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# Cladistics and mass extinctions: the example of conulariids (Scyphozoa, Cnidaria) and the End Ordovician Extinction Event

Heyo Van Iten<sup>ab</sup>, Matthew Burkey<sup>c</sup>, Juliana De Moraes Leme<sup>d</sup> & Antonio C. Marques<sup>ef</sup>

<sup>a</sup> Department of Geology, Hanover College, Hanover, IN 47243, USA;

<sup>b</sup> Department of Invertebrate Paleontology, Cincinnati Museum Center, 1301 Western Avenue, Cincinnati, OH 45203, USA

<sup>c</sup> Department of Geoscience, University of Iowa, 121 Trowbridge Hall, Iowa City, IA 52242, USA

<sup>d</sup> Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo, Rua do Lago-562 Cd. Universitária-São Paulo, SP, Brazil 05508-080

<sup>e</sup> Instituto de Biociências, Universidade de São Paulo, R. Matão, Tr. 14, 101, 05508-090 São Paulo, Brazil

<sup>f</sup> Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil

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## Cladistics and mass extinctions: the example of conulariids (Scyphozoa, Cnidaria) and the End Ordovician Extinction Event

HEYO VAN ITEN<sup>1,2</sup>, MATTHEW BURKEY<sup>3</sup>, JULIANA DE MORAES LEME<sup>4</sup> and ANTONIO C. MARQUES<sup>5,6</sup>

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**Abstract:** The End Ordovician Extinction Event (EOEE) had little impact on supra-specific diversity and disparity within the order Conulariida (Scyphozoa, Cnidaria). With two possible exceptions (*Exoconularia* and *Glyptoconularia*), all eight genera currently known from strata of middle or late Katian age survived the crisis, and nearly all of the discontinuous gross morphological features present in Ordovician and older genera are present in at least one of the surviving genera. A cladistic parsimony analysis of 17 genera, 12 of which occur in Ordovician strata, produced 3 major subclades and 7 less inclusive subclades within Conulariida. With one possible exception, the clade *Anaconularia* + *Baccaconularia*, all other monophyletic groups within Conulariida survived the EOEE. Moreover, additional, ghost lineages in the clade *Climacoconus* + *Holoconularia* + *Notoconularia* + *Paraconularia* + *Reticulaconularia* must have crossed the Ordovician–Silurian boundary. The minor impact of the EOEE on diversity and disparity within Conulariida probably reflects the eurytopic character and simple but efficient metabolism (possibly glycolysis-based) of this group.

**Keywords:** Cladistics; mass extinctions; conulariids; Scyphozoa; End Ordovician.

<sup>1</sup>Department of Geology, Hanover College, Hanover, IN 47243, USA; [vaniten@hanover.edu](mailto:vaniten@hanover.edu)

<sup>2</sup>Department of Invertebrate Paleontology, Cincinnati Museum Center, 1301 Western Avenue, Cincinnati, OH 45203, USA

<sup>3</sup>Department of Geoscience, University of Iowa, 121 Trowbridge Hall, Iowa City, IA 52242, USA

<sup>4</sup>Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo, Rua do Lago-562 Cd. Universitária-São Paulo, SP, Brazil 05508-080

<sup>5</sup>Instituto de Biociências, Universidade de São Paulo, R. Matão, Tr. 14, 101, 05508-090 São Paulo, Brazil

<sup>6</sup>Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil  
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### Introduction

Understanding the causes and consequences of mass extinctions may be facilitated by analysis of the phylogenetic relationships of species or genera within relevant monophyletic groups. In turn, analysis of extinction/survival patterns may shed additional light on the paleobiology of fossil clades of problematical affinities. The extinction of taxa entails the loss of morphological or other character states (at a minimum those diagnostic of particular species). Thus, knowing whether the states in question are homologous and derived may be useful in assessing whether the possession of such traits promoted survival or contributed to extinction. For example, the loss of states independently derived in multiple species or genera is interesting in that the states in question presumably originated in response to selection pressures, under paleoenvironmental conditions (potentially) quite different from those of the extinction event. At the very least, this possibility invites further analysis of such characters, perhaps through investigations of their functional significance (e.g., Fisher 1981). Conversely, character states that are

autapomorphic for eliminated higher taxa may have been disadvantageous to those groups, or their presence may have had little impact on the probability of survival (hence the usefulness of such similarities in tracing phylogenetic relationships). Finally, analyzing mass extinctions in the context of hypotheses of phylogenetic relationships enables one to predict the existence of additional, ghost lineages and thus (potentially) more accurately establish the time of origin of critical evolutionary novelties (see e.g. Rong et al. 2006).

