica (more specifically Sweden, Estonia and adjacent parts of Russia), which was located at mid-high palaeolatitudes within 15° of Armorica and Perunica (Fig. 5). However, the rock units from which these conulariids were originally described, for example the “Gray Vaginatum Limestone” (= the Holen Formation; Ebbestad and Högström, 2007) and the “*Orthoceras* Limestone”, have since been reassigned to the Middle Ordovician (see for example Ebbestad and Högström, 2007). Although Lower Ordovician marine deposits (e.g. the Latorp and Toyen formations; Ebbestad and Högström, 2007) are present in the Baltic Basin, as yet no conulariids have been found in these strata (Olle Hints, in litteris, 2015). Therefore, while *Archaeoconularia* and *Conularia* occur in Lower Ordovician rock units of other terranes (Table 1), *Pseudoconularia*, which was present and widespread in the Middle Ordovician Series (Van Iten and Vhylasova, 2004), is not currently known from Lower Ordovician strata. Finally, Sendino and Darrell (2008) listed *Metaconularia cf. punctata* (Slater, 1907) as occurring in Floian rocks in Wales. However, the specimens in question are from the Nant Ffrancon Subgroup, which is Middle Ordovician in age (Fortey et al., 2000).

Nearly all currently known Lower Ordovician conulariid localities are situated in Core Gondwana (Cocks and Torsvik, 2004) or in the peri-Gondwanan terranes of Armorica (Southern Montagne Noire), Avalonia (Wales) and Perunica (Bohemia), at high or very high palaeolatitudes (Fig. 5). One additional locality (Town of Sandu, Guizhou Province) is situated in South China, which lay astride 30°S in close proximity to Gondwanan India and the Arabian Shield (Cocks and Torsvik, 2013). Thus, nearly all known Lower Ordovician conulariid records were originally southward of 30°S. Furthermore, all occurrences are in siliciclastic sediments, predominantly mudstones, siltstones and fine sandstones, in some cases micaceous or with siliceous concretions/nodules (Table 1). In addition to conulariids, four localities, namely southeastern Morocco, the Southern Montagne Noire (France), South China and Korea contain *Sphenothallus* (Table 1; Figs. 2B, 6A): of these localities, three (Morocco, France and South China) contain both *Sphenothallus* and conulariids. *Sphenothallus* was also reported from the Prague Basin, Bohemia (Perunica) by Mergl (1997), but as the material was not illustrated, we have been unable to verify this occurrence.

