Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton

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Text: 30,435 words (including references and figure/table captions)
References: 336 (10,193 words)
Tables: 2
Figures: 12
Abbreviated title: Palaeozoic phytoplankton biogeography

Abstract: Early to mid Palaeozoic marine phytoplankton are represented by acritarchs and associated forms, which had a global distribution from the early Cambrian to the early Carboniferous (Mississippian). Palaeozoic phytoplankton assemblages show varying degrees of cosmopolitanism and endemism through time. A high degree of cosmopolitanism was evidently characteristic of the Cambrian and much of the Late Ordovician, Silurian and Devonian, but provincialism was more marked in the Early Ordovician and Hirnantian (latest Ordovician), the latter at a time of major palaeoenvironmental perturbations. Distribution patterns of Palaeozoic phytoplankton are attributed to a number of interacting factors, including
Palaeolatitude, palaeotemperature, oceanic circulation patterns, the disposition of continents, differentiation between oceanic and more cratonic (distal–proximal) assemblages, and sedimentary environments and facies. There are indications that biogeographical ranges of taxa shift over time. Moving our understanding of Palaeozoic phytoplankton biogeography forward requires targeted investigation of regions and time periods for which no or little data exist, quantitative analysis of data to investigate how similarity varies through time and how this might correlate with other datasets such as carbon isotope stratigraphy or sea level, and rigorous application of well-defined time slices to compare coeval assemblages, at least within the limits of resolution. (End of Abstract)

Early to mid Palaeozoic marine phytoplankton are represented in the fossil record largely by the acritarchs, an informal, probably polyphyletic group of organic-walled microfossils. Palaeozoic acritarchs are generally considered to have been cysts (Servais et al. 1997), analogous to the cysts of modern dinoflagellates but with probable affinities to green algae (Martin et al. 2008), although Kaźmierczak & Kremer (2009) and Moczydłowska (2010) have suggested that some were motile stages. A number of morphotypes previously assigned to the acritarchs are now provisionally assigned to green algal classes, including the Chlorophyceae, Prasinophyceae and Zyggnematophyceae (Colbath & Grenfell 1995; Grenfell 1995; Le Hérissè et al. 2009).

Acritarchs and related phytoplanktonic forms had a global distribution from the early Cambrian to the early Carboniferous (Mississippian), prior to the late Palaeozoic ‘Phytoplankton Blackout’ (Riegel 2008). Under favourable palaeoenvironmental conditions, they formed diverse and abundant assemblages. Changes in Palaeozoic phytoplankton diversity and abundance from proximal to distal positions along onshore–offshore gradients are well-documented (Jacobson 1979; Dorning 1981; Vecoli 2000, 2004; Li et al. 2004; Molyneux 2009). The most diverse and abundant assemblages are found in mid shelf depositional environments, with diversity and abundance declining towards nearshore settings on the one hand and outer shelf/basinal settings on the other.
In reviewing what was then known about the palaeobiogeography of mid Palaeozoic organic-walled phytoplankton, Colbath (1990a) highlighted some of the characteristics that made these organisms suitable for palaeobiogeographical studies. They can be abundant (up to $10^5$ specimens per gram under favourable circumstances), and are generally independent of lithofacies. Furthermore, as their motility is inferred to have been restricted, they were probably incapable of active dispersal against even relatively weak ocean currents so their distribution largely reflects physical processes. To explain why they were so little used in spite of these characteristics, Colbath pointed to a lack of taxonomic consensus, poorly documented biostratigraphical ranges, and sampling biases, both geographical and stratigraphical.

Progress has been made in the intervening period, but we are still not in a position to offer a definitive account of phytoplankton biogeography for the whole of the early to mid Palaeozoic. Nevertheless, we can now use the published record to frame and address a number of questions relating to biogeographical processes that might have influenced phytoplankton distribution, as well as suggesting ways to move the study of Palaeozoic phytoplankton biogeography forward. Such questions include, for example, whether there was always a degree of provincialism among phytoplankton throughout the Palaeozoic, or whether provincialism was more marked at some times and broke down at others. Also, if provincialism is recognized, is it related to palaeolatitude or to other controlling factors, such as the distribution of palaeocontinents, oceanic circulation patterns, or an oceanic versus continental (i.e. distal versus proximal) position?

In this contribution, we review published data and interpretations relating to Cambrian to Devonian phytoplankton biogeography and assess probable controls on phytoplankton distribution. This account is necessarily partial. Much of the published work dealing with Palaeozoic phytoplankton focuses on biostratigraphy and/or the taxonomic description of assemblages, and databases that would make the assessment of biogeographical ranges and distributions relatively straightforward do not yet exist. In addition, although many authors have commented on the palaeogeographical location and biogeographical affinities of their material, few papers have made early Palaeozoic phytoplankton biogeography their theme.

Maps used in this review for the Cambrian to Silurian (542 – 416 Ma) periods were generated using BUGPLATES software (Torsvik & Cocks 2013). Those used for the
Devonian Period are based on other sources, as indicated in the relevant figure captions.

Cambrian phytoplankton

Early Cambrian

Definitive evidence for acritarch provincialism in the early Cambrian is lacking. Acritarch assemblages from Baltica, described in a series of papers by Moczydłowska (1991, 1998, and references therein), comprise some of the best documented phytoplankton assemblages of that age and have been used to define a succession of lower Cambrian acritarch biozones. In upwards succession, the *Asteridium tornatum–Comasphaeridium velvetum*, *Skiagia ornata–Fimbriaglomerella membranacea*, *Heliosphaeridium dissimilare–Skiagia ciliosa* and *Volkovia dentifera–Liepaina plana* biozones span the Terreneuvian Series and Series 2 of the revised standard for the Cambrian System (Rushton & Molyneux 2011). Although our knowledge of early Cambrian acritarch assemblages is restricted to relatively few areas, the biozones have been identified widely within those areas, suggesting that biozonally diagnostic forms have similarly wide distributions.

The *Asteridium tornatum–Comasphaeridium velvetum* Biozone, which spans the Terreneuvian Series in Baltica (Rushton & Molyneux 2011), has been recognized in Cambrian successions of New Brunswick (Palacios *et al*. 2011) as well as Baltica. At the time, New Brunswick was situated on the margin of Gondwana at high southern palaeolatitudes (Torsvik & Cocks 2013, figs 5–7). The New Brunswick assemblages are of lower diversity than those from Baltica, but all the species and genera recorded by Palacios *et al*. (2011) also occur in Baltica. As yet, there is no evidence for biogeographical differentiation of earliest Cambrian phytoplankton between mid palaeolatitude Baltica and the high palaeolatitude Gondwanan margin.

Acritarch assemblages of Terreneuvian age from other palaeogeographical areas are not well known. Acritarchs recorded from basal Cambrian successions of South China and Tarim (northwest China) constitute the *Asteridium-Heliosphaeridium-Comasphaeridium* assemblage of Yao *et al*. 2005 (see also Dong *et al*. 2009), an association of small, morphologically simple, *Micrhystridium*-like acanthomorph acritarchs. Assemblages from China, New Brunswick and Baltica all contain the
genera *Asteridium* and *Comasphaeridium*, although only one species, *Asteridium tornatum*, has a biogeographical range that encompasses all three regions. In detail, however, there are also differences between the Chinese assemblages and those from New Brunswick and Baltica. *Heliosphaeridium*, for example, is not known from this level in New Brunswick or Baltica, where its First Appearance Datum (FAD) is higher in the stratigraphy. In contrast, *Granomarginata* was not recorded from South China or Tarim, although it is present at this level in both New Brunswick and Poland (East European Platform, Baltica). Hence, potentially subtle biogeographical signals emerge, but whether these signals are real or whether they are artefacts of sampling deficiencies, of variations in the facies sampled in each area, or of differences in taxonomic treatment is unclear.

Above the Terreneuvian Series, lower Cambrian acritarch assemblages from Gondwana (Stansbury and Arrowie basins of South Australia, South China, and the Armorican and Avalonian margins), Baltica (Norway, Sweden, Poland), Laurentia (northwest Scotland, Svalbard, Greenland) and Siberia (Anabar shelf) are reported to be taxonomically comparable (Moczydłowska 1998, fig. 19; Moczydłowska & Zang 2006). In her review of Cambrian acritarch palaeobiogeography, Moczydłowska (1998, p. 37) noted that lower Cambrian acritarch associations from South China and Australia, located at that time in northern Gondwana at equatorial palaeolatitudes, included cosmopolitan taxa that also occurred in successions deposited at higher palaeolatitudes on the Armorican and Avalonian margins of Gondwana (Torsvik & Cocks 2013, fig. 7) as well as on other palaeocontinents, including Siberia, Baltica and the eastern extremity of Laurentia (northwest Scotland, Svalbard, Greenland). She postulated that all of these areas might have been connected along their continental shelves, thus aiding phytoplankton dispersal, and pointed out that the most uniform global distribution of phytoplankton was during the later part of Stage 3 (*Holmia kjerulfi* Biozone of Scandinavia and equivalents), apparently coinciding with a maximum flooding event. This level also coincides with the widespread distribution of the acritarch genus *Skiagia*.

The FAD of *Skiagia*, at about the base of Series 2 and more or less coinciding with the FAD of trilobites (Moczydłowska & Zang 2006), is a significant biostratigraphical acritarch event in the lower Cambrian. The genus provides index species for two of the acritarch zones first determined in Baltica, namely the *Skiagia ornata*—
Fimbriaglomerella membranacea and Heliosphaeridium dissimilare–Skiagia ciliosa biozones, which together span Stage 3 and the lower part of Stage 4, both in Series 2 (Rushton & Molyneux 2011). The palaeogeographical reconstruction of Torsvik & Cocks (2013) for the early Cambrian places those areas yielding Skiagia at low to high palaeolatitudes in the southern hemisphere (Fig. 1), with their distribution outlining two trends, one along the margin of Gondwana and the second diverging to encircle the early Cambrian ocean bordered by Baltica and Laurentia.

Moczydłowska (1998, p. 37) and Moczydłowska & Zang (2006) drew attention to the similarity between lower Cambrian acritarch assemblages from South Australia and other Gondwanan and Baltic assemblages. At a slightly higher stratigraphical level, however, similarity between zonal assemblages from Baltica (Sweden, East European Platform) and an acritarch assemblage described by Zang & Walter (1992) from the Tempe Formation in the Amadeus Basin of central Australia is less evident. Six species from the Tempe Formation, Asteridium \([\text{Micrhystridium}]\) lanatum, Asteridium \([\text{Micrhystridium}]\) tornatum, Globosphaeridium \([\text{Baltisphaeridium}]\) cerinum, Dictyotidium birvetense, Lophosphaeridium tentativum and Skiagia ciliosa, have widespread distributions and have been recorded from the margins of more than one palaeocontinent. These six species, however, represent less than 20% of the assemblage described by Zang & Walter (1992) from the Tempe Formation. Zang & Walter (1992) referred to macrofossil evidence that indicated an “early middle Cambrian” age (Series 3, Stage 5?) for the Tempe Formation. Seriation of lower middle Cambrian data from Sweden, the East European Platform and the Amadeus Basin (Fig. 2) shows that a number of well-known middle Cambrian acritarch genera such as Adara, Cristallinium, Eliasum, Retisphaeridium and Timofeevia occur in Baltica but not in the Amadeus Basin. Conversely a number of acritarch genera are restricted to the latter.

