

Dissecting the global diversity trajectory of an enigmatic group: The paleogeographic history of tentaculitoids

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ABSTRACT

Tentaculitoids have long been recognized as a problematic group that diversified taxonomically and expanded geographically through much of the Ordovician–Devonian, only to become extinct toward the end of the Devonian. Perhaps because of uncertainties about their biological affinities, there has never been a definitive study of the diversity trajectories of tentaculitoids at either global or regional scales, and paleoecological analyses of the group are almost entirely lacking in the literature. Here, we present a much-expanded, paleogeographically-resolved database for tentaculitoids, which we use to present a first-ever assessment of their global history in a paleogeographic context.

The new data suggest an increase to a standing-diversity peak in the Devonian of 30 genera, preceded by a Silurian radiation that appears to have been focused mainly in Baltoscandia. Because most of the Silurian Baltoscandian data were derived from a single bibliographic source, the possibility cannot be ruled out that this concentration primarily reflects a monographic bias. The continued radiation in the Devonian was geographically broad-based, however, recognizable in several venues worldwide. Furthermore, whereas previous investigations suggested that a temporal transition could be recognized between the major tentaculitoid orders—Tentaculitida—thought to dominate in the Ordovician and Silurian, and Dacryoconarida and Homoctenida—thought to radiate in the Devonian—the new data point to a much broader overlap in the temporal trajectories of the groups. Coupled with information about differences in their life habits, this would appear to rule out any possibility that the three groups were ever in direct competition.

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1. Introduction

Long-term trends in biodiversity at multiple scales reflect a complex interplay between physical and biological processes, and the paleogeographic and paleoenvironmental underpinnings of diversification in many groups have now been well documented (e.g., Sepkoski, 1982; Miller and Sepkoski, 1988; Westrop and Adrain, 1998; Sepkoski, 2000; Novack-Gottshall and Miller, 2003; Patzkowsky and Holland, 2007; Martin et al., 2008; Rabosky and Sorhannus, 2009). In particular, after years of investigation, the diversity histories of bivalves, trilobites, gastropods, brachiopods, and many other marine invertebrate taxa have been successfully dissected quantitatively to understand patterns of extinction, origination, and evolutionary paleoecology (e.g., Thayer, 1979; Gould and Calloway, 1980; Thayer, 1985; Miller and Sepkoski, 1988; Novack-Gottshall and Miller, 2003; Kowalewski et al., 2005; Huntley and Kowalewski, 2007; Rong et al., 2007). Despite this progress, investigations of the so-called “problematic” taxa have lagged significantly.

Tentaculitoids, an enigmatic group restricted to the Ordovician through Devonian have long been noted as “present” in many paleoecological surveys (e.g., Wallace, 1969; Thayer, 1974; Antia, 1981; Pickerill and Hurst, 1983; Wiedman, 1985; Hurst and Pickerill, 1986; Baarli, 1987; Brett et al., 1991; Baarli et al., 1999; Cornell et al., 2003; Wehrmann et al., 2005; Botquelen et al., 2006; Holland and Patzkowsky, 2007), but there are no modern analogs to this long-extinct group and their associations with other, better-known groups such as brachiopods and trilobites should be considered tenuous at best (Dean, 1961; Hurst and Hewitt, 1977; Towe, 1978; Samtleben et al., 1996; Thomas and Lane, 1999; Rode and Lieberman, 2004; Ray and Thomas, 2007; Drapatz, 2010). There has never been a definitive diversity study of tentaculitoids at any scale, and paleoecological analyses focused specifically on this group are almost entirely lacking in the literature. This is somewhat surprising given the prominence of tentaculitoids in some marine environments during their brief existence. Detailed studies of tentaculitoids have focused mainly on their taxonomy and putative biological affinities (Lyashenko, 1955, 1959; Fisher, 1962; Bouček, 1964; Lardeux, 1969, 1986; Hajlasz et al., 1978; Larsson, 1979; Lukeš, 1985; Farsan, 1994, 2005; Kim, 2008).

Given continuing uncertainties about their taxonomic affinities, a more definitive analysis of their diversity trajectories and paleoecological affinities is warranted. Against this backdrop, we present in

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this paper the first-ever detailed paleogeographic dissection of the history of tentaculitoid global diversity. Using a literature-derived database that we compiled largely for the present study, we demonstrate that tentaculitoids were widely distributed in a suite of marine environments, especially in the Devonian. At the same time, their localized geographic distributions during the Late Devonian likely enhanced the probability of their extinction, except for homotenenids, which remained cosmopolitan in the Frasnian to the early Famennian. More generally, this study demonstrates that methods used to investigate diversity and geographic histories in more common taxa can be applied to problematic taxa through the careful assembly and analysis of data on their global occurrences. That said, some ambiguities remain concerning the extent to which the patterns observed reflect true biological signals versus preservational artifacts or the non-random interests of paleontologists in particular strata, although the same could be said of historical treatments of more common taxa as well (see [Concluding remarks](#)).

This study is a companion paper to a field-based, regional-scale, paleoecological analysis of tentaculitoids in the type Cincinnati, ([Wittmer and Miller, in preparation](#)).

2. Tentaculitoid paleobiology

Tentaculitoids have long been regarded as problematic taxa that diversified taxonomically and expanded geographically after the Ordovician Radiation and through much of the Silurian, only to become extinct during the Late Devonian at the onset of the Kellwasser Crisis ([Schindler, 1993](#); [Walliser, 1996](#); [Bond, 2006](#)). They have been described as *ringed, conical, shelled organisms of uncertain biological affinity* ([Fig. 1](#); [Fisher, 1962](#); [Larsson, 1979](#); [Farsan, 1994](#); [Bergstrom, 1996](#); [Cornell et al., 2003](#)). Previous researchers have classified tentaculitoids as the spines of brachiopods ([Towe, 1978](#)), as possible lophophorates ([Vinn and Mutvei, 2009](#); [Taylor et al., 2010](#)), as cephalopods lacking a siphuncle, or as pteropod-like pelagic gastropods ([Orlov et al., 1976](#); [Weedon, 1990](#); [Drapatz, 2010](#)). Others have informally designated them as a distinct class of Mollusca, the Tentaculitoidea ([Lyashenko, 1957](#); [Bouček, 1964](#); [Lardeux, 1969](#); [Drapatz, 2010](#)), although the molluscan affinity based on shell morphology and wall structure is still questioned. Even the life position of

tentaculitoids remains uncertain with most workers regarding tentaculitoids as either benthic or planktonic suspension feeders ([Fig. 2](#), [Fisher, 1962](#); [Cornell et al., 2003](#)). The present taxonomic position of tentaculitoids therefore remains contentious with a continued lack of consensus concerning their affinities ([Schindler, in review](#)), but ongoing research continues to address these persistent issues ([Schindler pers. comm.](#)).

The Class Tentaculitoidea [Lyashenko \(1957\)](#); (= Cricoconarida of [Fisher, 1962](#)) is divided into three orders, Dacryoconarida [Fisher \(1962\)](#), Homotenenida [Bouček \(1964\)](#), and Tentaculitida [Lyashenko \(1955\)](#) based on several distinctions by [Lyashenko \(1959\)](#), [Bouček \(1964\)](#), and [Lardeux \(1969\)](#). In general, Dacryoconarida have a smaller body size (0.8–20 mm), thinner shell, and bulbous apex ([Fig. 3](#)). The bulbous apex represents the embryonal stage of the organism that expands into the larval chamber. Dacryoconarids are generally thought to occur from the middle Silurian through late Devonian, although, as part of the present study, reports of occurrences were noted from as early as the Late Ordovician. The order includes the common Devonian groups Nowakiida [Lyashenko \(1955\)](#) and Styliolinida [Lyashenko \(1955\)](#) that can be found in Europe, North Africa, the Russian platform, Central Asia, South China, Australia, and eastern North America ([Lyashenko, 1953, 1955, 1959](#); [Alberti, 1971, 1980, 1981, 1982, 1988](#); [Lütke, 1974, 1979](#); [Lukeš, 1977, 1984, 1991](#); [Yochelson, 1983](#); [Lindemann and Yochelson, 1984](#); [Lyashenko and Lipatova, 1985](#); [Gessa, 1995, 1996, 1997](#); [Lindemann and Karabinos, 2002](#); [Kim, 2008](#)). Known as the ‘small-shelled and thin-walled’ tentaculitoids, they are common in black shales around the world but are also known to occur in light gray limestones, sometimes with exquisite preservation.