This study assesses the impacts of the two-phased End Ordovician Extinction Event (EOEE) on the monophyletic order Conulariida (Ediacaran–Triassic; Cnidaria, Scyphozoa), in the context of a phylogeny-based hypothesis involving 17 conulariid genera. The initial phase of the EOEE was triggered by continental glaciation on West Gondwana, with consequent rapid drops in eustatic sea level and water temperature, and the second phase resulted from an equally rapid return to greenhouse conditions (Brenchley 2004; Rasmussen & Harper

2011). Although it is estimated that 85% of all species present immediately prior to the EOEE were eliminated, higher taxa generally were not lost or replaced, and total species diversity was recovered during the succeeding Silurian Period. Four of the 12 conulariid genera present in Ordovician strata have not been recorded in strata of Silurian or younger age (Van Iten & Vhylasová 2004; Leme et al. 2008), and thus these conulariids may also have gone extinct during the EOEE. One of the problems addressed in this study is whether this hypothesis is true. In addition, we also investigate the impact of the EOEE on (1) the taxonomic diversity (richness) of suprageneric conulariid clades and on (2) conulariid morphological diversity (disparity), as measured by the change in the number of discontinuous gross morphological features across the Ordovician–Silurian boundary. Disparity traditionally has been measured with respect to homologous anatomical landmarks (Foote & Miller 2007). In the case of conulariids, however, such landmarks cannot be identified, and thus some alternative measure of disparity must be used. The alternative proposed here is the change in the number of discrete character states generally used in the diagnosis or description of conulariid genera. We refer to such a measure of disparity as cladistic disparity.

To better assess the possible causes of the extinction/survival patterns documented here, we present data on the paleogeographical and paleoenvironmental ranges of Ordovician conulariid genera. It should also be noted here that sampling for conulariids historically appears to have been uneven (with no reports of conulariids from Upper Ordovician rocks of Siberia or South America, for example), and that recently some genera previously known only from present-day Europe and/or North America have been discovered in Lower Ordovician strata of China or Morocco (Van Iten et al. 2013; H. Van Iten, unpublished observations).

## Distribution and relative abundance

Conulariid fossils probably represent the benthic polypoid life stage of medusozoan cnidarians that produced ephyrae through strobilation (Van Iten et al. 2006a). Late Ordovician conulariids collectively ranged from low to high paleolatitudes, from shallow subtidal to shelf slope and shale basin bottom environments, and inhabited a variety of substrates including carbonate and siliciclastic muds, silts and sands (Van Iten & Vhylasová 2004). Four genera – *Archaeoconularia*, *Conularia*, *Metaconularia* and *Pseudoconularia* – were cosmopolitan, occurring in at least four of the seven following paleocontinents and terranes: Armorica, Avalonia, Baltica, Laurentia, Perunica, the Pontides and West Gondwana. *Conularia* in particular was widely distributed, having been found in Upper Ordovician strata of most of the places listed above as well as Australia/Tasmania (Percival 2009). Paleobathymetrically, *Conularia* ranged from oxic shallow shelves to dysoxic shelf slopes and shale basins. Together, *Conularia* and the three other cosmopolitan genera were among the most abundant conulariids of Late (and earlier) Ordovician times, far outnumbering other genera in major museum collections and in rock units sampled by the present senior author (e.g., Van Iten et al. 1996).

Situated at the opposite end of the distribution spectrum are the genera *Anaconularia*, *Baccaconularia*, *Conulariella* and *Glyptoconularia*. These taxa are known from a single or at most two Ordovician paleocontinents and/or terranes, are represented in most cases by a small number (<20) of repositied museum

specimens, and occur in only one or two general lithologies (see also Discussion section).