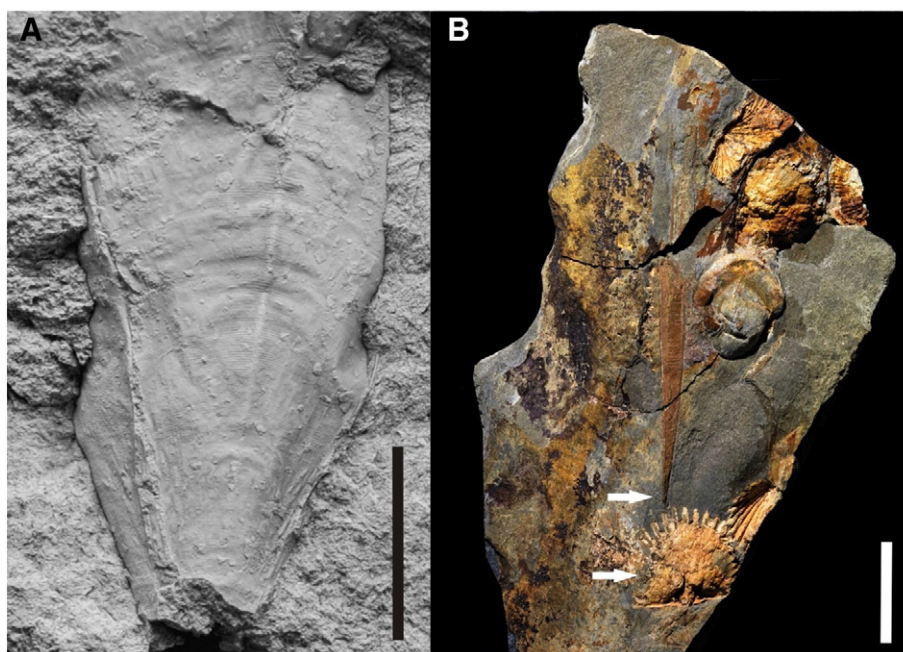


Fig. 2. A, *Conularia azaisi* Thorol, 1935 (upper Saint Chinian Formation, late Tremadocian, Southern Montagne Noire [Armorica]; UCBL-FSL 712799; specimen whitened with ammonium chloride). B, *Sphenothallus* sp. (Landeyran Formation, late Floian, Southern Montagne Noire [Armorica]; UCBL-FSL 712 485). This is the first *Sphenothallus* (upper arrow) reported from the Lower Ordovician System of Armorica, and it may have been attached at its apical end (upper arrow) to a rhynchonelliform brachiopod (lower arrow). Scale bars = 10 mm.

4. Fezouata Shale (EPF-bearing intervals)

4.1. Conulariids

At present the sole members of the phylum Cnidaria known to occur in the Fezouata Shale are *Sphenothallus* and conulariids, both sessile benthic medusozoans that were fully covered by a finely lamellar, organo-phosphatic periderm (Van Iten, 1992; Van Iten et al., 1992; Ford et al., in press). Destombes et al. (1985) were the first authors to report the presence of conulariids in the Fezouata Shale, but neither they nor subsequent authors (Van Roy et al., 2015) identified these fossils to lower taxonomical levels or reported the presence of *Sphenothallus* (though Van Roy et al., 2010 [fig. S2] misidentified their single illustrated *Sphenothallus* specimen as a “worm tube”). We here document the presence of one species each of *Archaeoconularia* and *Eoconularia* as well as at least one, possibly two, species of *Sphenothallus*.

Archaeoconularia sp. (Fig. 3A, B) and *Eoconularia* sp. (Figs. 3C–E, 4) are generally preserved flattened and aligned parallel to bedding, with nearly complete specimens preserving the gently arcuate apertural margin and tapering to within approximately 1 mm of the former apex. Comparisons of these specimens with previously described congeners from other terranes suggest that the Moroccan species are new. Specimens here identified as *Archaeoconularia* sp. (Fig. 3A, B) possess narrowly sulcate, non-thickened corners and midlines, and their faces exhibit minute, closely spaced nodes arranged in gently curving transverse rows that cross the midline without diminution or offset. From the corners the transverse rows trend toward the apical end of the periderm, but approximately half-way toward the midline they gradually change course to form shallow arcs that are convex toward the apertural end. While most specimens appear to have been on the order of 100–200 mm in length (Fig. 3B), one of the specimens examined in this study (YPM 530001) was originally at least 500 mm long. Relatively small specimens appear to be most similar to *A. fecunda* (Barrande, 1867) from the Upper Ordovician Zahořany Formation of Bohemia (Perunica) (Bouček, 1928), differing from this species in having the transverse node rows spaced farther apart. Specimens here identified as *Eoconularia* sp. (Fig. 3C–E, 4), originally <50 mm long, exhibit a broad, shallow corner sulcus, commonly darker in color

than the faces and slightly thickened internally, and their faces are crossed by smooth (non-nodose), non-thickened, sinusoidal (long.) transverse ribs similar to the primary transverse ribs of the type species, *E. loculata* (Holm, 1893) (see for example illustrations in Jerre, 1994). Features comparable to the finer, secondary transverse ribs of *E. loculata* were not discerned, but in any case these features were not noted in the original diagnosis of the genus (Sinclair, 1944).

4.2. *Sphenothallus*

The Fezouata Shale contains at least two species of more or less tubular fossils (Fig. 6), one of which can be assigned unequivocally to the genus *Sphenothallus*. Slender, straight to very gently curved specimens, here identified as *Sphenothallus* sp. 1 (Fig. 6A; see also Van Roy et al., 2010, fig. S2), exhibit the diagnostic pair of longitudinal thickenings situated at the end points of the tube's greatest diameter (Van Iten et al., 1992). Except for irregular, probably taphonomically induced wrinkling of the thin peridermal wall between the longitudinal thickenings, the tube appears to be smooth. In addition to the discovery of *Sphenothallus* in the Fezouata Shale, a smooth-walled specimen of this genus has been collected from the Landeyran Formation (late Floian) of the Southern Montagne Noire (Fig. 2B).