Tentaculitida are known as the ‘large-shelled and thick-walled’ tentaculitoids and members of the order have ringed, layered shells, tiny and narrow apices, and range in length from 1 to 80 mm (average 15–30 mm). The order Tentaculitida includes the most common genus designated in tentaculitoid paleoecological studies, *Tentaculites*. *Tentaculites* has the longest temporal range of all tentaculitoids, first appearing in the Early Ordovician ([Fisher and Young, 1955](#); [Corbett and Banks, 1974](#)) and ranging to the Late Devonian ([Wallace, 1969](#); [Cockbain, 1975](#); [Hajlasz et al., 1978](#); [Chen and Tucker, 2003](#)). Many researchers, however, have argued that *Tentaculites* is a “wastebasket” name because, without detailed examination, it has typically been

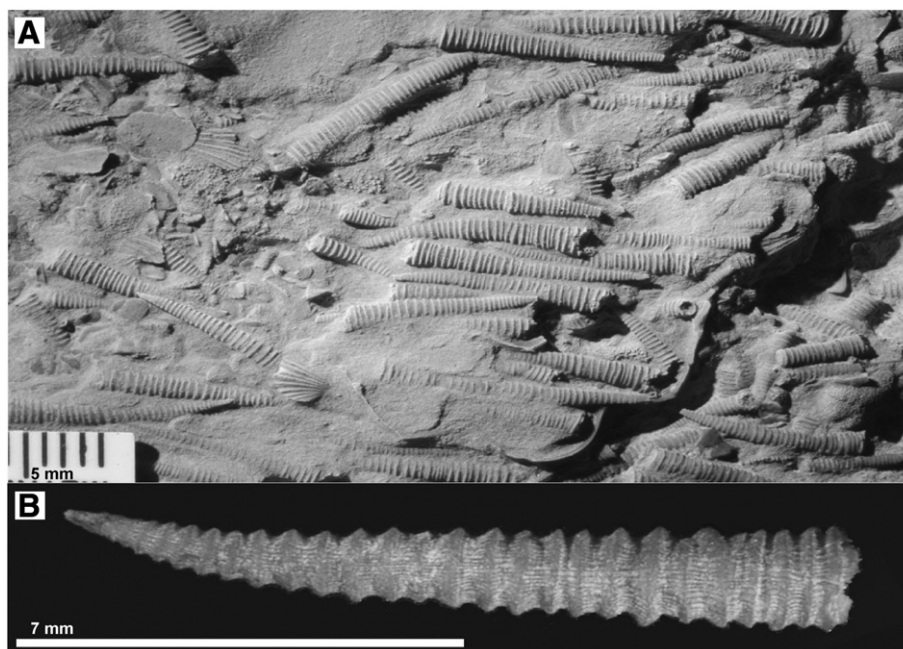


Fig. 1. Tentaculitoids from the Ordovician, Cincinnati Arch region. A) *Tentaculites richmondensis* (Miller), CMC IP 17551, Clinton Co., Ohio. Typical bed of tentaculitoids from the Cincinnati showing parallel alignment. Photo courtesy of D.L. Meyer. B) *Tentaculites* from the Waynesville Formation, Flemingsburg, Kentucky.

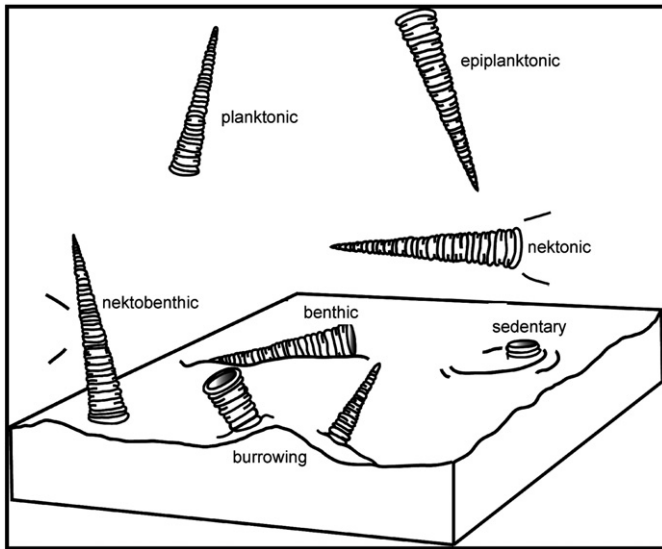


Fig. 2. Proposed modes of life for tentaculitoids. Tentaculitoids are commonly found oriented parallel the bedding planes, but can also be found vertically oriented. Modified from Fisher 1971, Cornell et al. (2003).

used in paleoecological studies as a designation for any conical fossil with annulations, along with *Cornulites* (see Plotnick and Wagner, 2006; Wagner et al., 2007). Tentaculitids are a globally occurring group most commonly found in Baltoscandia, the Mediterranean Province, Australasia, Laurentia, and South America (Driscoll, 1969; Hajlasz, 1974; Cockbain, 1975; Yoder and Erdtmann, 1975; Lukeš, 1977; Larsson, 1979; Ciguel, 1988; Ciguel et al., 1988).

Like Tentaculitida, the Homoctenida are calcitic 'large-shelled' tentaculitoids that are common in the Mediterranean Province, Laurentia, and South China (Bouček, 1964; Alberti, 1969, 1970, 1983; Chatterton and Perry, 1978; Zhang and Pojeta, 1986; Schindler, 1990; Ji and Ziegler,

1993). Homoctenids are different from tentaculitids in that they are 'thin-walled' and occur only in the Devonian. Commonly found in deep water limestones, shales, and siltstones, homoctenids are chiefly used for biostratigraphic studies in the Devonian because of their apparently high species turnover (Bond, 2006). Both dacroconarids and homoctenids are thought to have had a planktonic mode of life because of their widespread distribution in deep marine facies and occurrences with conodonts (Lyashenko, 1954; Fisher, 1962; Bouček, 1964; Lardeux, 1969; Lütke, 1974). For the present study, tentaculitids and homoctenids will be grouped together for analysis because of their similar morphological features and body size. Although both groups have different shell wall thickness and possible different modes of life, to some workers these two groups have enough in common that they can be grouped together (Farsan, 1994, 2005).

Documentation of vertically oriented tentaculitoids is rare, but has been noted in certain stratigraphic sequences (Driscoll, 1969; Cornell et al., 2003; Wittmer and Miller, in preparation). It has also been debated whether tentaculitids, homoctenids, and dacroconarids should even be grouped in the same class, but Lardeux (1969) and Larsson (1979) have found that all groups display a shell with the same distinctive accretion of each layer in relation to metamorphosis of the soft body. They argue that the size and morphological differences among the three groups likely reflect differences in lifestyle. As with dacroconarids, homoctenids are thought to have had a planktonic mode of life while tentaculitids are postulated to have been benthic. Some researchers have claimed to have found tentaculitoids in the Carboniferous, (Lineback, 1964; Roberts, 1964; Shul'ga et al., 1994; Niko, 2000), but there is a general consensus among tentaculitoid workers that the group became extinct in the Late Devonian and reports of younger tentaculitoids are generally considered suspect (Schindler, in review).