**Mid and late Cambrian**

The palaeobiogeography of acritarchs for the mid and late Cambrian (approximately Series 3 and the Furongian Series in the revised global Cambrian chronostratigraphy; Rushton 2011) was touched upon by Ghavidel-syooki & Vecoli (2008). These authors compared middle and upper Cambrian acritarch assemblages from southern
Iran with coeval assemblages from Baltica (East European Platform: Volkova 1990; northern Norway: Welsch 1986), the Avalonian margin of Gondwana (eastern Newfoundland: Martin & Dean 1981, 1984, 1988; Belgium and northern France: Vanguestaine 1973, 1978a; Ribecai & Vanguestaine 1993; England and Wales: Downie 1984; Upper Silesia: Moczydlowska 1998), Gondwana (North Africa: Albani et al. 1991; Vecoli 1996) and Laurentia (Missouri, Arkansas: Wood & Stephenson 1989). Most of these regions were at mid to high southern palaeolatitudes (Fig. 3), the exception being Laurentia which straddled the palaeoequator. Cluster analysis (Fig. 4) shows that a number of genera have widespread distributions, and that the important late Cambrian genera *Timofeevia* and *Vulcanisphaera* are known from all, or almost all, regions, including Laurentia. Laurentia and Kolguev Island (Baltica) are least similar to most other regions (Table 1), lacking significant upper Cambrian genera such as *Cristallinium*, *Cymatiogalea* and *Stelliferidium*, but including genera not reported from other late Cambrian assemblages, for example *Fimbriaglомерella* in the North American assemblage. The Laurentian assemblage also contains a number of species recorded in open nomenclature. Ghavidel-syooki & Vecoli (2008) acknowledged that the difference in composition between the Laurentian assemblage and those from the Gondwanan margin, Avalonia and Baltica could be attributed to sample bias, but noted also that the unusual taxonomic composition of the Laurentian assemblage might be due to palaeogeographical factors, namely the wide palaeolatitudinal and palaeogeographical separation between palaeocontinents.

An upper Cambrian assemblage from the Eastern Cordillera of northwest Argentina described by Rubinstein *et al.* (2003) is also dissimilar (Fig. 4, Table 1) to the upper Cambrian microfloras included by Ghavidel-syooki & Vecoli (2008) in their analysis. The assemblage from the Eastern Cordillera lacks independent age control, but is from a succession of late Cambrian to earliest Ordovician age, and is dated as late Cambrian. It includes genera such as *Acanthodiacrodium*, *Saharidia* and *Vulcanisphaera*, which are fairly widespread at this level, but also present are *Caldariola*, *Celtiberium*, *Granomarginata* and *Heliosphaeridium*, which are not so well known from upper Cambrian assemblages.

At present, it is difficult to draw any general conclusions regarding Cambrian phytoplankton biogeography. The distribution of the lower Cambrian *Skiagia*-bearing assemblages and that of the upper Cambrian assemblages both suggest a degree of
cosmopolitanism. The distinction between the lower middle Cambrian assemblage
from the Amadeus Basin and putative correlative assemblages from Sweden and the
East European Platform does point to the possibility that there was more
biogeographical differentiation in the early mid Cambrian, however, perhaps in this
case between intracratonic settings, as in the Amadeus Basin, and more oceanic,
continental margin settings. The distinction noted by Ghavidel-syooki & Vecoli
(2008) between Laurentia on the one hand and Gondwana, Avalonia and Baltica on
the other might also signify biogeographical differentiation in the late Cambrian, as
too does the distinctive character of the late Cambrian assemblage described by
Rubinstein et al. (2003) from northwest Argentina.

Ordovician

Early to Mid Ordovician

The Early to Mid Ordovician has been a focus for biogeographical studies of early
Palaeozoic phytoplankton. Early attempts to model Ordovician acritarch
biogeography by Cramer & Diez (1974a, b) distinguished an African Palynological
Unit, otherwise termed the Coryphidium bohemicum Province (Cramer & Diez
1974b), and an American Palynological Unit, described as having a “profoundly
different” acritarch assemblage from that of the Coryphidium bohemicum Province
(Cramer & Diez 1974b, p.142). Much of the ensuing discussion, however, has taken
Vavrdová’s (1974) assessment of the biogeographical differentiation of Early
Ordovician acritarch provinces in Europe as its starting point. The development of
ideas on Early and Mid Ordovician acritarch biogeography in the latter part of the 20th
century was reviewed and synthesized by Servais et al. (2003).

Vavrdová’s (1974) analysis of biogeographical patterns among European Ordovician
acritarchs recognized two provinces, the Mediterranean Province encompassing
Belgium, France, Spain, North Africa, southern Germany, Bohemia and Bulgaria, and
the Baltic (or Boreal) Province incorporating northern Russia, Poland, Sweden and
north Germany. Among the key criteria used to characterize these provinces,
Vavrdová (1974) pointed to the prevalence of acanthomorph acritarchs in the Baltic
Province, represented by species of Baltisphaeridium, Peteinosphaeridium,
Goniosphaeridium and Filisphaeridium, and the occurrence of diacromorph acritarchs
such as species of *Arbusculidium* and *Acanthodiacrodium* in the Mediterranean Province. This distinction is not always clear cut, however, and Vavrdová herself pointed out that the Baltic Tremadocian species *Dasydiacrodium monstrorsum* resembled the coeval Mediterranean species *Arbusculidium frondiferum* and *A. destombesi*. Conversely, she reported the occurrence of *Baltisphaeridium klabavense* and *Goniosphaeridium polygonale* in Arenig rocks of the Mediterranean Province.

She also highlighted, however, the occurrence of species of *Aureotesta*, *Coryphidium*, *Frankea* and *Striatotheca* in the Arenig–Llanvirn Mediterranean Province. None of these genera is known from the Lower Ordovician of the Baltic Province. The Mediterranean Province and the Baltic Province have been the topics of much subsequent work, the former now subsumed within a broader Perigondwana Province.

*From the Mediterranean Province to the Perigondwana Province*

Realization that Vavrdová’s (1974) Mediterranean Province extended beyond Europe came when Martin (1982a) commented on Tremadocian and Arenig acritarch assemblages from southern Europe and eastern Newfoundland. Based on her analysis of palynological data from the Tremadoc and Arenig series, Martin (1982a, p. 38) argued that the Mediterranean Province should include eastern Newfoundland, England and Wales, Spain, France, Belgium, Bohemia, North Africa and northwest Argentina. Martin (1982a) further noted that eastern Newfoundland and the Mediterranean area were located on the periphery of Gondwana at the beginning of the Ordovician, based on palaeogeographical reconstructions available at the time, and may have been the first to recognize the Mediterranean Province as a Perigondwanan province, at least implicitly if not explicitly (see Tongiorgi *et al.* 1995).

Li’s (1989) contribution to the debate, based on work on the Upper Yangtze region of South China, was twofold. First, he augmented Martin’s (1982a) observations by demonstrating that Vavrdová’s Mediterranean Province extended from eastern Newfoundland through southern Europe and the Middle East to South China. Second, he argued that affinity of acritarch assemblages to Vavrdová’s Mediterranean Province should be determined by the occurrence of the acritarch genera *Arbusculidium*, *Coryphidium* and *Striatotheca* rather than the prevalence of
diacromorph acritarchs, on the grounds that none of these genera had been reported from Baltic Province localities. In contrast, he noted that supposedly characteristic Baltic taxa such as species of *Baltisphaeridium*, *Goniosphaeridium* and *Peteinosphaeridium* had been reported from Mediterranean Province localities.

At about the same time, Albani (1989) noted that Arenig acritarch assemblages from Sardinia showed clear affinities with Vavrdová’s Mediterranean Province, but commented that the term ‘Perigondwanian Palaeoprovince’ was more appropriate, referring to Martin’s (1982a, in Martin & Dean 1988) earlier observations. Like Li (1989), Albani (1989) considered the genera *Arbusculidium*, *Coryphidium* and *Striatotheca* to be characteristic of the province, but also added the diacromorph genera *Acanthodiacrodium* and *Dasydiacrodium*.

The term ‘Perigondwanian Palaeoprovince’ and variants have been used by most subsequent workers, although Vavrdová (1997) introduced the ‘*Coryphidium bohemicum* acritarch bioprovince’ to cover essentially the same area during the same time period. Furthermore, use of the term ‘Mediterranean’ has persisted in some of the literature. Playford *et al.* (1995), for example, used ‘Mediterranean’ to delineate a subprovince of the Perigondwana Province, comprising the area originally specified by Vavrdová (1974) with the additions of England and Wales, the Arabian peninsula, eastern Newfoundland, southern Turkey and Karakorum (Pakistan). South America and South China were identified as separate Perigondwanan subprovinces. Also, from 1998 onwards, Tongiorgi and his co-workers (Tongiorgi *et al.* 1998, 2003a, b; Tongiorgi & Di Milia 1999) reverted to use of the term ‘Mediterranean Province’. In this paper, we use the term ‘Perigondwana Province’ to refer to the biogeographical unit defined by the distribution of the genera indicated above, principally *Arbusculidium*, *Coryphidium* and *Striatotheca*. As depicted in Figure 5, the Perigondwana Province extended along the margin of Gondwana from North Africa through southern Europe and the Middle East to Pakistan (Karakorum Terrane), and included Avalonia, South China and northwest Argentina (see also Playford *et al.* 1995; Tongiorgi *et al.* 1995; Vecoli 1999, fig. 9).
In contrast to the Perigondwana Province, recognition of Vavrdová’s (1974) Baltic Province has remained problematical, mainly because, as Li (1989) pointed out, many of the genera and species used in its original definition have much greater biogeographical ranges. Tongiorgi & Di Milia (1999), for example, noted that acanthomorph acritarch genera (*Baltisphaeridium*, *Liliospheridium*, *Peteinosphaeridium*, *Polygonium*) constituted inadequate criteria to characterize assemblages from the Baltic Province, given that acanthomorph acritarchs are also abundant in coeval assemblages from the Perigondwana Province. Similarly, they pointed out that the absence of diacromorph acritarchs as used by Vavrdova (1974) to define the province could no longer be regarded as diagnostic, given the presence of these forms in assemblages from Baltica (East European Platform, Baltoscandia).

Consequently, the Baltic Province came to be associated with the absence of taxa, and principally the absence of those genera and species regarded as characteristic of upper Tremadocian to lower Llanvirn (Darriwilian) Perigondwanan assemblages (Brocke et al. 1995), namely *Arbusculidium filamentosum* and species of *Arkonia, Striatotheca, Aureotesta, Coryphidium, Vavrdovella, Dicrodiacrodium* and *Frankea*. Servais & Fatka (1997), for example, used these genera and species to delineate the Trans-European Suture Zone, separating Perigondwanan terranes, including Avalonia and Armorica, from Baltica.

In separate developments and in contrast to the idea that the Baltic Province could only be recognized on negative evidence, Playford *et al.* (1995) and Tongiorgi & Di Milia (1999) offered positive criteria to identify the province based mainly on the distribution of species of *Peteinosphaeridium* and related genera. Thus, Playford *et al.* (1995) regarded *Peteinosphaeridium bergstroemii, P. dissimile, P. micranthum* and *P. trifurcatum* (s.s.) as being probably restricted to the Baltic Province, and Tongiorgi & Di Milia (1999) proposed that the Baltic Province could be defined by *Peteinosphaeridium bergstroemii, P. velatum, P. hymenoferum, Liliosphaeridium* spp., *Pachysphaeridium* spp. and ‘*Peteinosphaeridium macropylum* s.l.’. Tongiorgi & Di Milia (1999) further proposed that although the Baltic Province could be recognized primarily in Baltica, it also extended into South China (*Fig. 5*).

The criteria advanced by Playford *et al.* (1995) and Tongiorgi & Di Milia (1999) have not been universally accepted, and Li & Servais (2002) presented a critique of the use of species of *Peteinosphaeridium* as biogeographical markers. The latter authors
pointed particularly to the large amount of morphological variability often found within acritarch species (morphospecies) and to the influence of environmental conditions on the development of morphology among acritarchs in general. They considered that the variability observed between morphospecies, such as that between species of *Peteinosphaeridium*, could just as easily reflect local environmental conditions as palaeogeographical differences. They argued that it was difficult to justify the definition of a Baltic acritarch province based only on selected species of a single genus. Li & Servais (2002) concluded that detailed investigations of the variability of *Peteinosphaeridium* and related genera were needed to understand fully the palaeoecological and palaeogeographical distribution of that acritarch plexus.