The other tubular fossil (Fig. 6B), which is likewise very gently tapered and with a subelliptical transverse crosssection, nevertheless differs from non-ornamented *Sphenothallus* sp. 1 in exhibiting fine, regular, closely spaced transverse ridges or annulations that appear to fully encircle the tube. Also, development of the paired longitudinal thickenings appears to be very weak (and, again, the apical end is missing). For these reasons, we questionably assign this fossil to *Sphenothallus*, under the name ?*Sphenothallus* sp. 2.

5. Lower Ordovician palaeobiogeography

During Early Ordovician times, the peri-Gondwanan terranes of Armorica, Avalonia and Perunica lay in close proximity to each other and to Morocco (e.g. Nysæther et al., 2002; this paper, Fig. 5). It is not surprising, then, that *Archaeoconularia* is known from Tremadocian strata of Avalonia, Morocco and Perunica, or that *Eoconularia* has been

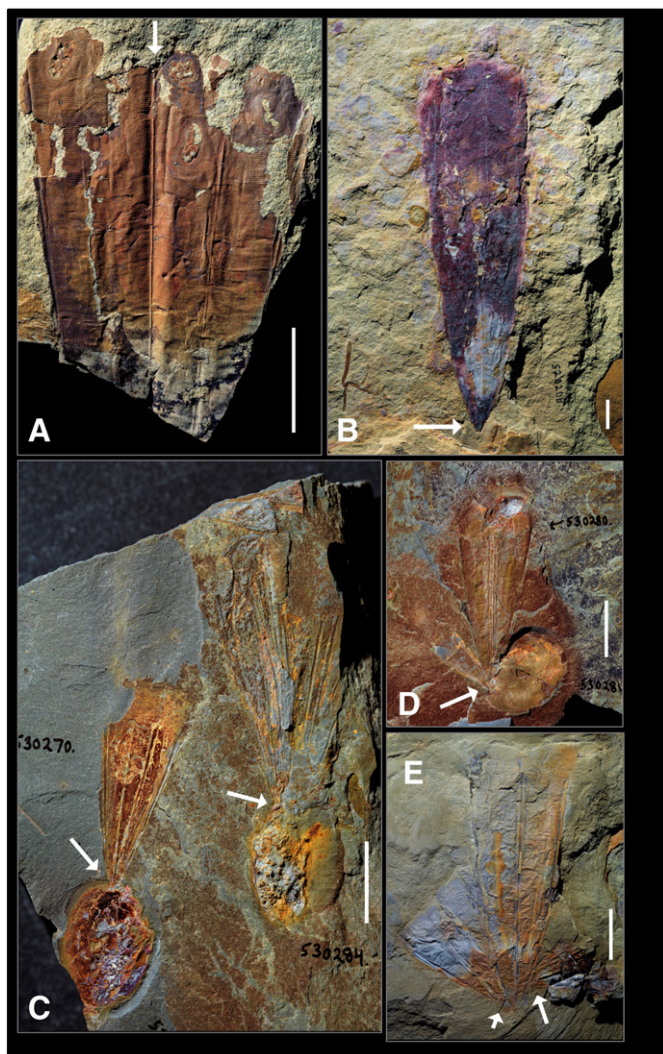


Fig. 3. *Archaeoconularia* sp. and *Eoconularia* sp. from the Fezouata Shale (Tremadocian–Floian) of southeastern Morocco (Core Gondwana; Anti-Atlas). A, *Archaeoconularia* sp. Single partial specimen (AA.BIZ12.03; lower EPF interval, late Tremadocian) clearly showing the transverse ornament (midline indicated by arrow). B, *Archaeoconularia* sp. Single nearly complete specimen (YPM 520208; upper EPF interval, mid Floian) preserving the arcuate apertural margin and broken just above the apex (arrow). C, *Eoconularia* sp. Single specimen (YPM 530270; left arrow) and a V-like pair (YPM 530283; left arrow), both originally attached at the apical end to a phosphatic brachiopod (arrows; lower EPF interval, late Tremadocian). D, *Eoconularia* sp. V-like pair (YPM 530280; lower EPF interval, late Tremadocian) composed of one small and one large specimen, both originally attached at their apical end to a phosphatic brachiopod (arrow). E, *Eoconularia* sp. Single nearly complete, relatively large specimen exhibiting two much smaller *Eoconularia* sp. arrayed along and possibly attached to one of its corners (long right arrow). Two additional, medium-sized specimens may be attached to another corner of the large specimen, closer to its apical end (short left arrow) (YPM 530272; lower EPF interval, late Tremadocian). Scale bars = 10 mm.