Finally, the known fossil record of Upper Ordovician conulariids occurs predominantly in strata of Sandbian or Katian age. Records of conulariids in strata of Hirnantian age are sparse, comprising, for example, the topmost part of the Upper Ordovician sequence on Anticosti Island, Quebec, Canada (H. Van Iten, unpublished observations).

## Phylogenetic analysis: materials and methods

We analyzed the phylogenetic relationships among the type species of 17 ingroup genera and 1 outgroup taxon, the coronate scyphozoans. The ingroup genera, 14 of which are listed in the Treatise on Invertebrate Palaeontology (Moore & Harrington 1956), are *Anaconularia* Bouček, *Archaeoconularia* Bouček, *Baccaconularia* Hughes et al., *Climacoconus* Sinclair, *Conularia* Miller in Sowerby, *Conulariella* Bouček, *Conularina* Sinclair, *Ctenoconularia* Sinclair, *Eoconularia* Sinclair, *Exoconularia* Sinclair, *Glyptoconularia* Sinclair, *Holoconularia* Hergarten, *Metaconularia* Foerste, *Notoconularia* Thomas, *Paraconularia* Sinclair, *Pseudoconularia* Bouček and *Reticulaconularia* Babcock and Feldmann. To date, 47 genera have been published as conulariids (Leme et al. 2008, table 1; Percival 2009). However, some of these have been removed from Conulariida or are of uncertain affinities (e.g., Babcock & Feldmann 1986a, 1986b; Van Iten et al. 2010), or have been (Babcock & Feldmann 1986a) or may be (we believe) interpreted as junior synonyms of *Conularia*, *Paraconularia* or other genera. One genus, *Vendocnularia* Ivantsov and Fedonkin (Ediacaran, Russia), was omitted because we were unable to examine the holotype and only known specimen directly.

Eighteen discrete, binary gross morphological characters of the periderm were scored for each taxon. For all genera including the outgroup, character state scores were determined through direct examination of actual (mostly type) specimens housed in the following institutions: the American Museum of Natural History (AMNH, New York), the Carnegie Museum of Natural History (CM, Pittsburgh), the Geological Survey of Canada (GSC, Ottawa), the Hunterian Museum (GLAHM, Glasgow University), the Museum of Comparative Zoology (MCZ, Harvard University), the Natural History Museum (NHM, London), the New Jersey State Museum (NJSM, Trenton) and the Royal Ontario Museum (ROM, Toronto). Our character matrix is available through the matrix repository, TreeBase, or from the authors, on request.

Cladistic analyses were carried out using branch and bound algorithms of PAUP\* 4.0b10 (Swofford 2001).

## Results

### *Conulariid phylogeny*

Our cladistic parsimony analysis yielded a single-most parsimonious cladogram for Conulariida (Fig. 1). This cladogram contains three major clades within Conulariida. One of these clades, composed of the genera *Conulariella*, *Conularina* and *Eoconularia*, is the most strongly supported group, being united by three nonhomoplasic synapomorphies: 1, derivation of sinusoidal transverse ribs; 2, termination of secondary (minor) transverse ridges; and 3, termination of the transverse ribs on the shoulders of the corner sulcus.