Previous studies have focused on tentaculitoids as paleocurrent indicators and biostratigraphic markers (Hajlasz, 1976; Hladil et al., 1991), sidestepping for the most part the group's diversity history or other biological attributes. As noted earlier, broader based paleoecological

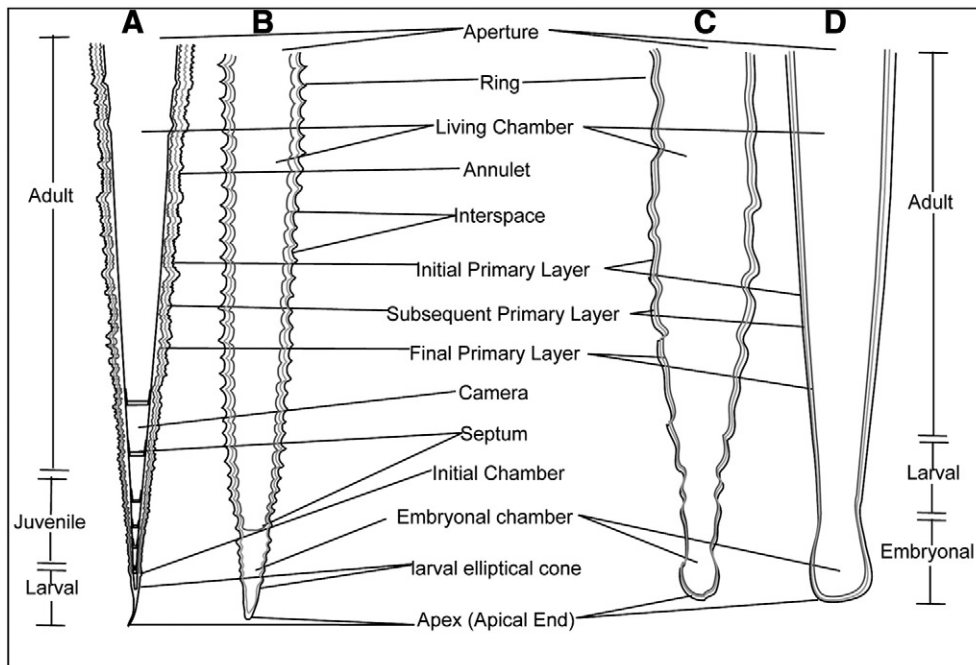


Fig. 3. Reconstructions of Tentaculitida (A), Homoctenida (B), and Dacroconarida (C and D) conchs in longitudinal section with important characteristics identified. The conchs include representative genera of Tentaculitoidea: A) *Tentaculites* B) *Homoctenus* C) *Nowakia* D) *Styliolina*. The layered shell is evident for both subclasses with the initial primary layer (black) making up the outer shell followed by a subsequent primary layer (light gray), and a final primary layer (dark gray) that makes up the internal cavity of the conch. The larval section of the Tentaculitida and Homoctenida contains a tiny narrow apex whereas Dacroconarida have a bulbous apex part of the embryonal chamber. The body of the tentaculitoid likely resided in the living chamber, which had an open aperture. Modified after Fisher (1962); Larsson (1979); Farsan (1994, 2005).

studies that document tentaculitoid fossils generally have lumped these organisms as *Tentaculites* sp. (Hurst, 1979; Wiedman, 1985). This problem is illustrated in the Paleobiology Database (PaleoDB: <http://paleodb.org/>), an online compendium of global fossil occurrences, derived largely from the paleontological literature. Before the present study in December 2007, there was a notable absence of tentaculitoid data in the PaleoDB: a total of 511 tentaculitoid occurrences gleaned from 120 publications, with 213 of the 511 occurrences designated as *Tentaculites* sp. This scarcity almost certainly reflects the focus of previous database contributors on other, more common groups, adding tentaculitoids only when they appeared in passing. Additionally, at regional levels, there has been little work on the paleoecological roles of tentaculitoids, thus limiting our understanding of their paleogeographic or paleoenvironmental attributes (Wittmer and Miller, in preparation). In the present study, an in-depth examination of the literature has uncovered a large number of additional references focusing specifically on tentaculitoids that permitted significant improvements to the previously deficient database.

3. Data collection

As noted earlier, some limited tentaculitoid data were already present in the PaleoDB prior to this study. These were augmented significantly through a comprehensive search and survey of references. Useful references included paleoecological and biostratigraphic studies, as well as systematic investigations of specific groups or individuals. In all, 1635 fossil occurrences representing 50 tentaculitoid genera and 117 species were collected from 240 references depicting occurrences around the world, and all data were incorporated into the PaleoDB (Table 1). Where possible, compiled data also included co-occurring taxa, as well as the number of individuals and/or specimens, and information on taphonomy, geography (latitude, longitude, country, state, and county), lithology, paleoenvironment, and stratigraphic interval. For each reference, collections (the fundamental units of the PaleoDB) were delineated based on occurrences at distinct stratigraphic intervals and/or from single geographic locations. Some references yielded only a single collection, whereas others, typically covering broader stratigraphic intervals or larger regions, yielded multiple collections.

Taxa encountered in this investigation, as well as those already listed in the PaleoDB, were updated to current phylogenetic and systematic interpretations based on work by Lyashenko (1959), Bouček (1964), Lardeux (1969), Farsan (1994), and Bergstrom (1996), and these systematic improvements were incorporated into the taxonomic opinion pages of the PaleoDB.

Because of current questions about systematic relationships, a few tentaculitoid references were excluded from this study. In particular, references to cornulitids, which have been viewed alternately as worm tubes or a distinct dactyloconarid order were not included, because there is currently no consensus about their affinities (Bouček, 1964; Larsson, 1979; Farsan, 1994). Other excluded references focused on conical forms not resembling tentaculitoids biologically or morphologically but nevertheless viewed by some previous workers as putative tentaculitoids (Weedon, 1991; Vinn, 2006, 2007).

Lithology and sedimentary structures were also noted for collections when these data were available in the literature sources. Assignment to temporal intervals was based on the literature sources, updated to

reflect current stratigraphic relationships and correlations. Latitude and longitude for collection localities were either provided by the literature sources or were determined by pinpointing localities in *Google Earth*. Paleolatitude and paleolongitude were determined by the PaleoDB, which incorporates rotations based on Scotese's PALEOMAP estimations (e.g., Scotese and McKerrow, 1990). Time bins for most of our analyses, except for those related to Fig. 9, were the global stages for the Ordovician through Devonian; many of the literature sources for tentaculitoid data accessed in this investigation did not permit higher resolution determinations, at least on a global scale. For the Ordovician, the "old" British standard was used, since references tended to report occurrences on this stratigraphic basis. Coverage of Ordovician and Silurian data in the PaleoDB was rather limited for some stages, orphaning important data at the time they were downloaded. To prevent the loss of essential data, ten million year time bins were used for Fig. 9.

Once assembled in the PaleoDB, tentaculitoid and other data for the analyses presented below were downloaded on February, 2011 and for Fig. 9 on September, 2011.

4. Data analyses

4.1. Diversity trajectories

Stage-by-stage diversity trajectories were developed from the tentaculitoid database using multiple methods of analyzing tentaculitoid occurrences, including *range-through* and *boundary-crosser* methods. The *range-through* method has typically been used to analyze global diversity, but less so for assessing regional diversity because of the possibility of immigration and emigration to and from the region affecting the number of taxa ranging through the interval in the area (Patzkowsky and Holland, 1996). By contrast, the *boundary-crosser method* assesses taxonomic richness at boundaries *between* intervals. By definition, this metric does not count singletons – taxa restricted to a single interval – and therefore somewhat mitigates sample-size differences from interval to interval, which are thought to reflect the number of singletons (Bambach, 1999; Bambach et al., 2004; Kiessling et al., 2007). The tentaculitoid data include a large number of singletons (20 genera), and the boundary-crosser method helps to diagnose more clearly how many taxa actually persisted from one interval to the next.

Classical rarefaction was performed on the raw diversity data of tentaculitoids to account for sampling inhomogeneities from interval to interval (Miller and Foote, 1996; Alroy et al., 2001, 2008). This sampling standardization technique mitigates the effects of differences in sample size by estimating the number of taxa that would have been found in stratigraphic intervals with larger numbers of occurrences if, instead, they had the same sample size as intervals with smaller numbers of occurrences. Classical rarefaction is likely inappropriate for sampling-standardization of diversity trajectories that span large portions of the Phanerozoic because of the likely confounding effects of secular changes in the abundance distributions of component communities (Alroy et al., 2008; Alroy, 2010), but it has been used effectively for investigating diversity trends over limited intervals within a single Phanerozoic era. Sampling quotas of 30 and 100 occurrences were used because of the variable amounts of data available in the Ordovician (typically less than 100 occurrences) relative to the Devonian (typically more than 100 occurrences). Rarefaction estimates at both quotas were based on 1000 iterations, and 95% confidence intervals were also calculated.