found in the Tremadoc of Avalonia and Morocco (Table 1). Likewise, *Sphenothallus* is now known from the Tremadoc of Armorica and Morocco as well as from South China and North China, which were located closer to the palaeoequator than were either of the two other terranes (but South China was still close to Core Gondwana). It is intriguing that neither *Archaeoconularia* nor *Eoconularia* has been found in Armorica. A possible reason for this absence is that the Saint Chinian Formation strata that host *C. azaisi* differ lithologically from those of all other Lower Ordovician localities (Table 1), representing perhaps a palaeohabitat that was not suitable for other conulariids.

The Tremadocian conulariid assemblage of southeastern Morocco is most similar to that of Avalonia (Wales), with both assemblages consisting of one species each of *Archaeoconularia* and *Eoconularia*.

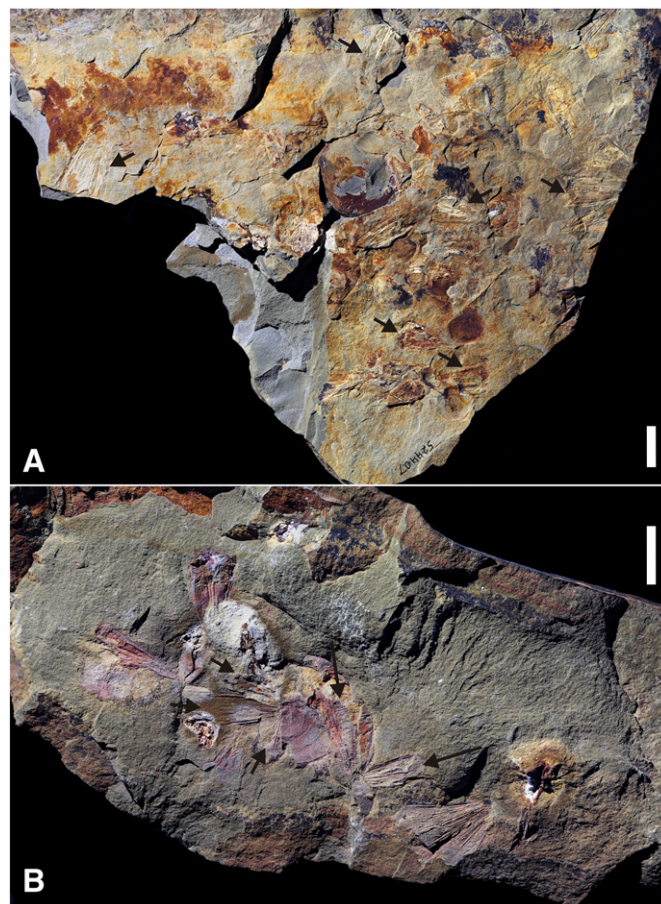


Fig. 4. *Eoconularia* sp. (Fezouata Shale, Anti-Atlas, southeastern Morocco). Examples of monospecific mass associations. A, Slab (YPM 524407; lower EPF interval, late Tremadocian) showing approximately 30 specimens (some indicated by arrows) in an area covering approximately 120 cm². B, slab (YPM 530276; lower EPF interval, late Tremadocian) showing 10 specimens in an area covering approximately 30 cm². The three specimens indicated by the short arrows form a radial cluster, and they converge on a common point situated within the margins of a phosphatic brachiopod. The two specimens indicated by the long arrows constitute a V-like pair likewise situated with the point of convergence of the component conulariid specimens located within the margins of a brachiopod. Scale bars = 10 mm.

Exoconularia, known from the Floian of Wales but not from the Fezouata Shale, probably is a close relative of *Archaeoconularia* (Van Iten et al., 2014b; this paper, Fig. 1). Although Lower Ordovician strata of Wales have not yielded *Sphenothallus*, we predict that eventually they will.