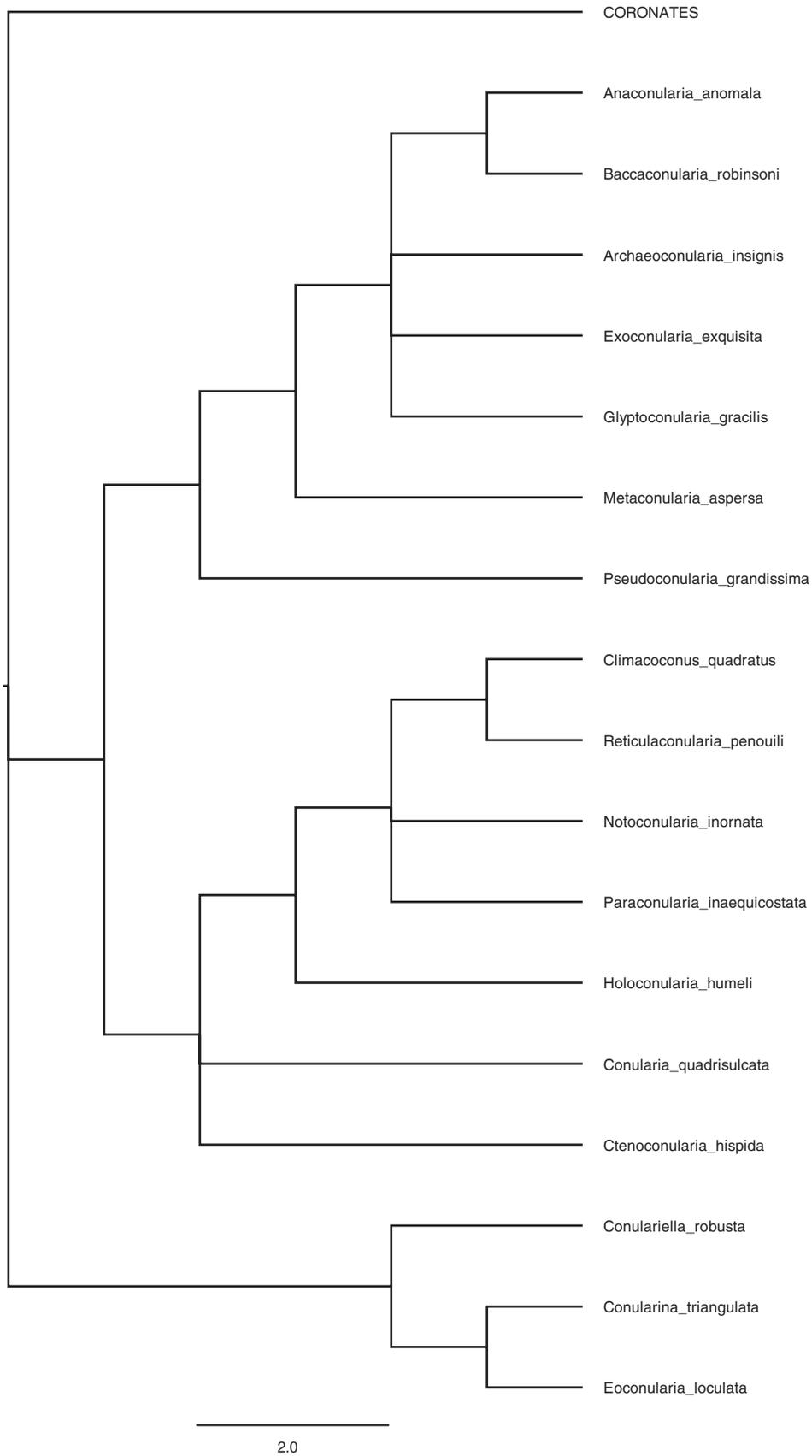


Fig. 1. Most parsimonious cladistic hypothesis of conulariid relationships based on 18 gross morphological characters of the periderm (length = 33, consistency index = 0.55, rescaled consistency index = 0.43).

A second major clade consists of the genera *Anaconularia*, *Archaeoconularia*, *Baccaconularia*, *Exoconularia*, *Glyptoconularia*, *Metaconularia* and *Pseudoconularia*, and is supported by two nonhomoplastic synapomorphies: 4, loss of trochoidal transverse ribs; and 5, loss of interspace ridges.

The third major clade, which consists of *Climacoconus*, *Conularia*, *Ctenoconularia*, *Holoconularia*, *Notoconularia*, *Paraconularia* and *Reticulaconularia*, is supported by a single nonhomoplastic synapomorphy – 6, loss of longitudinal alignment of the interspace ridges – recovered however in *Reticulaconularia*. Within this group, a less inclusive clade consisting of *Climacoconus*, *Holoconularia*, *Notoconularia*,

*Paraconularia* and *Reticulaconularia* is supported by the nonhomoplastic synapomorphy consisting of termination and alternation of the transverse ribs within the corner sulcus (see also Leme et al. 2008, text-fig. 4B).