**South China: Perigondwana, Baltica or mixed?**

The ‘Mediterranean’ (i.e. Perigondwanan) affinity of acritarch assemblages from the Lower to Middle Ordovician of South China had been recognized by Li (1987, 1989) and was reaffirmed by later workers (Playford *et al.* 1995; Tongiorgi *et al.* 1995, 1998, 2003; Tongiorgi & Di Milia 1999; Servais *et al.* 2003). But, although Tongiorgi *et al.* (1995) supported Li’s (1989) conclusion that South China belonged to the Perigondwana Province, they also indicated that the situation in South China was more complicated than attribution to that province might imply. Working on acritarchs from the Dawan Formation of Arenig age from the Yangtze Platform of South China, Tongiorgi *et al.* (1995) noted that the assemblage had a predominantly ‘Mediterranean’ character but also exhibited Australian and Baltic affinities. The largest component of the assemblage was described at the time as an endemic South Chinese component (42.2%), but this largely comprises endemic species assigned to genera with much wider distributions, including *Baltisphaeridium, Barakella, Cymatiogalea, Multiplicisphaeridium, Ordovicidium, Peteinosphaeridium, Pirea, Striatotheca, Tongzia* and *Veryhachium*. Species with known Perigondwanan affinities were identified as the second largest component of the assemblage (35.6%). These include forms regarded as diagnostic of the Perigondwana Province such as *Arbusculidium filamentosum, Coryphidium bohemicum, Striatotheca principalis parva* and *Striatotheca rarirrugulata*, and other forms such as *Cymatiogalea granulata* and *Petaloferidium florigerum*. The Australian component (13.3%) comprised species shared with assemblages from Australian basins (*Ammonidium*...
[Sacculidium] aduncum, Baltisphaeridium? coolibahense, Gorgonisphaeridium pusillum, G. miculum, Loeblichia heterorhabda, Polyancystrodorus radiosus and P. taleatus). A smaller component (8.9%) comprised species with Baltic affinities such as Ampullula suetica.

A number of these taxa have biogeographical ranges that are now known to extend beyond the limits as understood by Tongiorgi et al. (1995). Ampullula [Stelomorpha] erchunensis, for example, was listed among the taxa considered to be endemic to South China (Tongiorgi et al. 1995, table 1), but has since been reported from Perigondwanan and Baltic assemblages (Argentina: Achab et al. 2006; Pakistan: Quintavalle et al. 2000; Poland and Russia: Raevskaya et al. 2004; Norway: Tongiorgi et al. 2003b; see also Yan et al. 2010, who revised the genus Ampullula and its constituent species, including their palaeobiogeographical distributions). As a consequence, the detailed conclusions of Tongiorgi et al. (1995) might no longer be valid. Nevertheless, the broad conclusion that acritarch assemblages from South China include components that have affinities with biogeographical areas other than the Perigondwanan Province remains well founded (Fig. 5).

Tongiorgi et al.’s (1995) initial investigation was based on only one sample, but the biogeographical affinities of phytoplankton from South China were subsequently investigated further using more extensive datasets. Hence, Tongiorgi et al. (1998) documented assemblages with different affinities from the Arenig of the Yangtze Platform. Taxa that are characteristic of the Perigondwanan assemblage dominate microfloras from the middle Arenig Azygograptus suecicus Biozone (lower part of the Dawan Formation), accompanied by rare Baltic elements and a number of cosmopolitan taxa (Tongiorgi et al. 1998, p. 186). In contrast, assemblages from the upper Arenig Undulograptus austrodentatus Biozone contain taxa such as Liliosphaeridium kaljoi and other Baltic species, with the Baltic component entirely substituting the Perigondwanan taxa in the upper part of the section, near the top of the Arenig (Tongiorgi et al. 1998, pp. 186, 187). Consequently, Tongiorgi et al. (1998) concluded that inclusion of South China in the Perigondwanan Province could only be confirmed for the earlier Arenig.

The change in biogeographical affinity that Tongiorgi et al. (1998) observed up-section, however, is not so apparent elsewhere in South China. Brocke et al. (2000), for example, showed a greater Perigondwanan component in upper Arenig
assemblages from south-eastern Sichuan and northern Guizhou than was reported for
the sections studied by Tongiorgi et al. (1998). Subsequently, Tongiorgi et al.
(2003a) revisited the apparent change in biogeographical affinity from
Perigondwanan to Baltic among acritarch assemblages of the Yangtze Platform, and
proposed a model to explain why such changes might not be seen elsewhere (see
Factors controlling Early to Mid Ordovician acritarch provincialism).

Other provinces

Much of the discussion surrounding Early to Mid Ordovician acritarch biogeography
has focused on Perigondwana, Baltica and South China. Nevertheless, Playford et al.
(1995) recognized discrete North American and Australian provinces in addition to
Perigondwana and Baltica, making a total of seven acritarch biogeographical units
including their three Perigondwanan subprovinces (South America, Mediterranean,
South China). They also suggested that North China might be segregated from these
provinces, although it was virtually unexplored palynologically. They pointed out
that distinguishing a warm, subequatorial North China province from a more
temperate South China would be in accordance with other faunal, tectonic and
palaeomagnetic datasets (but note that the reconstruction from BUGPLATES used
here in Figure 5 also places South China at equatorial palaeolatitudes). In common
with their Perigondwana and Baltica provinces, Playford et al. (1995) considered
species of Peteinosphaeridium and related genera to be characteristic elements of the
microfloras from each province. Peteinosphaeridium? furcatum, for example,
tentatively referred to that genus and reported to be from the Arenig of Western
Australia, was identified as being characteristic of the Australian Province, whereas
Peteinosphaeridium? indianense and P.? spiralicum were considered to be
characteristic of the North American Province. Both of the latter species, however,
are from the Upper Ordovician, as Playford et al. (1995) acknowledged.

Volkova (1997) suggested that a separate warm-water (subequatorial) province could
be distinguished in the late Tremadocian (c. 480 Ma) based on co-occurrences of the
genera Aryballomorpha, Athabascaella and Lua and the absence of diacromorph
acritarchs. Upper Tremadocian assemblages with these characteristics were
documented from Laurentia (Alberta) by Martin (1984, 1992) and from North China
by Martin & Yin (1988), both areas situated at low subequatorial palaeolatitudes during the late Tremadocian (Torsvik & Cocks 2013, fig. 11). A further Laurentian occurrence, from Texas, was reported by Barker & Miller (1989) but not documented in full. *Aryballomorpha* and *Athabascaella* have also been reported from the upper Tremadocian of Baltica, however (Volkova 1995), which was situated at mid southern palaeolatitudes in the Early Ordovician (Torsvik & Cocks 2013, figs 10–12), and *Athabascaella* has been recorded from Perigondwanan successions that were at high southern palaeolatitudes, including the lower Tremadocian of Tunisia (Vecoli 2004) and the uppermost Tremadocian of Belgium (Breuer & Vanguestaine 2004). Other Perigondwanan records of *Athabascaella* are from the Arenig of Australia (Quintavalle & Playford 2006a, b), Oman (Rickards et al. 2010), South China (Li 1990; Yan et al. 2011), and possibly Argentina (Achab et al. 2006) and Bohemia (Vavrdova 1990a), demonstrating that the genus had a wide biogeographical range across palaeolatitude.

**Factors controlling Early to Mid Ordovician acritarch provincialism**

Cramer & Díez’s (1974a, b) cold African Palynological Unit and warm American Palynological Unit were depicted as being parallel to palaeolatitude and following climatic belts, but the palaeogeographical reconstructions on which they were based have since been superseded. Acritarch biogeography is no longer regarded as having a simple relationship with palaeolatitude or climate. More recent models, of greater complexity, invoke a range of interacting factors as controls on biogeographical distributions. Nevertheless, the biogeographical ranges of some acritarch genera and species are still regarded as being constrained by palaeolatitude. Latitude figured as a factor in the tentative model put forward by Li & Servais (2002) to explain the distribution of selected Lower to Middle Ordovician acritarch genera. Furthermore, Colbath’s (1990a) conclusion that the genus *Frankea* was restricted to relatively high palaeolatitudes remains largely true for the palaeogeographical reconstructions of Torsvik & Cocks (2013), as shown in Figure 5 (see also Servais 1993). The most northerly occurrences of *Frankea* in Arenig–Llanvirn (Floian–Darriwilian) Perigondwanan successions, including Avalonia, are from mid southern
palaeolatitudes. Its most northerly record on the margin of Gondwana is from Saudi Arabia, where it occurs in the Saq Formation and the Hanadir Member of the Qasim Formation (Le Hérissé et al. 2007). It occurs at similar mid southern palaeolatitudes in Avalonian successions of eastern Newfoundland (Dean & Martin 1978), Germany (Burmann 1968, 1970; Maletz & Servais 1993; Servais 1994), Belgium (Servais & Maletz 1992) and England and Wales (Downie 1984; Molyneux 1990, 2009). Even so, there are no known records of the genus from Baltica, which is placed at comparable mid southern palaeolatitudes as Avalonia and Saudi Arabia (Fig. 5).

Clearly, palaeolatitude cannot have been the only factor affecting the distribution of this genus.

Playford et al. (1995) postulated that acritarch distributions might be controlled by a palaeoenvironmental gradient across continental margins, possibly related to water temperature. They (p. 46) suggested that Perigondwanan assemblages might represent a widespread cold water flora that characterized ocean-facing settings, which they termed the Perigondwanan Oceanic Realm, and that different assemblages were present in warm shelf seas such as those of Baltica. Nevertheless, they also noted that successions in South China, which were deposited on a craton and had a similar facies evolution to that of the Baltic area, contained many Perigondwanan taxa that were missing from Baltica. Hence, they concluded that although water temperature might play a role in controlling acritarch biogeography (p. 44), ocean currents probably also played a role in the dispersal of acritarch taxa and might better explain differences between South China and Baltica than the palaeoenvironmental gradient model.

Tongiorgi et al. (1995) further considered the factors that were likely to affect acritarch distributions. They noted that a simple model such as that proposed by Cramer (1971) and Cramer & Diez (1974b), with biogeographical distributions controlled essentially by palaeoisotherms parallel to palaeolatitude, did not sit easily with the complex pattern of biogeographical affinities exhibited by the Yangtze acritarchs (see above). They proposed a modification of the model, in which the distribution of Arenig acritarch communities was indeed delimited by palaeoisotherms, but that the distribution of palaeoisotherms was in turn influenced by oceanic circulation. They postulated that: (1) a cold Perigondwanan current flowed northwards from the subpolar margin of Gondwana to South China, carrying typical
Perigondwanan taxa from high to low palaeolatitudes; (2) that the cold current gave
rise to a warm current northwest of South China which then returned southwards
through Baltica, with some shared taxa such as *Ampullula* originating in South China
and being carried to Baltica; and (3) that differences between Arenig acritarch
assemblages of South China and Australia could be explained by the former being
influenced by the cold Perigondwanan current whereas coeval deposits of the latter
were deposited in an inter-tropical epicontinental sea.

In a further development, Tongiorgi *et al.* (1998) presented two hypotheses to explain
the change from Perigondwanan to Baltic assemblages that they recorded on the
Yangtze Platform (see above). One hypothesis suggested that the change in
assemblages from Perigondwanan to Baltic affinity in the late Arenig was related to a
change in the pattern of ocean currents that might in turn be related to changes in
palaeogeography. They interpreted the occasional occurrence of Baltic taxa in the
middle of the section as indicating periodic infringement of warm water onto the
Yangtze Platform. Their second hypothesis, following Playford *et al.* (1995),
postulated that the Perigondwanan assemblage was a widespread cold water flora that
characterized ocean facing settings, whereas relatively warm-water shelf
environments such as the Baltic Province supported mostly endemic assemblages.
Excluding major tectonic movements, the successive occurrence of ocean-facing and
shelf assemblages would imply a change in sea level.