4.2. Paleogeographic dissection of diversity

Paleogeographic variations in diversification were analyzed by dissecting the global trajectory of tentaculitoids with respect to paleocontinental distributions. Paleocoastal designations and positions were based on Scotese's (e.g., Scotese and McKerrow, 1990) reconstructions of Laurentia, Avalonia, Baltoscandia, South China,

Table 1
Global tentaculitoid occurrences and unique genera.

	Global tentaculitoid	Number of unique genera
Ordovician	133	3
Silurian	274	13
Devonian	1228	35
Total	1635	51

Kazakhstan, Australasia, South America, and the Mediterranean Province (Fig. 4). For example, genera that occurred in strata located in France and Morocco were included in the Mediterranean Province, a set of microcontinents located at high southern latitudes in the early to mid-Paleozoic, whereas genera in Nova Scotia and Wales were placed in Avalonia, a small continent located in high-to-moderate southern latitudes during the study interval. Genus diversity for each paleocontinent was assessed using the range-through method and the percent contribution of genera shared among paleocontinents, the percent contribution of each continent to total global diversity through the study interval.

5. Results

5.1. Global tentaculitoid diversity trajectory

The range-through, boundary-crosser, and rarefied genus-level global diversity trajectories through the study interval (Fig. 5) show a rise and rapid fall in tentaculitoid diversity. Only one genus is documented prior to the Late Ordovician, *Tentaculites* in the Tremadocian. However, in the Late Ordovician two dactyloconarids, *Costatulites* and *Styliolina*, have been reported from Laurentia, increasing the aggregate diversity in all four analyses (Miller et al., 1954; Nitkin and Berger, 1989). Other studies have not recognized any dactyloconarids from the Ordovician, and it is more commonly thought that the subclass first appeared in the middle Silurian (Fisher, 1962; Norford, 1963; Plotnick, 1999). Miller et al. (1954) documented possible *Styliolina* occurrences in the Ordovician and these are included in the trajectory as appearing in the Hirnantian (latest Ordovician). It is important to note that the earliest occurrences of these dactyloconarids are speculative because of possible imprecise sampling and a contentious Ordovician origin for the group. These first occurrences are included in our analyses as a tentative start for the dactyloconarids, but further research on early dactyloconarids is still needed.

In general, a lack of information about the early history of Tentaculitida in the Ordovician might convey the impression that they were rather rare in the Ordovician, but based, at least on their regional abundances in strata of the type Cincinnati, this clearly was not the case (Holland and Patzkowsky, 2007; Wittmer and Miller, in preparation). Tentaculitoids were rare earlier, during the Tremadocian (Early Ordovician), with only

five collections present for the whole interval with no occurrences during the Middle Ordovician. The raw diversity trajectories in Fig. 5 suggest that tentaculitoids experienced a gradual increase in genus diversity from the base of the Silurian to the Early Devonian. During the Silurian, dactyloconarids and tentaculitids both contributed to the overall trajectory (Fig. 6), increasing diversity substantially to 30 genera by the Devonian, with the addition of homoctenids contributing most significantly to the overall diversity.

Diversity started to decline by the Middle Devonian (Eifelian) and, coupled with the onset of extinction events during the Late Devonian (Raup and Sepkoski, 1982; McGhee, 1996; Walliser, 1996; Bond et al., 2004; Jablonski, 2005), diversity plummeted rapidly, and tentaculitoids became extinct near the end of the period. The Silurian-to-Devonian increase observed in the raw diversity trajectories was muted substantially by rarefaction at a quota of 30 occurrences (Fig. 5C). All Silurian time bins contained at least 30 occurrences, but only one interval reached 100 occurrences, precluding a comparison between Silurian and Devonian at the higher quota. Given the relatively small sampling quota of just 30 occurrences on which the rarefied comparison between the Silurian and Devonian is based, this comparison should be interpreted cautiously, but it at least raises the possibility that the major Devonian increase observed in raw trajectories is partly an artifact of the increased sample sizes for Devonian time bins.

Dactyloconarida and Tentaculitida–Homoctenida range-through and rarefied diversity trajectories in Fig. 6 illuminate the different intervals of high diversity for each subclass. Tentaculitida–Homoctenida contributed a greater amount of total tentaculitoid diversity from the Ordovician to the Early Devonian, confirmed with the rarefied trajectory for the subclass. Tentaculitida–Homoctenida paralleled the increase in diversity and the gradual decline into the Late Devonian of the total curve, becoming extinct in the Frasnian (Fig. 6B). Dactyloconarids, on the other hand, gradually increased in diversity during the Silurian and added more genera to the total trajectory in the Late Devonian, as observed in the rarefied curve (Fig. 6D).

5.2. Paleogeographic diversity trajectories

The diversity trajectories of tentaculitoids appear, based on available data, to have been associated with radiations in particular paleocontinents at different times. Here, we analyze the apparent dispersal

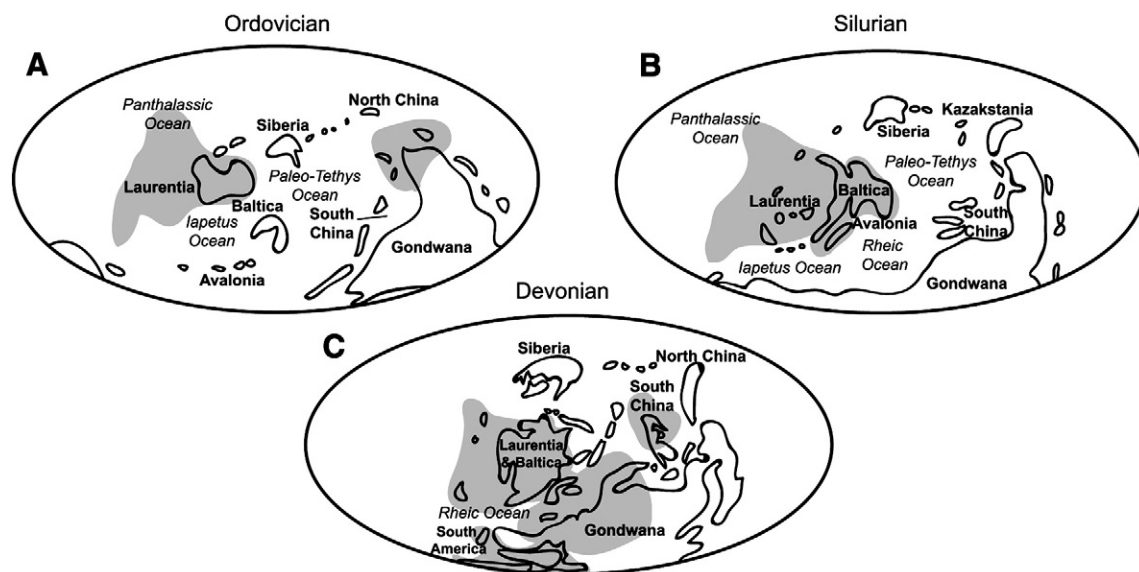


Fig. 4. Paleogeographic reconstruction of the ranges of tentaculitoid occurrences (light gray) in the Ordovician (A), Silurian (B), and Devonian (C). In the Ordovician (A) tentaculitoids appeared in Australasia (Gondwana) and Laurentia. By the Silurian (B) tentaculitoids appeared in Baltica in high abundance and in Laurentia and Avalonia. During the Devonian (C) tentaculitoids appeared throughout the world in South America, Laurentia, Avalonia, Baltica, South China and the Mediterranean Province.

Maps modified from Scotese and McKerrow (1990).