#### Impact on conulariid diversity

Of the 13 conulariid genera included in our phylogenetic analysis and present prior to the EOEE, all but five – *Anaconularia*, *Baccaconularia*, *Conulariella*, *Exoconularia* and *Glyptoconularia* – range into post-Ordovician strata (Fig. 2). However, *Baccaconularia* currently is known only from

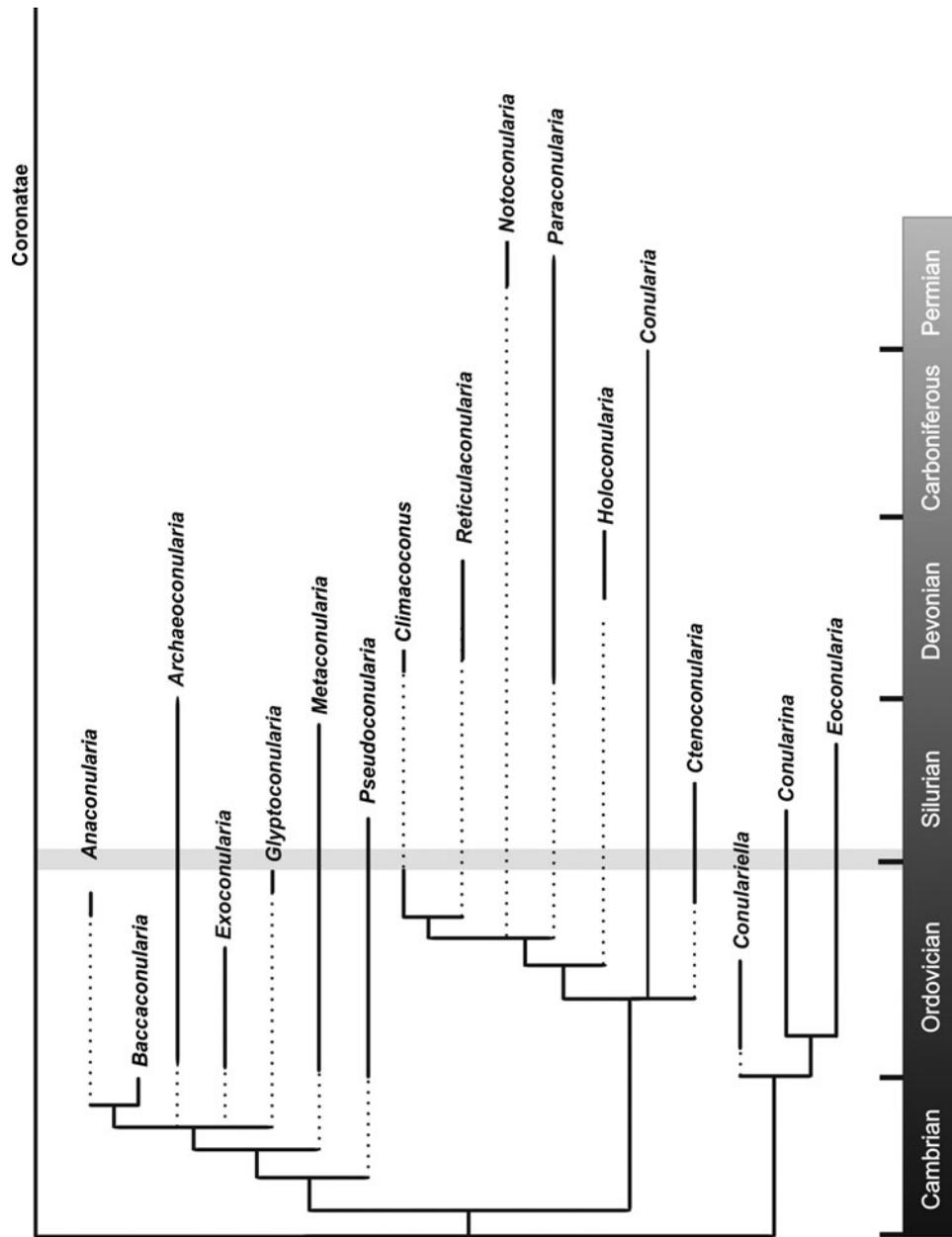


Fig. 2. Combined cladogram/stratigraphic range chart for the 17 conulariid genera discussed in the present study. In our phylogenetic hypothesis (Fig. 1), *Reticulaconularia* is the sister taxon of *Climacoconus*, and therefore the stratigraphic range of *Reticulaconularia* must be extended as a ghost lineage (dashed line) into the Ordovician Period. Likewise, there must be at least one ghost lineage leading to *Notoconularia* and *Paraconularia* that ranges downward into the Ordovician, and the range of *Holoconularia* must also be extended downward across the Ordovician–Silurian boundary. Data on stratigraphic ranges taken from Sinclair (1948), Thomas (1969), Babcock & Feldmann (1986b), Hughes et al. (2000), Van Iten & Vhylasová (2004) and Van Iten et al. (2013).