This theme was developed further by Tongiorgi *et al.* (2003a), who re-investigated
the apparent changes in biogeographical affinities of acritarchs in their data in order to
explain why such changes were not apparent in other studies of South Chinese
acritarchs (e.g. Brocke *et al.* 2000). Tongiorgi *et al.* (2003a) again argued that more
distal, oceanic settings around South China were characterized by Perigondwanan
microfloras, whereas more proximal settings were associated with assemblages that
exhibited Baltic characteristics. Consequently, a change from a distal to a proximal
environmental setting, either vertically within a section or laterally between sections,
might be accompanied by a change in assemblage-type from Perigondwanan to Baltic.
Hence, the upward change from Perigondwanan to Baltic assemblages recorded by
Tongiorgi *et al.* (1998) was correlated with a protracted regression from the mid to
late Arenig (late Floian to early Darriwilian) and the consequent development of more
proximal conditions. The evident lack of an equivalent change in the south-eastern
Sichuan and northern Guizhou sections (Brocke et al. 2000) was attributed to their more distal locations so that more proximal shelf conditions never developed.

Tongiorgi et al.’s (2003a) explanation for the upward change from Perigondwanan to Baltic microfloras on the Yangtze Platform introduces the problem of discriminating between biogeographical and palaeoecological controls. Changes in the composition of Palaeozoic phytoplankton assemblages along proximal–distal transects are well documented (Jacobson 1979; Dorning 1981; Vecoli 2000, 2004; Li et al. 2004; Molyneux 2009), so the change from Perigondwanan to Baltic microfloras recorded by Tongiorgi et al. (2003a) might be influenced by ecological factors as much as biogeography, or perhaps by a combination of ecological and biogeographical factors. Reflecting on this to some extent, Tongiorgi et al. (2003a) stated that they were inclined to abandon the terms ‘Mediterranean Province’ and ‘Baltic Province’, at least for the Arenig, in favour of ‘Mediterranean palynoflora’ and ‘Baltic palynoflora’.

The latter terms were considered to be more in keeping with a role for environmental and ecological factors as controls on assemblage composition. The Mediterranean palynoflora corresponded to the “…phytoplankton of the early Arenig transgressive oceans (‘Perigondwana Oceanic Realm’ of Playford et al. 1995...” (Tongiorgi et al. 2003a, p. 44). The Baltic palynoflora, on the other hand, comprises assemblages that developed during the late Arenig on mid to low palaeolatitude shelves, especially the more proximal parts, in response to repeated regressive episodes (Tongiorgi et al. 2003a, p. 45).

In the context of this discussion, it is notable that coeval assemblages from Argentina also contain genera and species with Baltic, South Chinese, Australian and more characteristic Perigondwanan affinities (Fig. 5). A microflora of probable Darriwilian age from the Capillas Formation of the Sierras Subandinas (Capillas River Section, Sierra de Zapla), northwest Argentina, for example, contains *Ampullula?* sp. and *Liliosphaeridium intermedium*, representing genera that are both more typical of Baltica and South China than Perigondwana. Also present, however, are species of the characteristic Perigondwanan genera *Arbusculidium*, *Arkonia* and *Striatotheca* (Rubinstein et al. 2011). A further example is provided by the record of *Ammonidium* sp. cf. *A. [Sacculidium] aduncum* in a Dapingian assemblage from the Famatina region of northwest Argentina (Achab et al. 2006), where it is associated with *Striatotheca* and other more typically Perigondwanan taxa such as *Vogtlandia*. 
Sacculidium aduncum has been reported from Sweden (Ribecai et al. 2002) and from the Canning Basin of Australia (Playford & Martin 1984; Quintavalle & Playford 2006a, b). Ampullula [Stelomorpha] erchunensis, which has been reported from Norway (Tongiorgi et al. 2003b), Poland and Baltic Russia (Raevskaya et al. 2004), South China (Yin 1994; Brocke et al. 1999, 2000; Tongiorgi et al. 1995, 2003a; Yan et al. 2011) and Pakistan (Quintavalle et al. 2000), is also present in the Famatina region, where it is associated with Arbuculidium filamentosum and Striatotheca. These records indicate that such associations of Baltic and Perigondwanan forms are not restricted to South China, but might be more widespread around the northern promontory of Gondwana, around northern and eastern Australia (Fig. 5). Palynological investigation of successions in south-eastern Australia, Tasmania and New Zealand might provide data to test this supposition.

Duration of Early to Mid Ordovician Provinces

Based on the stratigraphical ranges of diagnostic genera, Tongiorgi & Di Milia (1999) argued that the Mediterranean (i.e. Perigondwana) Province could only be recognized from the latest Tremadocian to a level in the Llanvirn. Furthermore, the Baltic Province as they defined it, namely by the presence of Peteinosphaeridium bergstroemii, P. velatum, P. hymenoferum, Liliosphaeridium spp., Pachysphaeridium spp. and ‘Peteinosphaeridium macropylum s.l.’, could only be recognized from the latest Arenig to early Llanvirn and therefore had a shorter duration. The same authors concluded that both Perigondwana and Baltica were characterized by a Mediterranean-type marine microflora during the Billingen (late Floian, mid Arenig) and that elements of the Baltic Province began to appear in South China no later than earliest Volkhov (early Dapingian, mid Arenig). They noted, however, that Baltic Province assemblages only became prominent from the late Dapingian–early Darriwilian (late Arenig; Baltoniodus norrlandicus Conodont Biozone) onwards, seemingly concurrently in Baltoscandia and South China. Hence, biogeographical units of the Early and Mid Ordovician had finite and different durations, depending on the biostratigraphical and biogeographical ranges of diagnostic elements.

Late Ordovician
Whereas a degree of phytoplankton provincialism is evident for the Early and Mid Ordovician (see above; Servais et al. 2003), the Late Ordovician was apparently a time of increasing cosmopolitanism (Wicander 2004). Even though some endemism remained, a breakdown in acritarch provincialism seems to have begun at the Darriwilian–Sandbian transition and continued through the Katian (Vecoli & Le Hérissé 2004). Only in the latest Ordovician, during the Hirnantian, did provincialism once again become prominent.

Sandbian and Katian

Hill & Molyneux (1988) were the first to report that Caradoc–Ashgill (Sandbian–Katian) acritarch assemblages from northeast Libya, situated at high palaeolatitudes on the margin of Gondwana, displayed some similarity with coeval assemblages from Laurentian North America, located at low palaeolatitudes (Torsvik & Cocks 2013, fig. 15). Two-thirds of their Gondwanan species are present in Upper Ordovician Laurentian rocks. Subsequently, Wicander et al. (1999), Playford & Wicander (2006) and Wicander & Playford (2008) confirmed these observations.

In their studies on lower Richmondian (middle Katian) strata of the North American Midcontinent (i.e. Sylvan Shale, Maquoketa Shale, Bill’s Creek Shale and Stonington Formation), Wicander et al. (1999), Playford & Wicander (2006) and Wicander & Playford (2008) compared their Laurentian acritarch assemblages with time-equivalent assemblages from Baltica, Avalonia, Gondwana and Perigondwanan terranes. They reported (Wicander & Playford 2008) that many of the constituent taxa of the Laurentian assemblages were geographically widespread during the Katian. The combined Bill’s Creek Shale and Stonington Formation acritarch assemblage, for example, was reported to include many taxa known from Upper Ordovician localities in Baltica, Avalonia, South China and Gondwana, “thus evincing Late Ordovician cosmopolitanism among marine microphytoplankton communities” (Wicander & Playford 2008, p. 62). Cosmopolitan species include Aremoricanium squarrosum, Baltisphaeridium aliquigranulum, B. perclarum, Dactylofusa ctenista, Diexallophasis denticulata, D. platynetrella, Dorsennidium hamii, Excultibrachium concinnum, Leiofusa fusiformis, L. litotes, Lophophosphaeridium edenense, Micrhystridium prolixum, Multiplicisphaeridium
irregulare, Orthosphaeridium rectangulare, Polygonium gracile, Veryhachium europaeum, V. oklahomense and Villosacapsula setosapellicula.

Hirnantian

Until recently, little was known about acritarch palaeobiogeography during the latest Ordovician Hirnantian Stage. Most investigations of acritarchs from Hirnantian strata have focused on Gondwanan or Perigondwanan successions in Morocco (Elaoud-Debbaj 1988), northeast Libya (Molyneux & Paris 1985; Hill & Molyneux 1988; Molyneux 1988; Paris 1988), northeast Algeria (Vecoli 1999; Le Hérissé in Paris et al., 2000), the Prague Basin (Dufka & Fatka 1993), Argentina (Rubinstein & Vaccari 2004; Rubinstein et al. 2008a), south Turkey (Le Hérissé in Paris et al. 2007) and Iran (Ghavidel-syooki et al. 2011a, b). There, preservation, reworking and dilution linked to the several advances and retreats of ice in local palaeovalleys during the Hirnantian glacial phases (e.g. Ghienne et al. 2007) can make it difficult to analyse and interpret palynological signals (Vecoli & Le Hérissé 2004; Vecoli 2008; Delabroye & Vecoli 2010). However, Vecoli & Le Hérissé (2004), in their extensive analysis of acritarch diversity patterns throughout the Ordovician of the periglacial Gondwanan margin, showed that standing diversity increased through the glacial interval with “new speciations […] of morphologically distinctive […] species […] such as Beromia clipeata, Eupoikilofusa [= Poikilofusa] ctenista, and Saharidia munfarida”. A burst of new netromorph species seems also to have occurred at that time (Vecoli & Le Hérissé 2004, fig. 6). Many of these new taxa were endemic to Gondwana (Delabroye 2010; Delabroye et al. 2011a; see below). In post-glacial Hirnantian strata, they co-occur with “new distinct [and endemic] morphotypes of Silurian ‘affinity’ such as Cymbosphaeridium spp., Tylotopalla spp. [e.g. Tylotopalla caelamericus], and Visbysphaera spp.” (Vecoli & Le Hérissé 2004). All of these species that appeared during the Hirnantian also occur with other species that were endemic to Gondwana at this level and which had their first appearances during the Sandbian and the Katian. The latter include Leprotolypa e vexa, Neoveryhachium carminae, Striatotheca sp. of Molyneux (1988) and Veryhachium subglobosum. A few Hirnantian localities at low palaeolatitudes have been studied for phytoplankton. Duffield (1982) studied samples from the Hirnantian Ellis Bay
Formation of Anticosti Island, Québec, Canada, although her work concentrated more on the local Silurian strata. Later, Martin (1988), who reprepared some of the samples from the Ellis Formation previously studied by Duffield (1982), observed that “a preliminary selection of taxa from ... strata on Anticosti Island, Québec, eastern Canada, indicates that the area has the most continuous palynological record from at least the Ashgill to the late Llandovery, with the best potential for establishing detailed acritarch systematics and interregional correlation”.

More recent work on acritarch dynamics across the Ordovician–Silurian boundary at low palaeolatitudes (Delabroye 2010; Delabroye et al. 2011a, b; Vecoli et al. 2011) has confirmed Martin’s (1988) observations. High-resolution investigation of acritarch distributions across the Ordovician–Silurian boundary on Anticosti Island (Laurentia) and at Valga, Estonia (Baltica) were complemented by literature reviews of Hirnantian assemblages from the Gondwanan and Perigondwanan localities mentioned above plus South China (Yin & He 2000), Sweden (Le Hérissé 1989a), north Estonia (Uutela & Tynni 1991) and Poland (Kremer 2001; Masiak et al. 2003); see Delabroye et al. (2011a, b). The more recent investigations show that the tendency towards speciation during the Hirnantian observed by Vecoli & Le Hérissé (2004) in Gondwana occurred also at low to mid palaeolatitudes during the Hirnantian, but involved different morphotypes (see also Vecoli 2008).