Of the other terranes/localities, southeastern Morocco shares a single genus, *Archaeoconularia*, with Perunica, but no genera with Argentina, the Southern Montagne Noire (Armorica) or South China (Table 1). Moreover, *Conularia* has been found only in the Tremadocian–Floian of Perunica, and *Conulariella* in the Floian of this terrane and South China. The latter genus does occur in Middle Ordovician (Darriwilian) strata of Armorica (Armorican Massif; Van Iten et al., 2013), which also yield *Archaeoconularia*, *Exoconularia*, *Metaconularia* and *Pseudoconularia* (Spain; Sendino and Santos, 2011).

6. Palaeoecology of conulariids

6.1. Monospecific mass occurrences

A striking characteristic of Fezouata Shale *Archaeoconularia* sp. and *Eoconularia* sp., particularly of the latter species, is their great abundance and areal density compared with congeneric specimens from other Ordovician (and younger) terranes and rock units. Many of the *Eoconularia* specimens occur in monospecific mass associations

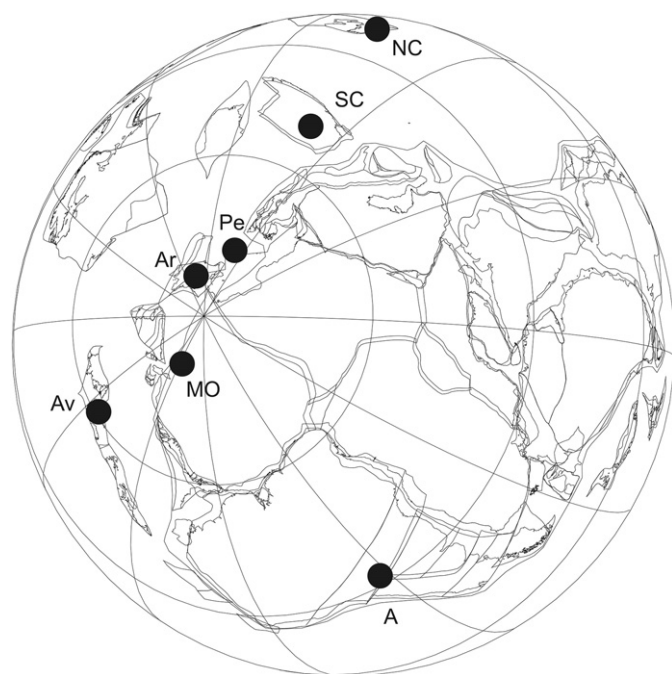


Fig. 5. Palaeogeographical distribution of Lower Ordovician conulariid and *Sphenothallus* localities. Oblique southern hemisphere view drawn for ~495 Ma (Tremadocian) using BugPlates (Torsvik, 2009) and with the position of South China modified following Cocks and Torsvik (2013). Terrane and other locality abbreviations: A, Argentina; Ar, Armorica (Southern Montagne Noire); Av, Avalonia (Wales); NC, North China (Korea); Pe, Perunica (Bohemia); SC, South China (Sandu, Guizhou Province); MO, southeastern Morocco.

consisting of up to approximately 50 specimens per 100 cm² (Fig. 4). No such associations of this genus or other conulariids have previously been documented or reported, and HVI found none in museum collections of *Eoconularia* from other localities (e.g. Ordovician strata near Girvan, Scotland [collections of the Natural History Museum, London; Sendino and Darrell, 2008] and the Early Silurian Manitoulin Dolostone of Drummond Island, Michigan, USA [uncatalogued material in the collections of the University of Michigan Museum of Paleontology, Ann Arbor; Sinclair, 1948]). In short, the assemblages of *Eoconularia* sp. from the EPF-bearing intervals of the Fezouata Shale appear to contain the most abundant and densely packed specimens of this or any conulariid genus ever documented (see also discussion below).