Furongian quartz siltstones in the Upper Mississippi Valley Region of the USA (Hughes et al. 2000); it is also an extremely rare faunal element, being represented by fewer than 20 repositied specimens collectively assigned to two species. *Anaconularia*, while represented by approximately 2000 repositied specimens, is monospecific and is known only from micaceous quartz sandstones of the Bohemian Massif (Perunica), last appearing there in beds of late Sandbian age (Van Iten & Vhylasová 2004). *Conulariella*, last recorded from Darriwilian shales of Perunica and Armorica (Pillet & Beaulieu 1998; Van Iten & Vhylasová 2004), is extremely rare, being represented by fewer than 20 repositied specimens collectively assigned to four species. *Glyptoconularia* ranges upward relatively close to the base of the Hirnantian Stage, having been identified in mid-late Katian shales in the Upper Mississippi Valley (Van Iten et al. 1996). Again, though, this monotypic genus is extremely rare, being represented by fewer than 20 repositied specimens, all from just three localities in cratonic North America. In short, while the known stratigraphical ranges of the two extremely rare genera may be sampling artifacts, it still seems likely that they and *Anaconularia* became extinct before the onset of the EOEE. Finally, while *Exoconularia* has not been recorded from post-Ordovician strata, this genus is nearly identical morphologically to *Archaeoconularia*, differing from the latter taxon solely in the possession of a pair of longitudinal sulci flanking the midline sulcus on each of the four faces (Moore & Harrington 1956). Thus, even if *Exoconularia* is a monophyletic group that did not survive the EOEE, its probable nearest relatives, namely species assigned to cosmopolitan *Archaeoconularia*, did survive.

With the possible exception of the single minor clade consisting of the genera *Anaconularia* and *Baccaconularia*, all of the suprageneric monophyletic groups nested within Conulariida (Fig. 1) survived the EOEE. Again, however, both *Anaconularia* and *Baccaconularia* may have gone extinct well before the EOEE. These and the two other genera (*Conulariella* and *Glyptoconularia*) with restricted distributions may have been eliminated owing to their having inhabited narrow niches.

All four genera that first occur after the EOEE, namely *Holoconularia*, *Notoconularia*, *Paraconularia* and *Reticulacconularia*, together form a single clade that includes *Climacoconus*. This clade, nested within our third major group, is supported by a single nonhomoplastic synapomorphy (presence of a unique type of corner anatomy, mentioned above).

### Impact on conulariid cladistic disparity

A striking aspect of conulariid evolution is that only one of the 36 genus-level character states here and generally recognized (e.g., Moore & Harrington 1956; Leme et al. 2008) was (apparently) lost across the Ordovician–Silurian boundary. This state is the absence of a sulcus at the corners (perradii), a synapomorphy supporting *Anaconularia* + *Baccaconularia* but homoplastic with the outgroup coronates. Only one genus-level evolutionary novelty, namely the presence of a mesial ridge in the corner sulcus (an autapomorphy of *Notoconularia*), first appears in post-Ordovician strata. However, our hypothesis of phylogenetic relationships (Figs. 1 and 2) implies that this feature evolved during Ordovician times (see also Discussion section). In short, then, nearly the entire known set of discrete conulariid peridermal anatomical features first appeared prior to

the end of the Ordovician Period, and all of the discrete anatomical features uniquely evolved among conulariids continued to be present in post-Ordovician conulariids.

Among the conulariid genera that do not range across the Ordovician–Silurian boundary, all but one (*Conulariella*) are characterized by the absence of transverse ribs and the possession of longitudinally aligned nodes. Again, however, at least two of these four genera (*Anaconularia* and *Baccaconularia*) may have gone extinct well before the EOEE. *Exoconularia*, while ranging upwards close to the base of the Hirnantian Stage, may not be monophyletic, and if this is indeed true then no supra-specific groups having only nodes went extinct during the EOEE.