New species common to Laurentia and Baltica that appeared during the Hirnantian are *Ammonidium* sp. in Delabroye et al. (2011b), *Leiofusa granulicatis quincunx, Evittia* sp. A in Delabroye et al. (2011b), *Helosphaeridium longiorgii, Hoegklintia visbyensis* and *Oppilatala* sp. in Delabroye et al. (2011b). These species occur together with other taxa that were endemic to the two low to mid latitude palaeoplates, but which appeared earlier during the Sandbian and the Katian, such as *Baltisphaeridium curtatum, Buedingiisphaeridium balticum, Dilatisphaera wimanii, Likropalla adiazeta* and *Peteinosphaeridium septuosum*. In contrast to Gondwanan successions, Hirnantian successions in Laurentia and Baltica have yielded numerous large forms of *Baltisphaeridium* spp., ‘giant’ acritarchs such as *Hoegklintia* spp. or *Estiastra* spp. that are typical of low to mid palaeolatitude carbonate environments, several large species of the *Goniosphaeridium-Stellechinatum-Polygonium* plexus, and *Dilatisphaera wimanii*, a giant precursor of smaller *Dilatisphaera* species that evolved during the Silurian (Delabroye et al. 2011b). As in Gondwana, however, the
Laurentian and Baltic Hirnantian assemblages also contain endemic species that belong to genera of Silurian affinity, in this case including Ammonidium, Evittia, Hoegklintia, Oppilatala and Tylotopalla.

Whereas much of the Late Ordovician was characterized by cosmopolitan taxa and assemblages, these recent data seemingly show that a new phytoplankton provinciality began to develop during the latest Ordovician (i.e. Hirnantian), at a time of major palaeoenvironmental perturbations (Munnecke et al. 2010 and references therein) that culminated in the glacial maximum of the Early Palaeozoic Icehouse (Vandenbroucke et al. 2010a, b and references therein). Pairwise comparisons of taxonomic similarity for the latest Katian and Hirnantian, pre-glacial, syn-glacial and deglacial/post-glacial phases, based on data published by Delabroye et al. (2011a, figs 5, 6, 7 and 8) from Anticosti, Estonia and high palaeolatitude Gondwana, show a decrease in similarity throughout this interval (Fig. 6). Delabroye et al. (2011b) designated two distinct Baltic/Laurentian and Gondwanan palaeoprovinces during the latest Ordovician “possibly caused by limited water masses exchange between Gondwana and Laurentia/Baltica due to the presence of a bathymetric ridge associated with the opening of the Rheic Ocean [of which the] effect would have intensified during the Hirnantian glacially-driven sea level drop” (Delabroye et al. 2011b, p. 39).

Nevertheless, several important areas have not yet been investigated for Hirnantian phytoplankton, such as Siberia at low palaeolatitudes in the northern hemisphere, or have produced only poorly preserved Hirnantian assemblages, for example Avalonia (Whelan 1988) or South China (Li, pers. oral comm. 2007). Our understanding of latest Ordovician acritarch palaeobiogeography would be improved considerably if well-preserved assemblages could be obtained from such areas in the future.

Recent investigations of acritarch assemblages from the Hirnantian of Iran (Ghavidel-syooki et al. 2011a, b) highlight some species of particular interest for our understanding of the factors controlling their distribution, i.e. whether they are latitudinally distributed and/or follow palaeocontinental margins. Iranian assemblages of Hirnantian age share a high proportion of species in common with those of other Gondwanan and Perigondwanan localities, but also share species in common with latest Ordovician assemblages from Laurentia and Baltica (Ghavidel-syooki et al. 2011a, b). Of particular interest here is the species from the Eastern Alborz Range, northern Iran figured as Tylotopalla sp. (Ghavidel-syooki et al. 2011a, pl. 5, figs 9–
10), and also found in the Zagros Mountains of southern Iran (Ghavidel-syooki et al., 2011b, fig. 4B). This is morphologically close to *Tylotopalla heterobrachiifera nomen nudum* from the Ellis Bay Formation of Anticosti (Delabroye 2010; Delabroye et al. 2011a). *Cheleutochroa diaphorosa* from the Eastern Alborz Range (in Ghavidel-syooki et al. 2011a, pl. 2, fig. 6, pl. 3, fig. 8) also resembles the *Oppilatala* specimens found in the uppermost Ordovician of Anticosti and Estonia (Delabroye et al. 2011b, pl. 11, figs 6–7; *Oppilatala anticostiana nomen nudum* in Delabroye et al. 2011a; Delabroye 2010) in having conspicuous plugs at base of the processes. These two species have not been recovered from other Gondwanan or Perigondwanan localities. During the latest Ordovician, the Alborz Terrane and Zagros Basin of Iran were situated on the margin of Gondwana at low to mid southern palaeolatitudes, comparable with the palaeolatitudes of Anticosti in Laurentia and Estonia in Baltica (Torsvik & Cocks, 2013, figs 15, 16). Hence, these observations might show that the composition of the Iranian assemblages was controlled by a mixture of factors, including continental physiography (see Servais et al. 2003), i.e. following the continental margin of Gondwana, to account for the Perigondwanan aspect, and a restriction to low to mid southern palaeolatitudes to account for the elements in common with Laurentia and Baltica.

**Silurian**

Analysis of Silurian acritarch biogeography dates back to the work of Cramer and Cramer & Diez (for reviews see Cramer 1971; Cramer & Diez 1972, 1974a, b), but as noted for the Early–Mid Ordovician, their analysis was based on out-dated palaeogeographical reconstructions and has been superseded by later work. Papers by Le Hérissé & Gourvennec (1995) and Le Hérissé et al. (1997a) focused on the biogeography of mid Silurian and late Silurian acritarchs respectively, and constitute the basis of this review.

**Mid Silurian (late Llandovery – Wenlock)**

Cramer (1971) and Cramer & Diez (1972, 1974a, b) identified six acritarch ‘biofacies’ in a late Llandovery–Wenlock palynological province model, which they
termed (i) the Baltic palynofacies, (ii) the *Gloeocapsomorpha prisca* facies, (iii) the *Deunffia eisenackii* facies, (iv) the *Domasia* facies, (v) the *Neoveryhachium carminae* facies (subdivided into Iberian, Transitional and Brazilian-Libyan realms), and (vi) the *Pulvinosphaeridium-Estiastra* facies. As with their interpretation of Ordovician acritarch biogeography, they considered these units to be delineated by palaeoisotherms, which they regarded as being parallel to palaeolatitude, and so showed the boundaries of these units as also being parallel to palaeolatitude.

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Cramer’s (1971; Cramer & Díez (1972, 1974a, b) latitude-parallel model, however, was at least partially dependent on the palaeogeographical reconstruction used as a base map (Colbath 1990a). When plotted on a reconstruction of Llandovery palaeogeography by Scotese (1986), data from Cramer (1971) show major deviations from the palaeolatitude-parallel model, particularly with regard to the distribution of the *Neoveryhachium carminae* biofacies and the combined *Deunffia-Domasia* biofacies (Colbath 1990a).

The distribution of the four principal biofacies of Cramer’s model, namely the *Neoveryhachium carminae* facies, the *Deunffia* facies, the *Domasia* facies and the *Pulvinosphaeridium-Estiastra* facies, was re-evaluated by Le Hérissé & Gourvennec (1995). Their analysis of late Llandovery–Wenlock distribution patterns, which used quantitative methods to supplement qualitative assessments, again questioned the latitudinal controls advocated by Cramer (1971) and Cramer & Díez (1972, 1974a, b) and reached different conclusions regarding controlling factors. Based on data from eastern North America, South America, western Europe, Baltoscandia, Siberia, North Africa and adjacent regions and China, Le Hérissé & Gourvennec (1995) concluded that acritarch distribution resulted from the combined effects of continental distribution, latitude, environment and oceanic circulation. They also concluded that the main contributory factors influencing the distribution of *Gloeocapsomorpha prisca* and *Deunffia eisenackii* blooms were related to local environmental factors rather than palaeotemperature, in contrast to Cramer’s model.

The *Neoveryhachium carminae* biofacies

In terms of the palaeogeographical reconstructions of Torsvik & Cocks (2013), *Neoveryhachium carminae* occurs, albeit rarely, on the Rheic Ocean margin of
Laurentia and the adjacent continental masses of Avalonia and Baltica (Fig. 7). In addition to the rare occurrences in the south-eastern United States (Alabama, Georgia and Virginia) reported by Cramer & Diez (1972), *Neoveryhachium carminae* has been recorded from the Llandovery Series of Belgium (Avalonia: Martin 1969, 1974, 1989) and the upper Wenlock and Ludlow series of Gotland (Baltica: Le Hérissé 1989b; Stricanne et al. 2004).

The biogeographical range of *Neoveryhachium carminae* also extended along the facing margin of Gondwana, where it occurs in rocks of Llandovery to early Wenlock age from Bolivia and Peru (Díaz-Martínez et al. 2011) through North Africa (Libya: Deunff & Massa 1975; Hill & Molyneux 1988) to Turkey (western Taurides: Dean & Monod 1990; Dean et al. 1993), Iran (Zagros Basin: Ghaivdel-syooki 1997) and Saudi Arabia (Le Hérissé et al. 1995; Le Hérissé 2000). Other records are from Silurian successions in Algeria (Argiles à Graptolites, Formation de Medarba, Formation de l’Oued Tifist: Jardiné & Yapaudjian 1968; Jardiné et al. 1974), Jordan (Khushsha Formation: Keegan et al. 1990), Egypt (Gueinn & Rasul 1986) and Iraq (Akkas Formation: Al-Ameri 2010), and from rocks dated as late Silurian (upper Wenlock–Ludlow series) in Libya (Richardson & Ioannides 1973; Wood & Tekbali 1987).

*Neoveryhachium carminae* has also been recorded from rocks of mid Llandovery to early Wenlock age in the intracratonic Paranaíba and Paraná basins of Brazil and Paraguay respectively (Brito 1967; Quadros 1982; Wood & Miller 1991; Rubinstein 1997), and from rocks of Ludlow age in Bolivia (Cramer et al. 1974c) and the Precordillera Basin of Argentina (Rubinstein 2001).

Le Hérissé & Gourvennec (1995, p. 116) noted that *Neoveryhachium carminae* was found preferentially at high palaeolatitudes. However, they also reported evidence for facies control, with a tendency for the species to occur in turbid environments and clastic sedimentary regimes of shallow shelf seas. Furthermore, they noted that the species was found in environments with similar sedimentary conditions in Laurentian North America and on Gotland. They pointed out that facies control to account for the species’ distribution had been advocated by Cramer (1971) but not considered subsequently, and concluded that a correspondence could be established between the distribution of the species and platform mudstones and fine-grained clastic sediments deposited in shelf environments. Rubinstein (1997), however, questioned whether this interpretation of facies control could be used to explain the distribution of
Neoveryhachium carminae in South American basins, arguing that there were no marked differences in depositional environments between basins to explain the presence or absence of the species. She suggested that the distribution of *N. carminae* there might be related to conditions in each basin, citing in particular connection to or isolation from other basins or an oceanic environment.

The Deunffia-Domasia biofacies

Le Hérissé & Gourvennec (1995, fig. 3) considered the *Deunffia* and *Domasia* biofacies in combination and plotted the late Llandovery–Wenlock distribution of the two genera on a paleogeographical reconstruction based on that of Scotese & McKerrow (1990). Cramer's interpretation (e.g. Cramer & Díez 1974b, fig. 2) placed the *Domasia* and *Deunffia* biofacies at low, tropical to subtropical palaeolatitudes, with sporadic occurrences at higher palaeolatitudes attributed to either sporadic irregularities in the thermal regime or to post-Silurian deformation. Le Hérissé & Gourvennec (1995), however, showed that both genera were found in Gondwanan as well as Laurentian successions, a point already illustrated by Colbath (1990a, fig. 1), albeit that they comprised fewer species at higher palaeolatitudes. Their map of species diversity (Le Hérissé & Gourvennec 1995, fig. 3) shows two maxima, one at low palaeolatitudes, between 0° and 30°S, covering eastern Canada (South Ontario), Great Britain and Gotland and reaching a maximum of nine species, and the second at higher southern palaeolatitudes, between about 45° and 70°S, centred on south-west Europe and north-west Africa with a maximum of five to six species. Species diversity decreases away from these maxima, but extends along both the Gondwanan margin and the opposing Laurentian margin (Fig. 7). Rubinstein (1997), however, also reported six species of the *Domasia-Deunffia* association of late Llandovery to early Wenlock age from the La Chilca Formation of the Argentinian Precordillera Basin, suggesting that there might be more maxima elsewhere.