The frequent occurrence of *Archaeoconularia* sp. and *Eoconularia* sp. in monospecific mass associations, in strata deposited in a low-energy environment well below fair-weather wave base (Martin et al., in press), suggests that the living conulariids were distributed in monospecific clumps or patches that were possibly clonal in origin (Van Iten and Cox, 1992; Rodrigues et al., 2006; Van Iten et al., 2012). Although the conulariids probably underwent limited transport (as indicated by the observation that they are now oriented parallel to bedding; Van Iten et al., 2012), the alternative hypothesis that clumping resulted from purely taphonomical factors seems unlikely, especially considering the occurrence of some specimens in V-like pairs (which probably would have been disrupted had they undergone appreciable transport). In general, biological processes leading to clumping constitute reproductive strategies, either sexual (i.e. settlement of planulae) or asexual (e.g. budding, settlement of pseudo-planulae). As discussed for example by Marques and Collins (2004), most medusozoan cnidarians have an asexual benthic stage in their life cycle. Within this stage, one or more of the following asexual modes of reproduction may occur: polyp budding (formation of modular organisms), profuse medusa budding (including scyphozoan strobilation), and dormant cyst production (podocysts, reinforcing seasonal maintenance of benthic populations) (Arai, 1997; Robinson et al., 2014). Medusozoans



Fig. 6. Tubular phosphatic fossils from the Fezouata Shale (Tremadocian–Floian) of southeastern Morocco (Core Gondwana; Anti-Atlas), A, *Sphenothallus* sp. 1. Single slightly twisted and wrinkled specimen (YPM 518162; lower EPF interval, late Tremadocian) missing the apical holdfast. B, ?*Sphenothallus* sp. 2. Single specimen (YPM 518106; arrow; exact age uncertain) showing numerous fine, closely spaced transverse annulations. Scale bars = 10 mm.

collectively exhibiting these reproductive modes/strategies are similar in morphology and clustering to *Archaeoconularia* and *Eoconularia* (see for example Miranda et al., 2012). In the conulariids, three scenarios could have led to biological clumping: a) attachment of groups (clusters) of conulariids to other species such as brachiopods or to other conulariids (see discussion below); b) clustering of individual conulariids that were not connected to biological substrates or to each other; or c) formation of clonal colonies, with each clump constituting a single integrated body.

6.2. Conulariid/brachiopod associations

Six of the specimens of *Eoconularia* sp. examined here form three V-like pairs (Van Iten et al., 2012), with the two members of each pair converging adapically toward a common point and nearly touching each other at the apical end (Fig. 3D, E). An additional six specimens form two radial clusters (Van Iten and Cox, 1992), each consisting of three specimens that converge adapically on a common point (Figs. 3E, 4B). Unfortunately, all of these specimens have been broken approximately one mm above the apex, which is now missing. Nevertheless, both members of one of the V-like pairs preserve their apertural margin, and one of these specimens is approximately three times longer than the other; furthermore, the point of convergence of the pair lies within the margins of a phosphatic brachiopod (Fig. 3D). The same is also true of one of the radial clusters (Fig. 4B). Eleven other *Eoconularia* specimens, four of them solitary and the rest arrayed in V-like pairs (e.g. Fig. 4B), form similar associations with a phosphatic brachiopod shell (Fig. 3C, E). In all 16 cases, the apicalmost portion of the conulariid lies immediately adjacent to the brachiopod and close to its commissural margin, and the long axis of the conulariid is inclined at a high angle to this margin. Also in all cases, brachiopod specimens are sparse

(i.e. the areal density of brachiopods on the host slab is low). Importantly, similar conulariid/brachiopod associations, involving *Conularia trentonensis* Hall, 1847 and *Onniella* sp. (a rhynchonelliform brachiopod), occur in the Upper Ordovician (Katian) Collingwood Shale Formation of southwestern Ontario, Canada. For example, the small slab illustrated here in Fig. 7 bears three radial clusters, each composed of three *Conularia* converging on a common point. In all three clusters, the apical regions of the component conulariids lie directly beneath the shell of a single *Onniella* sp., a configuration that closely resembles that of the aforementioned *Eoconularia* sp. Together with the *Eoconularia* sp./phosphatic brachiopod associations, these are the first such intimate associations of conulariids and brachiopods ever documented (see discussion below).

The largest of the five *Eoconularia* sp. illustrated here in Fig. 3E exhibits two much smaller *Eoconularia* sp. arrayed along one of its corners. The two small specimens nearly touch the larger specimen at their apical ends (again broken just above the tip), and their long axes are aligned parallel to each other. On the other side of the large specimen, two additional, mutually parallel *Eoconularia* sp. appear to touch their larger neighbor, though closer to its apical end. This occurrence is highly similar to a conulariid/*Sphenothallus* association illustrated by Van Iten et al. (1996, pl. 1, fig. 8) and consisting of two mutually parallel

Climacoconus quadratus (Walcott, 1879) touching one of the longitudinal thickenings of the *Sphenothallus* tube.