## Discussion

The impact of the EOEE on the cladistic disparity of conulariids was very minor, and so too it seems was its impact on conulariid diversity at the genus and higher levels. With the possible exception of *Glyptoconularia*, it appears likely that at least three genera (*Anaconularia*, *Baccaconularia* and *Conulariella*) went extinct well before the onset of the EOEE. *Exoconularia*, which ranges up into the middle Katian (lower Ashgill), may also have gone extinct before the EOEE. One way to investigate whether the five noncrossover genera actually did go extinct before the EOEE is to examine acid digestion residues of carbonate rocks (Jerre 1993; Van Iten et al. 1996, 2006b) straddling the Ordovician–Silurian boundary. Such work has already yielded sub-microscopic fragments of conulariid species and genera in strata in which macrofossil specimens of these taxa had not previously been recorded.

Perhaps not surprisingly, those genera that did survive the EOEE include the most speciose, most abundant and most broadly distributed conulariids of the Late Ordovician world, namely *Archaeoconularia*, *Conularia*, *Metaconularia* and *Pseudoconularia*. Interestingly, the remaining four crossover genera may have been restricted to tropical latitudes. Thus, Ordovician *Ctenoconularia* currently are known only from Laurentia (cratonic North America and Scotland; Sinclair 1948; Van Iten 2012), and Silurian species of this genus are known only from Laurentia and Avalonia (England; Sinclair 1948; Sendino & Darrell 2008). Ordovician *Climacoconus* and *Conularina* have been found only in Laurentia and Baltica (Sinclair 1948; Jerre 1994). Finally, Ordovician *Eoconularia* are known from these two paleocontinents (Sinclair 1948) as well as from Upper Ordovician strata of Avalonia (Wales; Sinclair 1948) and Lower Ordovician strata of West Gondwana (H. Van Iten, unpublished data on conulariids from the Fezouata Formation (Floian) of Morocco).

The minor impact of the EOEE on conulariids may have been due in part to the group's world-wide distribution. In addition to a substantial fall in eustatic sea level and consequent loss of shallow marine habitat, the initial, cooling phase of the EOEE produced changes in oceanic structure and circulation that may have affected levels of marine nutrients (Barnes 2004; Brenchley 2004). The subsequent warming phase was associated with regional anoxia. The initial phase should have exerted its greatest impact on organisms adapted to relatively warm (shallow tropical) waters, but again nearly all Late Ordovician conulariid genera currently known only from tropical paleocontinents (Laurentia and Baltica) survived both the cooling phase and the subsequent warming phase. As noted above, conulariids are now generally interpreted as a major group of scyphozoan cnidarians. The most recent research on the metabolism of these organisms

(e.g., Childress & Seibel 1998) indicates that coronate and certain other medusa, as well as scyphozoan polyps, deal well with low concentrations of dissolved oxygen, at least over short periods of time (De Zwaan & Putzer 1985). In addition, scyphozoans have efficient anaerobic metabolism (possibly glycolysis; Condon et al. 2001; Ishii et al. 2008 and references cited therein). Such characteristics may have benefitted conulariids, especially during the second, warming phase of the EOEE. Our phylogenetic analysis yielded little evidence that any particular character state of the conulariid periderm, save possibly the absence of transverse ribs, conferred reduced fitness under the conditions of the EOEE. Selective pressures may have acted on other traits, perhaps on continuous ones or on aspects of soft-part anatomy.

Finally, assuming that the genera constituting the clade *Climacoconus* + *Holoconularia* + *Notoconularia* + *Paraconularia* + *Reticulaconularia* are collateral descendants of common ancestors, then because the latter four genera currently are known only from post-Ordovician strata, the lineages leading to them must be extended deep into the Ordovician Period as ghost lineages. Thus, our hypothesis of phylogenetic relationships implies the survival of even more conulariid lineages across the Ordovician–Silurian boundary than suggested by merely considering the known stratigraphical ranges of actual fossils alone. Again, this possibility may be tested by examining acid digestion residues for conulariid microfossils showing anatomical characteristics of the terminal post-Ordovician genera.

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