Based on this distribution pattern, Le Hérissé & Gourvennec (1995, p.121) argued for dispersal of taxa belonging to the *Deunffia-Domasia* association between low and high palaeolatitudes, and an increase in diversity from high to low palaeolatitudes. They also noted, however, that although there were differences in diversity between the Laurentian and Gondwanan margins, there was no real evidence for provincialism
within the group. They observed that the spatial distribution of the combined
\textit{Deunffia-Domasia} biofacies was more closely related to depositional environment
than palaeolatitude, with better representation of the biofacies in outer shelf
environments on both the Laurentian and Gondwanan margins. Le Hérissé &
Gourvennec (1995) concluded that the wide distribution of the biofacies was likely to
have been influenced by oceanic circulation patterns that transported the \textit{Deunffia-}
\textit{Domasia} association between the relatively homogeneous outer shelf environments of
both continental margins.

Le Hérissé & Gourvennec (1995) noted that there were transitions from the
\textit{Neoveryhachium carminae} biofacies to the \textit{Deunffia-Domasia} biofacies in both
Laurentian North America and Gondwana. Based on cluster analysis of assemblages
from eastern North America, Le Hérissé & Gourvennec (1995, fig. 4) showed that the
distribution of biofacies was parallel to the margin of the depositional basin rather
than palaeolatitude, complementing Colbath’s (1990a) earlier observation of the same
pattern.

Based on their analyses, Colbath (1990a) and Le Hérissé & Gourvennec (1995)
concluded that depositional environment and facies exerted greater controls on the
distribution of the \textit{Neoveryhachium carminae} and \textit{Deunffia-Domasia} biofacies than
palaeolatitude. Le Hérissé & Gourvennec (1995) also concluded that the
\textit{Pulvinosphaeridium-Estiastra} biofacies, which they noted was also characterized by
abundant \textit{Hoegklintia}, was probably restricted to fairly shallow, carbonate-rich
environments at low palaeolatitudes (Fig. 7) and was therefore also subject to controls
exerted by depositional environment on its distribution.

Although they had demonstrated that the \textit{Neoveryhachium carminae} and \textit{Deunffia-}
\textit{Domasia} biofacies had widespread distributions on the Laurentian and Gondwanan
margins of the Rheic Ocean, Le Hérissé & Gourvennec (1995) argued that other taxa
might have more restricted biogeographical distributions. They cited, in particular,
the apparent restriction of \textit{Dilatisphaera williereae} in the late Llandovery–Wenlock to
a subtropical zone that encompassed the Brabant Massif of Belgium, Gotland, the
Llandovery type area of Wales, western Ireland, and the Gaspé Peninsula and
Anticosti Island of eastern Canada (Fig. 7). They also noted that the distribution of
\textit{Dilatisphaera} was subsequently modified in time and space, with dispersal from low
to high palaeolatitudes. Among other taxa identified as having potential
biogeographical significance, Le Hérissé & Gourvennec (1995) suggested that
Gracilisphaeridium might be used in addition to other taxa to define a “Euramerican”
(i.e. Laurentian/Avalonian/Baltic) province at the Llandovery–Wenlock boundary,
and that other distinctive taxa, notably Dactylofusa maranhensis and Tyrannus
 giganteus might be restricted to Gondwana (Fig. 7). Dactylofusa maranhensis, for
example, is widespread in Gondwanan successions, where it occurs in the
intracratonic Paranaiba and Paraná basins of Brazil and Paraguay (Brito 1967;
Quadros 1982; Gray et al. 1992; Rubinstein 1997) and in the Central Andean Basin of
northwest Argentina (Rubinstein 2005; Rubinstein et al. 2008a; Rubinstein & Muro
2011) as well as along the margin of Gondwana as depicted by Le Hérissé &
Gourvennec (1995, fig. 2).

In summary, the distribution of late Llandovery–Wenlock acritarch biofacies parallel
to palaeolatitude, as depicted by Cramer (1971) and Cramer & Díez (1972, 1974a, b),
is incompatible with more recent palaeogeographical reconstructions. The biofacies
are widespread and, based on current evidence, their distributions are evidently
controlled by depositional environment and facies rather than biogeography (but see
Rubinstein 1997, p. 615, for an alternative view that plays down the role of facies
control for South American basins). Other taxa such as species of Dactylofusa,
Dilatisphaera, Gracilisphaeridium and Tyrannus might have biogeographically
significant distributions, but this remains to be tested.

Late Silurian (Ludlow–Přidoli)

Le Hérissé et al. (1997a) used methods similar to those employed by Le Hérissé &
Gourvennec (1995) to investigate the biogeography of late Silurian phytoplankton in
the context of the base maps published by Scotese & McKerrow (1990). Their
analysis highlights some of the complexities introduced by the interplay of different
factors affecting biogeographical distributions of Palaeozoic phytoplankton. On the
one hand, Le Hérissé et al. (1997a) referred to the apparent homogeneity of late
Silurian assemblages from southern Baltica and the Gondwanan margin. However,
they also referred to the degree of endemism that was evident among late Silurian
phytoplankton assemblages from either side of the Rheic Ocean. Le Hérissé et al.
(1997a) also pointed out that cluster analysis enabled delineation of a biogeographical
unit encompassing part of South America (Bolivia), the Gondwanan margin (Florida, Algeria) and Perigondwana (Armorican Massif), comparable to the Malvinokaffric Realm of invertebrate biogeography.

For the Ludlow Series, Le Hérissé et al. (1997a) noted that microfloras from northern Europe, such as those from the British type section or Gotland, were less varied taxonomically than those from higher palaeolatitude Gondwanan sections, but contained some apparently endemic forms such as *Eisenackidium ludloviense*, *Helosphaeridium latispinosum*, *Visbysphaera foliata* and *V. whitcliffense*. In contrast, they commented that coeval high palaeolatitude assemblages had a higher proportion of endemic forms, with about 30% endemism. They reported *Anomaloplaisium johnsium*, *Baltisphaeridium areolatum areolatum*, *B. areolatum laevigatum*, the coenobial form *Deflandrastum*, *Morcoa cantabrica*, *Triangulina sanpetrensis*, *Pardaminela crassicosta*, *Perforella perforata*, *Tyrannus giganteus*, *Visbysphaera bonita* and *V. jardinei* to be typical of Ludlow successions in North Africa and adjacent regions (Fig. 8). Subsequent work, however, has shown that species previously considered to be endemic to high palaeolatitudes have wider distribution. Le Hérissé (2002), for example, citing Jachowicz (2000), pointed out that *V. bonita* and *V. jardinei* occurred in the Přídolí Series in Pomerania, north-west Poland, which would place them in proximity to the Trans-European Suture Zone between Baltica and Avalonia on the Laurussian margin of the Rheic Ocean (Torsvik & Cocks 2013, figs 3, 18). Le Hérissé et al. (1997a) also noted that Ludlow assemblages from the upper part of the Dadas Formation in Turkey, from a Perigondwanan terrane, contained a mixture of Balto-Scandinavian and Gondwanan taxa together with a high proportion of endemic forms.

The Ludlow assemblages discussed by Le Hérissé et al. (1997a) thus exhibit an endemic component restricted to opposing continental margins on either side of the Rheic Ocean, but also a high degree of apparent homogeneity. The latter was attributed by Le Hérissé et al. (1997a) to a narrowing of the Rheic Ocean in the late Silurian, which brought the Gondwanan margin into proximity to the Laurentian (or Laurussian) margin, and to oceanic circulation patterns that might have influenced the distribution of microfloras.

Le Hérissé et al. (1997a) also distinguished an outer, deep-water belt on the Perigondwanan margin of the Rheic Ocean (Fig. 8), characterized by a low diversity
assemblage with *Cymbosphaeridium* or *Evittia*, cysts of prasinophycean algae

*(Cymatiosphaera, Dictyotidium)* and mazuelloids. This assemblage was documented from Bohemia, with other possible examples from the Carnic Alps, Sardinia, the Vendée (southern Brittany, Aquitaine) and Spain.

**Devonian**

Notable papers dealing with Devonian phytoplankton biogeography include those by Colbath (1990a), who examined the biogeographical distribution of Frasnian microfloras, and Le Hérissé *et al.* (1997a), who analysed the biogeography of Early Devonian acritarchs and prasinophytes. These studies made use of quantitative methods, principally cluster analysis, as well as more qualitative assessments, but were subject to the limitations imposed by the available data. As Le Hérissé *et al.* (1997a) noted, there were, at that time, relatively few publications on Lower Devonian (Lochkovian and equivalent ‘Gedinnian’) acritarch assemblages, and that they were also geographically limited.

Although some of the problems pertaining to Devonian acritarch palaeobiogeography still exist, progress has been made, and many stratigraphically well documented, diverse, and well preserved organic-walled microphytoplankton assemblages have since been published. However, just as for other organisms, the quality of palaeobiogeographic reconstructions based on acritarchs, largely depends on the “quantity and quality of information on assemblages from each sampled locality” (Le Hérissé *et al.* 1997a, p. 106).

Only those Devonian acritarch papers germane to the discussion of Devonian acritarch palaeobiogeography were used for this review. Papers dealing with Devonian acritarchs and prasinophytes that contain poorly preserved assemblages, those representing environments generally unfavourable to diverse assemblages (both preservational and morphological), those in which assemblages are not illustrated, and those that describe only one or several new taxa are not included. Many of the papers cited do, however, contain extensive bibliographies that include papers not referenced here.

Lastly, Le Hérissé *et al.* (2000) reviewed the biostratigraphical, palaeoecological and palaeogeographical status of Devonian acritarchs in general, as well as plotting the
stratigraphical range and geographical distribution of some 180 selected acritarch species. These species were classified as being Cosmopolitan, Gondwanan, European (primarily from Belgium), North American, South American or Australian.

Early Devonian

In their pioneering investigation of the Early Devonian biogeography of acritarchs and prasinophytes, Le Hérissé et al. (1997a) applied cluster analysis to assemblages from eastern North America (single location, Oklahoma), Bolivia, North Africa (Algeria, Libya, Tunisia), the Armorican Massif, north-west Spain, the Moesian platform (Romania), and the Estonian and Podolian block (Le Hérissé et al. 1997a, fig. 6).

Their analysis distinguished three groups of assemblages. One cluster comprised Podolia and Romania. A second cluster consisted of north-west Spain, the Armorican Massif and North Africa, with Bolivia linked at lower similarity values. The third cluster, eastern North America, was clearly isolated from the other two groups (Le Hérissé et al. 1997a, fig. 4). Le Hérissé et al. (1997a, p. 120) concluded that eastern North America and Gondwana were characterized by distinctive acritarch assemblages during the Early Devonian. They went on to write “Taking into account more recent palaeogeographic reconstructions, it seems that this provincialism was not controlled by water temperature differences, but rather influenced by physical barriers (e.g. emergent land) between these areas, preventing seaway connections and the dispersal of acritarchs. In spite of the limited data available, particularly from northern Europe, close similarities exist between this region and the North Gondwanan margin. This linkage reflects the low latitudinal positioning of this region and the narrowing of the Rheic Ocean during the Early Devonian.” As shown below, this conclusion has had to be modified as more sections became available.

Studies of Lower Devonian acritarchs still remain relatively sparse. Le Hérissé et al. (2009) examined phytoplankton biodiversity changes for the late Silurian to earliest Devonian (Lochkovian) based on published and unpublished data from key stratigraphic sections where independent age control was firmly established. Regional biodiversity for Lochkovian phytoplankton communities was determined for Laurentia (Oklahoma, western Newfoundland), Armorica (Crozon Peninsula and Normandy, France; northern Spain) and Gondwana (Libya, Bolivia). Le Hérissé et al.
(2009) concluded that there was an initial radiation of new acritarch taxa during the Lochkovian and an increase in cosmopolitan species in both hemispheres. When plotted on the Early Devonian palaeogeographical map of Cocks & Torsvik (2002, fig. 8; see also Rubinstein et al. 2008b, fig. 3 and Le Hérisse et al. 2009, text-fig. 3), published acritarch records form two distinct groups. One group comprises records from mid palaeolatitudes, about 30°–40°S, from Laurentia, Armorica and northern Gondwana (North Africa). The second group consists of assemblages from high palaeolatitudes (>60°S) and mainly from South America (Fig. 9).