Van Iten et al. (1996) argued that associations similar to those described above constitute compelling circumstantial evidence of original attachment of the conulariids to the associated fossils, probably at the apical end of the conulariids. Previously documented associations consist of one or more conulariids and the shell of a hyolith or nautiloid, a crinoid stem or *Sphenothallus* tube, or possible vertebrate bone (Van Iten and Südkamp, 2010; see also Van Iten et al., 1996 and references cited therein). Even though direct evidence of apical attachment is not evident (in all cases the tips of the conulariids are missing), it seems unlikely that such associations, with their multiple, spatial coincidences, are fortuitous or taphonomic in origin. This is particularly evident for the V-like pairs (Fig. 3D) and radial clusters (Fig. 7). The fact that the conulariids converge on a common point, situated within the margins of the brachiopod, tends to rule out the hypothesis that the fossils were brought together by bottom currents, as this mechanism requires either (a) multiple cases of originally solitary conulariids being deposited in such a way as to be contiguous at their apices, or (b) specimens originally arranged in V-like pairs and radial clusters undergoing transport without disruption of their original apical convergence. Additionally, the low areal density of the specimens in question argues against these associations being merely fortuitous. Similar reasoning applies to the alternative hypothesis that the conulariid/brachiopod associations are an artifact of transport by biological agents. In short, then, it seems that the most likely explanation of multiple occurrences of conulariid/brachiopod associations such as those here documented, is that the spatial patterns now exhibited by these fossils reflect original attachment of the conulariids to brachiopod shells, most likely at the apical or adoral end of the conulariids. The same line of argument leads us to conclude that it is most probable that the two small *Eoconularia* sp. arrayed along a corner of a larger individual of this species (Fig. 3E), were originally attached or connected at their apex to the larger specimen. Moreover, because all three of these specimens are conulariids and members of the same species, it seems possible that the two small conulariids may not simply have been attached to the larger specimen, but rather budded from it. This hypothesis can potentially be corroborated by the discovery of specimens preserving the apex.

7. Conclusions

A literal reading of the fossil record of conulariids leads to the conclusion that this medusozoan clade underwent a radiation during Early Ordovician times. However, our cladistic analysis demonstrates that the two known pre-Ordovician genera, *Baccaconularia* (Furongian) and *Paraconularia* (latest Ediacaran), occupy apical positions in the conulariid tree (Fig. 1). If this interpretation is correct, then the most recent common ancestor of all conulariids originated still deeper within the Neoproterozoic Era, and therefore multiple conulariid ghost lineages extend downward through the Cambrian and Ediacaran periods. Rocks of the Cambrian System are widespread and have been sampled intensively, but thus far the only definitely known Cambrian conulariid locality (Hughes et al., 2000) has yielded but a single genus. Even the Cambrian Konservat-Lagerstätten have yet to produce a single specimen of a conulariid. Notwithstanding, the fact that the mid Cambrian Burgess Shale has yielded extremely rare *Sphenothallus* sp., a finely lamellar phosphatic taxon that appears to be isotaphonomic with conulariids, suggests that conulariids likewise may be present but extremely rare, occurring possibly as minute fragments (conulariid “microfossils”; Jerre, 1993; Van Iten et al., 1996, 2006b), which could be recovered by means of the same rock preparation techniques used for extraction of conodonts.