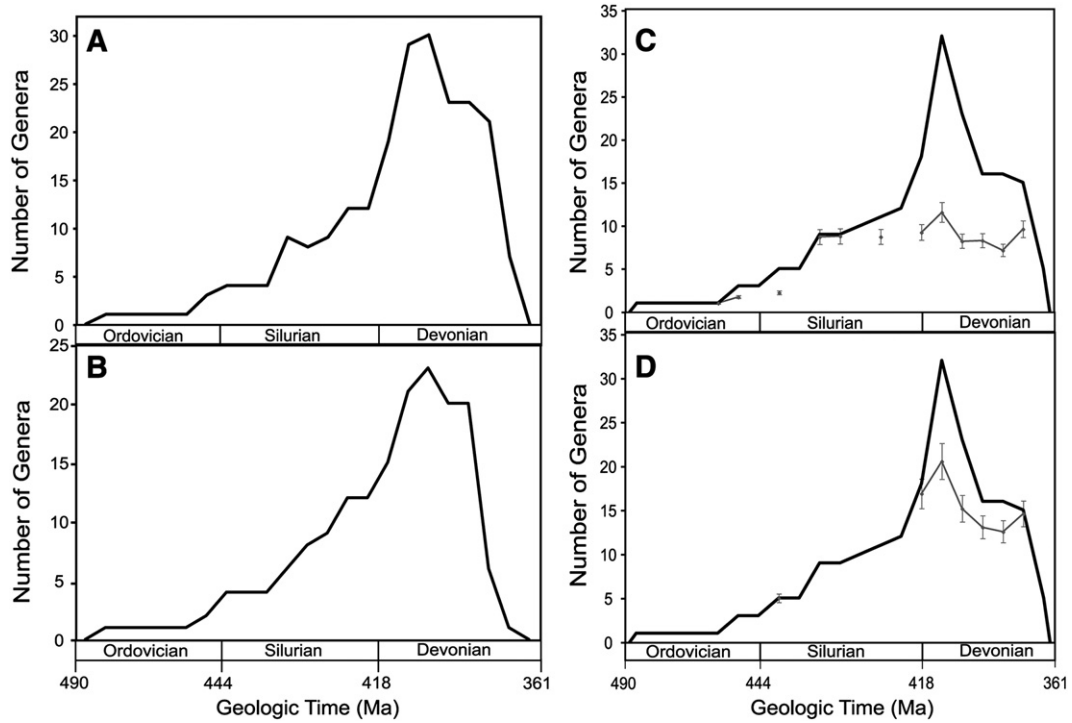


Fig. 5. Diversity trajectories of tentaculitoids from the Ordovician through the Devonian. A) Range-through analysis. The diversity of tentaculitoids climbed from one genus in the Early-Middle Ordovician to a maximum of 30 genera in the Early Devonian. Tentaculitoids declined in diversity throughout the Devonian, culminating in their extinction in the Late Devonian. B) Boundary-crosser analysis of tentaculitoid diversity; note lower standing diversity with the removal of singletons, with a maximum of 23 genera in the Early Devonian. C) Rarefied diversity to a quota of 30 occurrences of time bins that contained 30 or more occurrences (gray with diamonds) with 95% confidence intervals in gray along with the raw, sampled-in-bin diversity (black) of tentaculitoids. Note the relatively flattened pattern from the Silurian to the Devonian. D) Rarefied diversity to a quota of 100 occurrences of time bins containing 100 or more tentaculitoid occurrences (gray with diamonds) with 95% confidence intervals in gray along with raw diversity of tentaculitoids (black). The Devonian rarefied diversity closely resembles the raw trajectory.

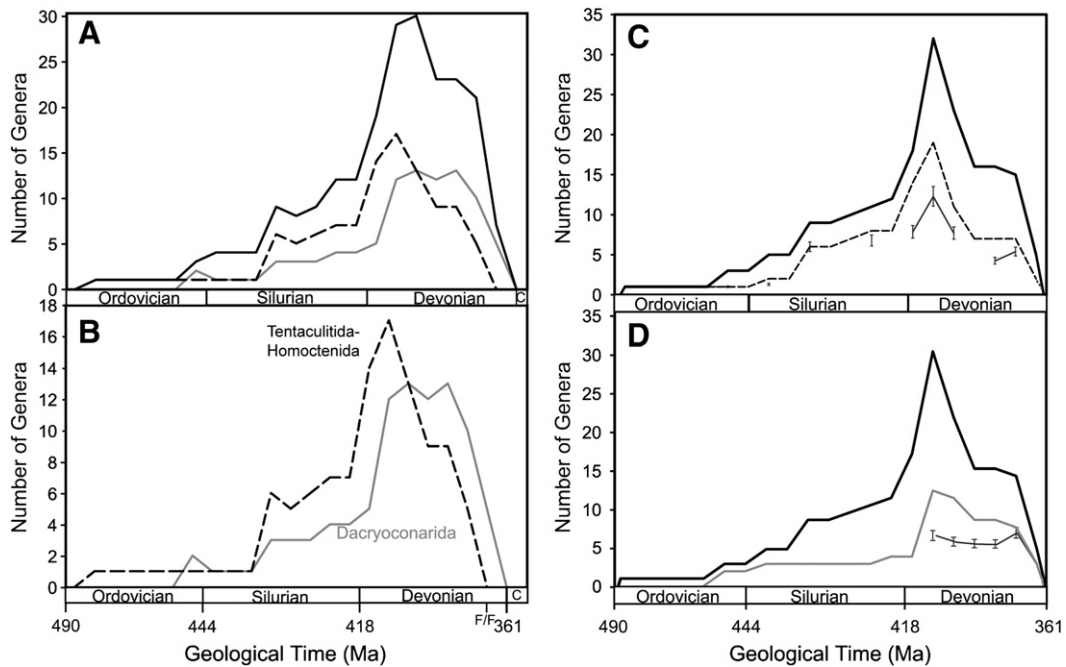


Fig. 6. Diversity trajectories for subclasses. A) Total range-through for all tentaculitoids (black) as well as the order components, the tentaculitids-homoctenids (dashed) and dacyroconarids (gray). All three orders contributed to the overall trajectory, particularly building the Early Devonian maximum. B) Range-through diversity trajectory for the orders; Tentaculitida-Homoctenida (dashed) and Dacyroconarida (gray). Tentaculitids appeared in the Early Ordovician and reached peak diversity in the Early Devonian with the addition of homoctenids, becoming extinct by the Frasnian. Dacyroconarids did not appear until the Late Ordovician and were highly diverse in the Devonian only to become extinct by the mid-Famennian. C) Tentaculitida-Homoctenida rarefied diversity of time bins that contained 30 or more occurrences (gray) with 95% confidence intervals in gray along with the total raw, sampled-in-bin diversity of Tentaculitoidea (black) and raw Tentaculitida-Homoctenida diversity (dashed). The rise in the Early Devonian was slightly muted in the rarefied trajectory, but shows that tentaculitids-homoctenids contributed significantly to the overall increase in diversity. D) Dacyroconarida rarefied diversity of time bins that contained 30 or more occurrences (gray) with 95% confidence intervals in gray along with the total raw diversity of Tentaculitoidea (black) and raw Dacyroconarida diversity (light gray). The rarefied Early Devonian rise is more muted than that of the Tentaculitida-Homoctenida and shows a slow decrease through most of the period.

of tentaculitoids through time, through a paleogeographic dissection of their diversity trajectories (Fig. 7).

5.2.1. Ordovician paleobiogeography

As noted earlier, the Ordovician was a time of very limited tentaculitoid diversity, despite their considerable abundance in some regions. In the Early Ordovician (Tremadocian), *Tentaculites* occurred in Australasia (Australia, Malaysia, and Thailand), which was located near the northeastern coast of Gondwana close to the equator (Fig. 4; Cocks, 2001). Environments here were dominated by a mix of siliciclastic and carbonate sediments (Scotese and McKerrow, 1991; Cocks, 2001). Interestingly, after the Tremadocian, *Tentaculites* was not documented in younger Ordovician strata of Australasia. In other parts of the world, tentaculitoids are not documented again until the Late Ordovician in Avalonia, located at that time in the southern subtropics adjacent to Baltoscandia (Fig. 4; Torsvik, 1998). *Tentaculites* is, again, the only genus documented in Avalonia for that interval, with only one species, identified as *Tentaculites anglicus*, along with occurrences of another undesigned species assigned to *Tentaculites*. Despite the paucity of distinct taxa, the paleocontinent yielded a considerable number of Late Ordovician tentaculitoid occurrences, suggesting that they were quite abundant at that time.