At mid palaeolatitudes, well-preserved and diverse Lochkovian acritarch assemblages from Laurentia are known from the Haragan and Bois d’Arc formations of Oklahoma (Loeblich & Wicander 1976; Wicander 1986). Similarly well-preserved and diverse Lochkovian acritarch assemblages have been recorded from the Landévennec Formation, Crozòn Peninsula, Brittany (Deunff 1980) and the San Pedro Formation, northern Spain (Cramer 1964; Rodriguez Gonzalez 1983), both in Armorica, and from various formations in the Algerian Sahara (Jardine & Yapaudjian 1968; Jardine et al. 1972, 1974) and the Tadrardt Formation of western Libya (Le Hérissé 2002), both in northern Gondwana. These are not the only published records of Lochkovian acritarch assemblages (see Rubinstein et al. 2008b for additional references), but constitute the most diverse and best preserved Lochkovian assemblages described to date. As environmental conditions play an important role in the distribution of acritarchs, some of the published acritarch assemblages are of little or no use in helping to delineate palaeogeographic realms and so are not discussed here.

At high paleolatitudes, Lochkovian acritarch data are from South America (Fig. 9) but, as indicated by Rubinstein et al. (2008, p. 170), are still scarce and are restricted to Argentina (Le Hérissé et al. 1997b), Bolivia (Vavrdová et al. 1996; Vavrdová & Isaacson 1997; Melo 2000, 2005; Le Hérissé et al. 2004), Brazil (Brito 1967; Daemon et al. 1967; Lange 1967; Quadros 1982, 1988, 1999; Dino & Rodrigues 1995) and Uruguay (Martínez Macchiavelo 1968; Pöthe de Baldis 1978). In addition, Rubinstein & Steemans (2007) reported on a palynomorph assemblage of late Pragian to early Emsian age from the Precordillera of Mendoza, Argentina. More recently, Rubinstein & Muro (2011) discussed the biostratigraphy and diversity trends of Silurian to Lower Devonian organic-walled phytoplankton and miospores from Argentina.
The mid palaeolatitude acritarch record seemingly indicates some provincialism between Laurentia and Armorica on the one hand, and Gondwana on the other, with about 35% of the species endemic to Laurentia (Le Hérissé et al. 1997a). However, some of this is probably due to lack of a robust published record, and what were earlier reported to be endemic species have now been recorded elsewhere. Nonetheless, commonly occurring, distinctive species that are restricted to Laurentia include, among others, *Ectypolopus elimatus, Multiplicisphaeridium amplitatuum, Nanocyclopia aspraritis, Pterospermella malaca* and *Pterospermella verrucaboia*. Other common and distinctive Laurentian taxa that have been recorded elsewhere include *Cymatiosphaera reticulosa* (Podolia), *Dictyotidium biscutulatum* (Podolia), *Ecthymapalla echinata* (Libya) and *Oppilatala vulgaris* (Libya). Commonly occurring and distinctive taxa that are restricted to Armorica and North Africa include *Candelasphaeridium insolitum, Fulgisphaeridium bristokii* and *Perforella perforata*. Assemblages from Gondwana include a number of genera and species that are seemingly endemic to the palaeocontinent, for example *Schizocystia*, which has been reported from Lower Devonian strata of South America and North Africa. Its occurrence on the west and north Gondwana margin makes this genus a possible marker for the Lower Devonian in Gondwanan successions (Rubinstein et al. 2008b). Those taxa that have a widespread geographical distribution, are restricted to the Lochkovian, and can be used for worldwide stratigraphic correlations (Rubinstein et al. 2008b), include the distinctive *Demorhethium lappaceum, Riculasphaera fissa* and *Thysanoprobolus polykion*. Other Devonian acritarch taxa that either first occur in the upper Silurian or extend into the Pragian and Emsian stages and are commonly reported include, among others, the *Diexallophasis remota* group, *Evitta* spp., *Hapsidopalla sannemannii*, *Pterospermella circumstriata*, *Quadraditum fantasticum* and *Winwaloeusia distracta* (e.g. Playford 1977; Le Hérissé et al. 2000). All of these taxa also have wide geographical distributions. Notwithstanding the restricted distribution of some genera and species, as noted above, it now appears, based on the diverse (47 species) and well-preserved Lochkovian acritarch assemblage reported from the Solimões Basin, northwestern Brazil, and Lower Devonian acritarch assemblages elsewhere, that there was a more cosmopolitan nature to the Early Devonian microphytoplankton community than
previously suggested, and “the variations in composition are most probably
progressive from high to low (palaeo)latitudes” (Rubinstein et al. 2008b, p. 176).

Mid Devonian

The amalgamation of Avalonia and Baltica with Laurentia in the mid Silurian led to
the formation of Laurussia, which then continued to move southward and rotate
counterclockwise. By the Early–Mid Devonian transition (397.5 Ma), Laurussia and
its overlying epeiric seas were located at low to mid southern palaeolatitudes (Fig.
10). In contrast, Gondwana rotated in a northwesterly direction, with the result that
the Rheic Ocean between Laurussia and Gondwana continued to close, bringing the
two continental masses closer together. The mountain building that began during the
late Silurian continued along the eastern margin of Laurussia.

The literature on Middle Devonian acritarch assemblages, particularly from well-
dated and stratigraphically constrained sections, is more extensive than for the Lower
Devonian, but still of uneven geographical and stratigraphical distribution, with most
of the studies from Givetian rather than Eifelian sections. Publications on well-
preserved Middle Devonian acritarch assemblages from sections with good
stratigraphic control in North America include Legault (1973; Givetian, Ontario,
Canada), Playford (1977; upper Pragian–Givetian, Ontario, Canada), Wicander &
Wood (1981; Givetian, Ohio, U.S.A.), Wicander & Wright (1983; Eifelian–Givetian,
Ohio, U.S.A.), Wood & Clendening (1985; Givetian, Kentucky, U.S.A.), Turner
(1991; Givetian–Frasnian, Alberta and Northwest Territories, Canada), Huysken et al.
(1992; Givetian–Famennian, Kentucky, U.S.A.) and Wicander & Wood (1997,
Givetian, Iowa, U.S.A.).

Middle Devonian acritarch assemblages from South American are not as well studied
as those from North America and do not always have the best stratigraphic
information. Nonetheless, the following references offer reasonable to good
Brazil), Póthe de Baldis (1974; Eifelian–Givetian, northwestern Paraguay), Barreda
(1986; Givetian–Frasnian, Argentina), Quadros, (1988; Lower–Upper Devonian,
northern Brazil), Wood (1995; Givetian–Frasnian, Bolivia), Ottone (1996; Eifelian–
Frasnian, northwestern Argentina), Vavrdová et al. (1996; Lochkovian–Famennian, Bolivia) and Rubinstein (1999, 2000; Eifelian-Givetian, western Argentina).

The same can be said for Africa, where some of the described acritarch assemblages have good stratigraphic control, and others not as good but still contain diverse acritarch assemblages that are very much characteristic of the Middle Devonian. These include: Jardiné & Yapaudjian (1968; Emsian–Givetian, Algeria), Jardiné (1972; Lochkovian–Famennian, Algeria), Jardiné et al. (1972, 1974; Lochkovian–Famennian, Algeria), Anan-Yorke (1974; Middle Devonian, Ghana), Moreau-Benoit (1984; Givetian–Famennian, Libya) and Streel et al. (1988; Eifelian–Famennian, northeast Libya).

Several acritarch assemblages have been described from Armorica by Deunff (1954, 1968, 1981; Middle Devonian), Rauscher (1969; Devonian), Moreau-Benoit (1972, 1974; Silurian–Devonian) and Le Hérissé & Deunff (1988; Givetian–Frasnian), but will not be discussed below because of their paucity of species or poor preservation.

In a preliminary study, Riegel (1974) described an upper Emsian and Eifelian acritarch assemblage from the Rhineland, Germany, which contained mostly long-ranging taxa.

Colbath (1990b) described and illustrated a beautifully preserved Givetian–Frasnian acritarch assemblage from the Canning Basin of Western Australia. More recently, Zhu et al. (2008) described and discussed an Eifelian acritarch assemblage from the Junggar Basin, China, at the time part of the Kazakhstan Plate and situated in mid northern palaeolatitudes between Laurussia to the west, North China and South China to the east, and Gondwana to the south (Fig. 10).

Selected taxa that occur in at least three of the previously reported Middle Devonian diverse acritarch assemblages from North America listed above (excluding Turner, 1991), and are thus geographically widespread and abundant in North America, include: Arkonites bilixus, Baltisphaeridium distentum, Cymatiosphaera winderi, Dictyotidium variatum, Diexallophasis simplex, Duvernaysphaera angela, D. tenuicingulata, Estiastra rhytidoa, Exochoderma arca, Hapsidopalla chela, H. exornata, Lophosphaeridium ochthos, Muraticavea munificus, Navifusa bacilla, Oppilatala sparsa, Ozotobrachion fircillatus, Palacanthus ledanoisii, Polyedryxium decorum, P. fragosulum, P. pharaonis, Pterospermella reticulata, Stellinium...
 comptum, S. micropolygonale, Triangulina alargadum and Veryhachium polyaster. Other species are abundant in the same Middle Devonian North American assemblages, but these are cosmopolitan taxa with long stratigraphic ranges such as Diezallophasis remota, Multiplicisphaeridium ramispinosum, Tunisphaeridium tentaculaferum, Veryhachium europaeum, V. lairdi, V. trispinosum complex and numerous species of Micrhystridium.

The most diverse Middle Devonian acritarch assemblage from South America was described by Ottone (1996) from the Los Monos Formation of the Tarija Basin, Argentina. Based on the published record of Middle Devonian South American acritarch assemblages (see above), there are many similarities to those from North America. Comparing the Los Monos Formation acritarch assemblage, consisting of 51 species (Ottone (1996), to the seven Middle Devonian North American acritarch assemblages reported above (excluding Turner, 1991), shows a total of 21 species in common between the two regions. Such a high degree of similarity suggests that a somewhat narrow and temperate oceanic link developed between Laurussia and Gondwana (South America) during the late Mid (Givetian) and early Late Devonian (Frasnian).

In addition to the similarities, a number of species seem to have been restricted to the higher southern Gondwana palaeolatitudes (but see below). These include Bimerga bensonii, Duvernaysphaera radiata, Maranhites brasiliensis, M. mosesii and Pterospermella pernambucensis, among others that have been reported but are not particularly abundant. Furthermore, Ottone (1996) reported Umbellasphaeridium deflandrei from the Los Monos Formation, and Wood (1984, p. 199) stated that the distribution of the Umbellasphaeridium recurrent species association indicated a closeness of Africa and South America and that “Umbellasphaeridium displays a ‘southern hemisphere endemism’ in the Middle and Upper Devonian.”