Conulariids and *Sphenothallus* in the EPF-bearing intervals of the Fezouata Shale of southeastern Morocco, introduced herein, represent the first records of these two medusozoan groups from the Lower

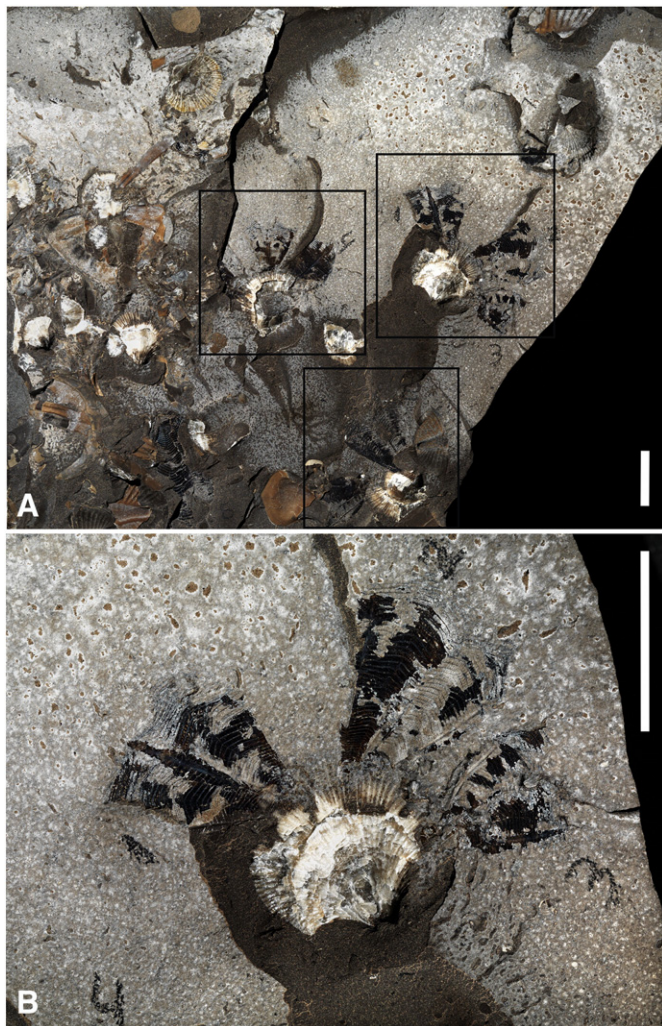


Fig. 7. *Conularia trentonensis* Hall, 1847 (Upper Ordovician [Katian], Collingwood Shale Formation, Lake Huron shoreline, southern Ontario, Canada; UMMP 73817). A, single bedding plane bearing three radial clusters (outlined by rectangular boxes), each composed of three conulariids originally attached to the shell of an *Onniella* sp. B, detail of one of the clusters. Scale bars = 10 mm.

Ordovician of Africa. Two genera of conulariids—*Archaeoconularia* and *Eoconularia*—are present, and there may also be two species of *Sphenothallus* (one smooth-walled and another with fine transverse ridges). Sample sizes for nearly all Lower Ordovician localities are relatively large (>30 repositied specimens per species per locality), and thus differences in the taxonomic composition of conulariids between Morocco and the four other Lower Ordovician localities (Argentina, Armorica, Perunica and South China) may reflect differences in the original palaeoenvironments and/or factors promoting faunal endemism. *Archaeoconularia* and *Eoconularia* are also present in the Lower Ordovician of Wales (Avalonia), which was located adjacent to northwestern Africa; however, the sample sizes available for the Avalonian sites are much smaller than for other palaeocontinents. Thus, there may be significant undiscovered conulariid diversity in Avalonia.

In addition to being relatively diverse, Lower Ordovician conulariids may also be locally abundant. In the Fezouata Shale, *Archaeoconularia* sp. and *Eoconularia* sp. commonly occur in monospecific mass associations, with observed *Eoconularia* sp. concentrations containing up to about 50 specimens in an area of approximately 100 cm², on the same bedding plane/lamina. Moreover, some *Eoconularia* sp., including specimens forming V-like pairs, show orientational evidence of original apical attachment to phosphatic brachiopods and even to other *Eoconularia* sp. Similar evidence of original apical attachment to rhynchonelliform brachiopods (*Onniella* sp.) is exhibited by radially clustered *C. trentonensis* from the Upper Ordovician Collingwood Shale of Ontario, Canada. This is the first time that evidence of original apical attachment of conulariids to brachiopods or to other conulariids has been documented. Finally, even though most conulariids and *Sphenothallus* in the EPF-bearing intervals of the Fezouata Shale probably underwent limited (local) transport immediately prior to final burial, the present occurrence of *Archaeoconularia* sp. and *Eoconularia* sp. in monospecific mass associations probably reflects an original clumped distribution of these two conulariids on the shallow seafloor.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.03.008>.

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