In the Late Ordovician, *Tentaculites richmondensis*, a common tentaculitoid found in multiple collections from the type Cincinnati strata characterized by carbonate, siliciclastic, and mixed systems contribute to the slight increase in regional diversity in Laurentia (Holland and Patzkowsky, 2007). Tentaculitoid abundances are very high in the Cincinnati, but are sporadic at the outcrop scale. In

our companion study (Wittmer and Miller, in preparation), tentaculitoids are highly abundant within certain stratigraphic horizons and do not typically persist in abundance laterally even at the scale of individual localities. While many occurrences of *Tentaculites* have been documented for the Late Ordovician of Laurentia, only one occurrence of *Styliolina* has been documented in the collections of the PaleoDB (Miller et al., 1954) marking the first appearance of the dactyloconarids. However, this early occurrence is debatable. By the end of the Ordovician, *Tentaculites* also occurred in Baltoscandia and the Mediterranean Province. Finally, the dactyloconarid genus *Costatulites*, is known from the Upper Ordovician of Kazahkastania (Nitkin and Berger, 1989).

5.2.2. Silurian paleobiogeography

The Early Silurian marked the beginning of a notable increase in genus diversity for tentaculitoids worldwide (Fig. 7). As the number of genera increased, so did their collective geographic range. Greater numbers of occurrences and unique genera appeared in Baltoscandia, in particular (Fig. 7D). The Early Silurian marked the first appearance, in Avalonia, of *Nowakia* (Dactyloconarida), which was the most common dactyloconarid in the Silurian and Devonian.

Baltoscandia, which appears to have been something of an epicenter for the first appearances of Silurian tentaculitoids, was located in the tropics south of the equator during the Silurian and represents a carbonate-dominated platform. In all, nine genera first appeared in this paleocontinent (Larsson, 1979) during the Silurian, primarily tentaculitids.

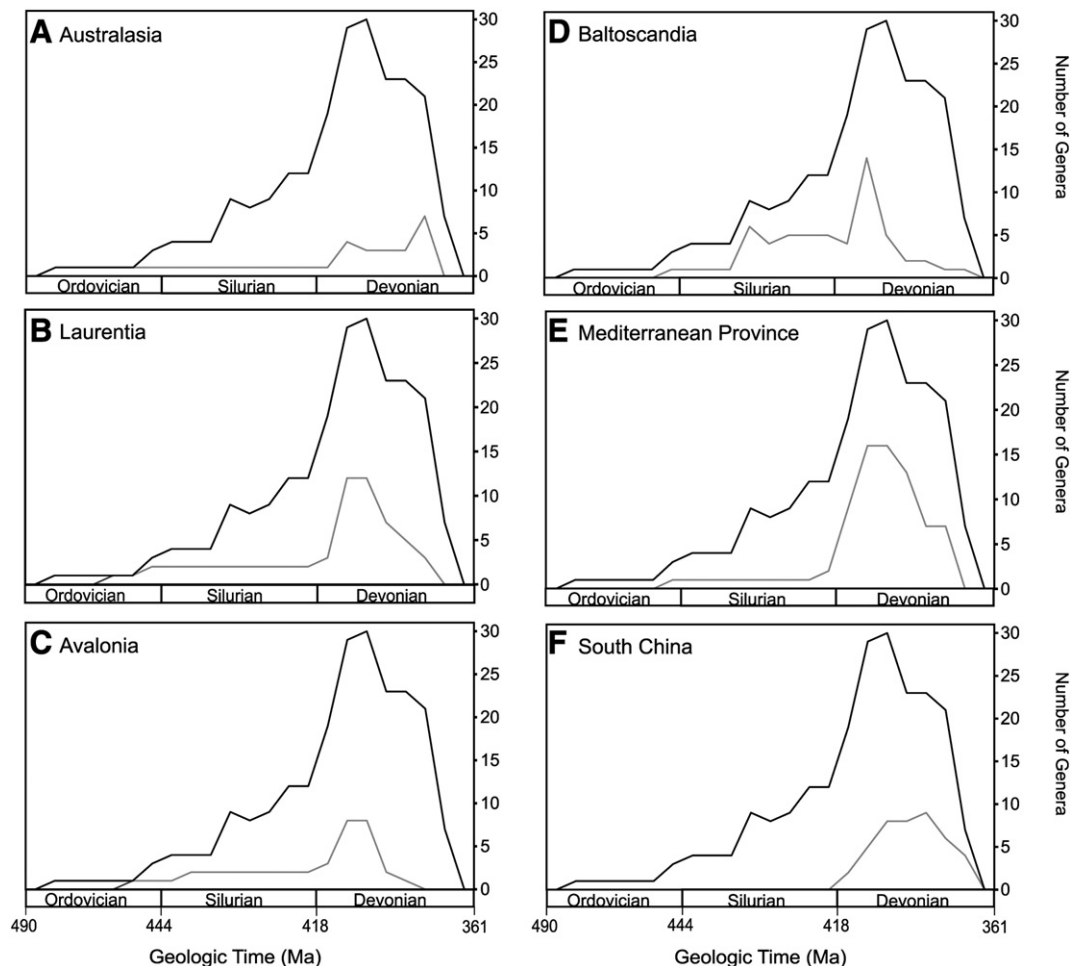


Fig. 7. Tentaculitoid range-through diversity trajectory for individual paleocontinents (gray), versus global range-through diversity (black). A) Australasia. B) Laurentia. C) Avalonia. D) Baltoscandia. E) Mediterranean Province. F) South China.

5.2.3. Devonian paleobiogeography

As noted earlier, the Devonian was characterized by an extensive global radiation of tentaculitoids (Fig. 5), although the size of the increase may have been exaggerated in raw compilations because of increased Devonian sample size. That said, the diversity increase paralleled a broadening distribution of tentaculitoids around the world, with the geographic range of rich tentaculitoid faunas expanding to all paleocontinents (Fig. 7).

Interestingly, tentaculitoid diversity increased during the onset of the Acadian orogeny (Scotese and McKerrow, 1990; Soper et al., 1992; Murphy, 2007), in siliciclastic-dominated areas of Avalonia and Laurentia. Dacryoconarid, homoctenid and tentaculitid genera were present in virtually equal numbers in the Early Devonian. During the Pragian, five new genera appeared in Avalonia, but, after that time, the regional diversity of tentaculitoids gradually declined. It is possible that this regional diversity increase is at least partly a sampling artifact associated with the increased availability of siliciclastics. However, the overall Devonian increase in tentaculitoid diversity transcended these regions (see below) suggesting that it was not simply tied to an increase in rock volume (see Discussion and Concluding remarks sections for additional consideration of the rock-volume issue).

Laurentia harbored many types of dacryoconarids, especially styliolinids in black shales. By the Late Devonian, however, only *Styliolina* and *Tentaculites* were present, and by the Frasnian, Laurentia was devoid of tentaculitoids. In the Pragian, Baltoscandia exhibited an increase of 14 genera, but, diversity then apparently declined there throughout the latter part of the Devonian.

The Mediterranean Province was the major contributing region for tentaculitoid genus diversity during the Devonian, with a standing diversity of 16 genera in the Lower Devonian (Fig. 7E). Prior to that, however, the province did not contain substantial numbers of tentaculitoids. The majority of Devonian tentaculitoids in the Mediterranean Province were dacryoconarids (*Nowakia*, *Styliolina*, and other thin-shelled forms); most of the later occurrences are known from the Prague Basin, where multitudes of tentaculitoid species and genera were described in a series of studies (Bouček, 1964; Lukeš, 1977, 1982, 1984, 1985, 1989, 1991; Lardeux, 1986; Farsan, 1994). Occurrences were limited from the Givetian to the Famennian because of an absence of older marine rocks in the Prague Basin. Earlier Devonian occurrences for the Mediterranean Province were mainly from the Russian platform (Lyashenko, 1953, 1955, 1957, 1959; Lyashenko and Lipatova, 1985) and North Africa (Dubois and Mazelet, 1964; Alberti, 1969; Lütke, 1979; Pashko, 2004). By the beginning of the Frasnian, however, tentaculitids were apparently absent from the region with homoctenids persisting until the Early Famennian (Schindler, 1990, 1993).

Frasnian tentaculitoids remained widespread and abundant in Australasia (Cockbain, 1975), Laurentia (Baird, 1976), and in South China (Li and Hamada, 1987; Wang, 1990; Li, 2000; Chen and Tucker, 2003). However, by the end of the Frasnian, the remaining tentaculitoid occurrences documented in the present study are from South China, in particular from Frasnian and Famennian strata (Fig. 7F). Tentaculitida (*Tentaculites*) were present there until the end-Frasnian extinction. *Styliolina* and *Striatostyliolina* were the most common tentaculitoid in the carbonate rich environments of South China (Li, 2000) and persisted up until to the Famennian.

6. Discussion

6.1. Global diversity trajectory

It is instructive to compare the tentaculitoid diversity curve that could have been constructed based on the PaleoDB prior to this investigation to the new curve that includes that data reported here (Fig. 8A). Before the present study was initiated, only 13 tentaculitoid

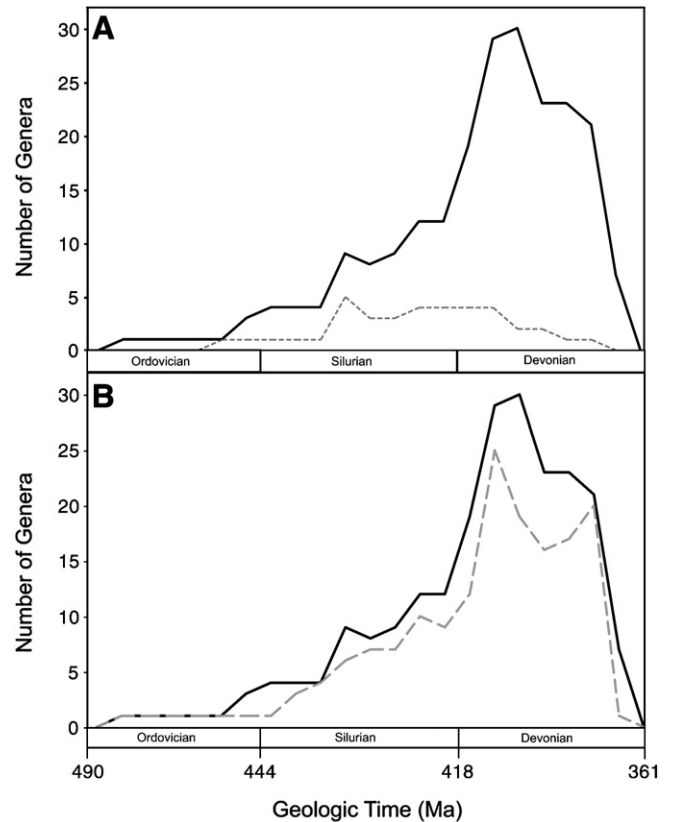


Fig. 8. A) Range-through global diversity trajectory of tentaculitoids from the PaleoDB in December 2007 before the present study was initiated (gray), compared with the updated diversity trajectory as of February 2009 (black). B) Range-through diversity of tentaculitoids from data acquired in this study (black) versus the pattern based on Sepkoski's (2002) global compendium data for tentaculitoids (dashed).

genera were represented in the PaleoDB, with almost no data from the Devonian. Updated taxonomic information from several papers revealed at least 97 genera within the Tentaculitoidea (Lyashenko, 1955, 1957, 1967; Bouček, 1964; Larsson, 1979; Lardeux, 1986; Farsan, 1994), but, currently, only 50 of these 97 have collection data associated with them in the PaleoDB. At least some of the remaining 47 genera were documented only once in a systematic investigation, and were not accompanied by information required for proper cataloging in the context of the PaleoDB (i.e. stratigraphic data, location, and lithology).

Our aggregate global curve for tentaculitoids is, however, fairly congruent with a curve based on Sepkoski's (2002) global genus compendium (Fig. 8B). Because Sepkoski's compendium includes information on only the first and last global appearances of genera, it cannot be used for the kind of paleogeographic dissection conducted in the present study. Furthermore, our curve exceeds that based on Sepkoski's compendium curve in the Silurian because of updated taxonomic and occurrence data not available to Sepkoski when his compendium was completed. Eleven new genera were added from studies that were obscure or were not available at the time (Churkin and Carter, 1971; Ludvisgen, 1972; Lavrusevich et al., 1973; Breyvel et al., 1977; Farsan, 1981; Ruan and Mu, 1983; Li and Hamada, 1987; Niko, 1998; Gerreine et al., 1999; Li, 2000). Importantly, the concordance between the global diversity curves compiled independently from Sepkoski's global compendium and our updated data added to the PaleoDB suggests that the PaleoDB now effectively captures the global signal for tentaculitoids available from the fossil record, at least as cataloged to date (see Concluding remarks, below). This, in turn, suggests that the paleobiogeographic and lithological patterns described earlier are direct reflections of the state of the art with respect to the global tentaculitoid record.

6.2. *Tentaculitida–Homoctenida and Dacryoconarida diversity trajectories*

Prior to this study, the tentaculitoid orders, *Tentaculitida*, *Homoctenida* and *Dacryoconarida*, were thought to exhibit patterns of diversification quite different than those illustrated here (Bouček, 1964; Farsan, 1994; Berkyová et al., 2007). In the literature, tentaculitids were characterized as comprising most of the Ordovician and Silurian diversity of tentaculitoids, and then declining subsequently in conjunction with the growing diversity of dacryoconarids and homoctenids (Bouček, 1964; Farsan, 1994). Dacryoconarids were thought to have diversified rapidly in the Devonian, subsequently collapsing during the Frasnian–Famennian mass extinction (Fisher, 1962). Based on the present study, however, this does not appear to be the case, and there is no indication that either group had any effect on the other's trajectory. Because of the possibility that tentaculitids, homoctenids and dacryoconarids had different lifestyles and, therefore, were not likely in direct competition, some researchers have surmised that dacryoconarids and homoctenids were offshoots of tentaculitids and, ultimately, became more successful. Both groups have been thought to have had planktonic larval stages, but differed after reaching juvenile development according to Farsan (1994). Tentaculitids supposedly settled to the substrate and maintained a benthic habit during their juvenile and adult lives. Dacryoconarids, however, are commonly associated with conodonts in more fine-grained sediments representing the outer shelf, leading many to regard them as having been planktonic (Fisher, 1962; Lütke, 1974; Alberti, 1993; Gessa and Lecuyer, 1998). Despite a lack of soft-body evidence to bolster these claims, the distribution and spatial association of tentaculitids with other benthic organisms (e.g., brachiopods) suggest a benthic lifestyle (Hurst and Hewitt, 1977; Wittmer and Miller, in preparation).

Berkyová et al. (2007) considered dacryoconarids and homoctenids to be among the most important macrozooplankton in the Paleozoic. The shells have been intensely studied, revealing repair scars reminiscent of shell repair in planktonic gastropods, leading to the conclusion that they were preyed upon by other organisms in the Silurian and Devonian (Larsson, 1979; Berkyová et al., 2007). Berkyová et al. (2007) hypothesized that the decline of this group was related to the rise of the gastropods with planktotrophic larvae. It is safe to at least assume that dacryoconarids and homoctenids were planktonic based on the findings of Berkyová et al. (2007) and other dacryoconarid workers (Alberti, 1997a,b, 2000; Drapatz, 2010; Schindler, in review). A planktonic mode of life may have permitted an increase in geographic range for a given species, and with it, increased opportunities for speciation, thereby promoting their increased diversity in the Devonian (Lipps, 1970; Jablonski and Lutz, 1983; Jablonski et al., 1985; Jablonski, 1986). While homoctenids radiated in the Devonian, they were critically reduced by the Kellwasser Crisis (Bond, 2006). This crisis has been cited as a possible general cause of the demise of tentaculitoids, although it has also been argued that they were outcompeted by planktonic gastropods, which were radiating at that time (see Schindler, 1993; Bond, 2006; Schindler, in review). Recognized as a stepwise extinction, the Kellwasser crisis first affected benthic communities through widespread marine anoxia and euxinia (Schindler, 1993; Walliser, 1996; Bond, 2006). Subsequent anoxic pulses eventually reduced the extent of habitable pelagic and hemi-pelagic environments (Schindler, 1993).

6.3. *Tentaculitoid paleogeographic patterns*

Documented Ordovician occurrences of tentaculitoids are limited mainly to Laurentia (Cincinnati Arch) and Avalonia (United Kingdom), although they were occasionally quite abundant in these regions during the Late Ordovician (Wittmer and Miller, in preparation). The earliest documented global occurrence is in Australasia but the range-through curve for Australasia (Fig. 7A) is somewhat misleading because it

conveys the impression that tentaculitoids were present from their first occurrence in the Early Ordovician through the Late Ordovician. However, there is a gap observed in the record of tentaculitoids between the Arenigian and Caradocian (Fig. 9B). It is likely that their Middle Ordovician “absence”, reflects their scarcity, and it is probable that continued sampling of fossiliferous Middle Ordovician strata will ultimately yield tentaculitoids somewhere. What is clear, however, is that the number of documented occurrences of tentaculitoids increased dramatically in the Late Ordovician.

In general, well-sampled areas should tend to yield more data, as appears to be the case for Baltoscandia during the Silurian, which displayed the greatest Silurian genus richness of all paleocontinents. In fact, what is known of Silurian richness from Baltoscandia is derived from a single, in-depth study by Larsson (1979) on tentaculitoids from Gotland and the Swedish mainland. The majority of newly named genera came from this study and added appreciably to the overall global diversity trajectory, which otherwise would show relative stagnation at that time. It remains to be determined whether this pattern reflects a sampling/monographic bias, or whether Gotland and Swedish mainland were unusually rich in tentaculitoids at that time (Raup, 1977).

By contrast Devonian patterns are based on numerous studies from four different paleocontinents; the Mediterranean Province, Avalonia, Laurentia, and South China. It is important to note that all of these regions have been well-studied for the Ordovician and Silurian as well, yet do not yield substantial tentaculitoid Silurian richness, suggesting that tentaculitoids genuinely did not occur at great diversity in those regions prior to the Devonian. Devonian occurrences were compiled from many localities worldwide, and global tentaculitoid diversity increased in association with the increased contribution from multiple paleocontinents. That said, there may be some hints of monographic effects in the Devonian, in that two tentaculitoid workers, Lyashenko (1953–1967) and Alberti (1969–2000) exhaustively identified Devonian tentaculitoids for the Mediterranean Province from the Russian platform and North Africa respectively. Both workers played significant roles in naming Devonian tentaculitoid species and genera. Although the aforementioned monographic biases may have affected the tentaculitoid trajectory observed in some intervals, the extensive Devonian increase appears to be biologically meaningful not only because it was broad-based on several paleocontinents, but also because it is undergirded by a trajectory in the number of in-bin occurrences that is rather different than that observed for a composite based on all marine taxa (Fig. 9). If we take the composite occurrence trajectory as a reflection of the aggregate

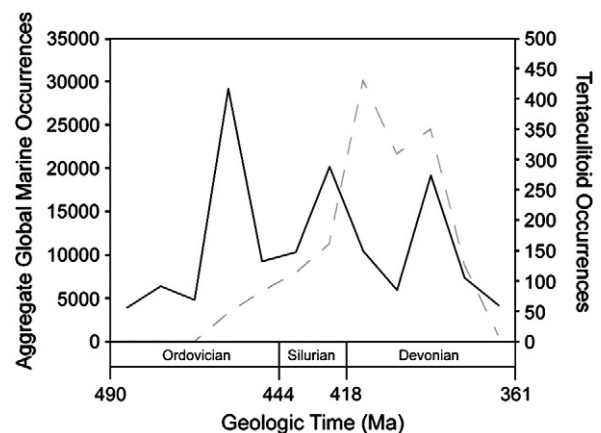


Fig. 9. Aggregate global marine invertebrate occurrences compiled from the Paleodb (September 2011) (black) versus tentaculitoid global occurrences (dashed) using Paleodb stratigraphic/temporal ten million year time bins. Note the uniqueness of the overall trajectory for tentaculitoid occurrences through the study interval, relative to that for all marine taxa in aggregate.

extent of paleontological sampling from interval to interval, it can be seen clearly that neither the global tentaculitoid occurrence trajectory nor the diversity trajectory (Fig. 4) mimic this pattern. The Devonian increase is far in excess of what one would expect if it were simply tracking changes in the aggregate availability of fossils.

7. Concluding remarks

There have been longstanding concerns that patterns of Phanerozoic diversity observed in space and through time might be biased by the selective focus of paleontologists on some strata and not on others (Sheehan, 1977; but see Raup, 1977). And, of course, concerns persist about the effect on observed patterns of fundamental biases in the record itself (e.g. Raup, 1976; Peters and Foote, 2001). Nevertheless, new analytical frameworks, such as Peters' macrostratigraphic approach (e.g., Peters, 2006), have pointed to ways of circumventing longstanding questions about whether apparent correlations between spatio-temporal changes in sedimentary rock volume and biodiversity pattern reflect a joint bias or, alternatively, a joint, biologically meaningful "common cause". Peters (2008) provided a particularly compelling demonstration of a strong similarity in the nature and volatility of the Paleozoic extinction record and that of coeval gap-bound carbonate packages for North America. In this case, the intermittent loss of carbonate platforms in association with sea-level declines appears to have directly promoted extinction through the loss of habitat, thereby providing support for the common-cause hypothesis.

With respect to worker bias, valuable perspective about diversity dynamics has come from assessing the effects of the accumulation of new data on decadal time scales for groups of interest. In the cases of tetrapods (Maxwell and Benton, 1990) and brachiopods (Foote and Miller, 2007, Fig. 1.22 therein), for example, there is compelling evidence that period-to-period trajectories have been stable for several decades, suggesting that the addition of new data is unlikely to change these data significantly in the future.

Seen in this light, the present study should be viewed as a beginning, rather than an end. As much as anything, it is the first-ever, synthetic statement about the current stage of tentaculitoid paleobiology and paleobiogeography and, as such, provides a framework and basis for future investigations as new data on tentaculitoids and the strata in which they are found continue to become available.

Based on the data available at present, it appears that following their origination in the Ordovician, the global diversity of tentaculitoids increased in the Silurian, and then more substantially in the Early Devonian, when a peak diversity of 30 genera is currently recognized. After the Middle Devonian, the group began to decline, particularly in the face of the Frasnian/Famennian extinction and the Kellwasser crisis. Dissecting tentaculitoid diversity further, Tentaculitida–Homoctenida (large-shelled) and Dacryoconarida (small-shelled) suggested slightly different times of peak diversity. Tentaculitids were the first group to arise in the early Ordovician and reached their highest level of diversity in the Early Devonian, whereas homoctenids radiated throughout the Devonian, becoming extinct by the early Famennian. Dacryoconarids may have arisen in the Late Ordovician, with most occurrences in the Silurian and increased diversity through the Early and Middle Devonian, persisting until the mid-Famennian.

The paleogeographic distribution of tentaculitoids was limited in the Ordovician to small regions, but as genus diversity increased during the Silurian and Devonian, the geographic range of tentaculitoids expanded globally. Contrasting patterns in the Silurian and Devonian reveal potential differences of sampling. The Silurian increase may reflect a monographic bias because of the addition of new genera and species contributed by a single extensive study in Baltoscandia (Larsson, 1979). By contrast, the Devonian increase was characterized by a broad based expansion of tentaculitoids to all paleocontinents investigated, although a majority of occurrences were from the Mediterranean Province, where monographic efforts of two workers may have also been important.

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