Elsewhere in Gondwanan successions, Anan-Yorke (1974) described an acritarch assemblage consisting of 37 species from three exploratory oil wells on the shelf and coastal region of Ghana. Taking into account synonymies, there are at least 11 species in common with published North American and South American acritarch assemblages. The common, characteristic Middle Devonian species found in all three regions include Polyedryxium pharaonis, Stellinium micropolygonale and Triangulina alargada, as well as the cosmopolitan species Diezallophasis remota,
Multiplicisphaeridium ramispinosum, Tunisphaeridium tentaculaferum, Veryhachium europaeum, V. lairdi and V. trispinosum complex. Bimerga bensonii, Maranhites brasiliensis, Navifusa brasiliensis and Umbellasphaeridium saharicum are also present in the Ghanaian assemblage, reinforcing the view based on their South American records that at least some, notably Bimerga, are restricted to higher Southern Hemisphere palaeolatitudes (Fig. 10). As noted by Rubinstein (2000), the presence of Bimerga bensonii in Bolivia, Argentina and Ghana confirms the presence of an oceanic connection between the Gondwanan regions of South America and Africa during the Mid Devonian. Middle Devonian acritarch assemblages from western Libya were reported by Moreau-Benoit (1984). Species that have also been reported from North America, South America, and, in several cases, Ghana include Cymatiosphaera winderi, Diexallophasis remota, Multiplicisphaeridium ramispinosum, Navifusa bacilla, Polyedryxium fragosolum, P. pharaonis, Tunisphaeridium tentaculaferum, Tyligmasoma alargadum, Veryhachium europaeum, V. lairdi, V. polyaster and V. trispinosum complex. Maranhites brasiliensis and Umbellasphaeridium deflandrei are also present, but their occurrence at mid southern palaeolatitudes (c. 30°S, Fig. 10) suggests that they might have been endemic to Gondwana in the Mid Devonian rather than just high southern Gondwanan palaeolatitudes. Jardiné & Yapaudjian (1968), Jardiné (1972) and Jardiné et al. (1972, 1974) also recorded some of the same taxa from Algeria as those mentioned by Moreau-Benoit (1984) from Libya. Among the Givetian taxa recorded by Colbath (1990b) from the Canning Basin of Western Australia are Daillydium pentaster, which first appears in the upper Givetian in North America, France and North Africa, and Lophosphaeridium ochthos, which is present in the Givetian of North America. Multiplicisphaeridium ramispinosum, Navifusa bacilla, Stellinium micropolygonale and Unellium winslowiae, variously known from the upper Givetian of North America and North Africa, and the widespread Veryhachium trispinosum complex are also present. From the Junggar Basin of Xinjiang, northwest China, Zhu et al. (2008) reported on a poorly preserved Middle Devonian (Eifelian) miospore and acritarch assemblage from the Ulusubasite Formation. The acritarch assemblage consisted of 19 species, most of which are cosmopolitan. Comparing the Ulusubasite Formation acritarch assemblage to the seven reported North American acritarch assemblages (excluding Turner,
1991), there are 13 species in common. For South America, there are eight co-
occurring species with the assemblage described by Ottone (1996), and five common
species between China and western Libya (Moreau-Benoit 1984) and the Algerian
Sahara (Jardiné et al. 1974) respectively. Although the degree of similarity between
the Ulusubasite Formation and those of comparable age is not high, perhaps due in
part to preservation, there are nonetheless many species in common such as

Based on the palaeogeographical distribution of acritarch species recorded from the
Ulusubasite Formation, Zhu et al. (2008) confirmed the previously reported marine
link between Laurussia and Gondwana, as well as including the Junggar Basin in that
warm, lower palaeolatitude, temperate marine connection.

In summary, it appears there was a reasonably high degree of cosmopolitanism within
the acritarch assemblages of mid to high palaeolatitudes during the Mid Devonian, as
evidenced by the numerous acritarch species in common between Laurussia (North
America, Avalonia, Baltica), Gondwana (primarily Argentina, Ghana, Libya, Algeria,
western Australia) and western China (Junggar Basin) (**Fig. 10**). In addition to the
similarities between assemblages, however, a number of endemic species seem to be
restricted to the higher southern Gondwana palaeolatitudes or at least to high to mid
palaeolatitudes on the margin of Gondwana. These include **Bimerga bensonii**, **Duvernaysphaera radiata**, **Maranhites brasiensis**, **M. mosesii**, **Pterospermella pernambucensis** and **Umbellasphaeridium deflandrei**.

**Late Devonian**

By the Late Devonian, the Rheic Ocean had narrowed significantly such that
Laurussia and Gondwana were in very close proximity (**Fig. 11**). Mountain building,
which began in the late Silurian (the Acadian orogeny), continued along the eastern
margin of Laurussia, and also in the northern portion of Laurussia as a result of the
Ellesmere orogeny (**Fig. 11**). Sedimentological and palaeontological evidence
indicates a rather uniform global climate during this time interval.
Upper Devonian acritarch assemblages have received greater attention than those of the Lower Devonian or Middle Devonian, although preservation and stratigraphical control vary. Many of the earliest acritarch studies were from Upper Devonian sections, but preservation, processing techniques and brief descriptions, as well as poor illustrations in many cases, render many of the early, pioneering studies difficult to use. For comprehensiveness, all of those publications that describe and illustrate Upper Devonian acritarch assemblages are listed, even if many of the taxa erected are of dubious quality. In discussing the palaeobiogeography of Upper Devonian acritarch assemblages, discussion, as for the Lower and Middle Devonian acritarch assemblages, is restricted to those taxa that can be used in a regional or global setting.


Publications dealing with Upper Devonian acritarch assemblages from South America include Brito (1971, 1976, 1978; Middle–Upper Devonian, northern Brazil), Daemon (1974; Upper Devonian, Brazil), Pöthe de Baldis (1979; Upper Devonian, Paraguay), Vavrdová et al. (1996; Lochkovian–Famennian, Bolivia), Quadros (1999; Frasnian–Famennian, northern Brazil), Oliveira & Burjack (1997; Frasnian, Brazil), Le Hérissé (2001; Frasnian–Famennian, northern Brazil) and Wicander et al. (2011; Famennian, Bolivia).

Many of the earliest acritarch studies focused on Europe, and particularly on Upper Devonian assemblages. Those, and more recent publications, include Stockmans & Willière (1960, 1962a, b, 1966, 1967, 1969, 1974; Frasnian–Famennian, Belgium), Bain & Doubinger (1965; Famennian, France), Deunff (1965, 1981; Upper Devonian, France), Górka (1974a, b; Famennian, Poland), Vanguestaine (1978b; Famennian, Belgium), Deunff (1981; Givetian–Frasnian, France), Martin (1981, 1982b, 1985; Frasnian–Famennian, Belgium), Loboziak et al. (1983; Frasnian–Famennian, France),
Upper Devonian acritarch assemblages from Africa and the Middle East have been described by Jardiné (1972; Lochkovian–Famennian, Algeria), Jardiné et al. (1972, 1974; Lochkovian–Famennian, Algeria), Moreau-Benoit (1984, Givetian–Famennian, Libya), Paris et al. (1985, Emsian–Famennian, Libya), Streel et al. (1988, Eifelian–Famennian, northeast Libya), Ghavidel-syooki (1994; Frasnian–Famennian, northern Iran), Hashemi & Playford (1998; Upper Devonian, Iran), Ghavidel-syooki (2001; Frasnian–Famennian, central Iran), Ghavidel-syooki (2003; Lochkovian–Frasnian, southern Iran) and Ghavidel-syooki & Owens (2007; Frasnian–Famennian, northern Iran).

In Australia, Colbath (1990b) described a Givetian–Frasnian acritarch assemblage from the Canning Basin of Western Australia, and Playford (1981) and Playford & Dring (1981) described a Frasnian acritarch assemblage from the Carnarvon Basin, also in Western Australia. Li et al. (2002a) reviewed research on Devonian acritarchs in China, and details on Upper Devonian acritarchs were published by Gao (1986) and Lu & Wicander (1988).

Several general papers deal with the palaeobiogeographical distribution of acritarchs during the Late Devonian. Colbath (1990a) examined the biogeographical distribution of Frasnian assemblages based on 10 well-documented microfloras, all from open-shelf, cratonic deposits. Similarity in composition between the assemblages was computed using the Simpson Index, and then clustered using weighted average linkage pair-group analysis. Based on this analysis, Colbath concluded that the clustering reflected biogeographical, rather than local ecological differences between the assemblages. Earlier, Wood (1984) had discussed the stratigraphical, palaeoecological and palaeobiogeographical distribution of Umbrellasphaeridium deflandrei and Umbrellasphaeridium saharicum from North America and South America, as well as from Africa. Vanguestaine (1986b) synthesized 80 publications relating to Upper Devonian and Carboniferous acritarchs and their stratigraphical and palaeogeographical distribution. Vavrdová & Isaacson (1997, 1999, 2000) considered the previously established Umbrellasphaeridium saharicum Bioprovince (Wood 1984) as a possible indicator of a close connection.
between the eastern North American region and South America’s Central Andes, based on high palaeolatitude-generated cold-water currents. Finally, Clayton et al. (2002) discussed regional differences in Upper Devonian palynomorph assemblages from southwest Portugal, Algeria, Libya and North America.

The references listed above show that the majority of acritarchs had a global distribution during the Late Devonian, but with some evidence for an endemic province at high southern palaeolatitudes, and with periodic incursions of the high palaeolatitude assemblage into the low palaeolatitude regions of Laurussia and northern Perigondwanan areas (Vavrdová & Isaacson, 1999).

Based on analysis of data contained in the numerous publications listed above, plus the syntheses by Wood (1984), Vanguestaine (1986b), Streel et al. (1988) and Vavrdová & Isaacson (1997, 1999, 2000), Upper Devonian acritarchs can be categorized as cosmopolitan, those that occurred primarily in the low palaeolatitude region of Euramerica (Laurentia, Baltica, Avalonia), Australia and Iran, and those that were typically confined to the higher palaeolatitude Perigondwana region.

The majority of reported Frasnian and Famennian acritarchs can be considered cosmopolitan, ranging from the low to mid palaeolatitudes and into higher palaeolatitudes (60°S or higher). Furthermore, many of these species were restricted to the Late Devonian, or first appeared in the Mid Devonian in one region and extended their latitudinal and palaeogeographical range during the Late Devonian. Le Hérissé et al. (2000) list 60 acritarch species that are restricted to the Upper Devonian or extend slightly into the lowermost Carboniferous.

Cosmopolitan acritarchs are found at a number of localities in both the broadly defined Euramerican and Gondwanan regions, including Australia and China, and thus cover a wide range of palaeolatitudes. They include Chomotrietes vedugensis, Cymatiosphaera perimembrana, Daillydium pentaster, Dictyotidium litum, Diexallophasis remota, Gorgonisphaeridium ohioense, G. plerispinosum, Multiplicisphaeridium ramispinosum, Palacanthus ledanoisii, Polyedryxium pharaonis, Solipsphaeridium spinoglobosum, Stellinium comptum, S. micropolygonale, Tornacia sarjeantii, Unellium lunatum, U. piriforme, U. winslowiae, Veryhachium lairdii, V. pannuceum, V. polyaster and V. trispinosum complex. Other species reported from these areas are possibly endemic, but they may occur only in one or a
small number of localities and are not particularly common and so are not included here.

Some acritarch species, however, are abundant and seem to be limited to the low palaeolatitudes of the Euramerican region, Australia, Iran and China. These include, among others, *Craterisphaeridium sprucegrovense*, *Deltotosoma intonsum*, *Gorgonisphaeridium condensum*, *G. discissum*, *G. winslowiae*, *Lophosphaeridium diminutum* and *Papulogabata annulata*. There is a high degree of similarity between the Euramerican region and Australia and China, with 17 out of 48 species from the Frasnian of Western Australia (Playford 1981; Playford & Dring 1981) and 27 out of 29 species from China (Lu & Wicander 1988) also reported from Upper Devonian Euramerican acritarch assemblages.

Taxa recorded from Perigondwanan localities include *Crassiangulina tesselita*, *Horologinella horologia*, *H. quadrispina*, *Maranhites brasiliensis*, *M. mosesii*, *Pyloferites pentagonalis*, *Umbellasphaeridium deflandrei* and *U. saharicum*. Of these, *Crassiangulina tesselita*, *Horologinella horologia*, *H. quadrispina* and *Pyloferites pentagonalis* were apparently restricted to high palaeolatitude Perigondwana regions and were not dispersed into lower palaeolatitudes during the Late Devonian. *Maranhites brasiliensis*, *M. mosesii*, *Umbellasphaeridium deflandrei* and *U. saharicum*, however, appear to have been characteristic of, but not limited to high palaeolatitude Perigondwana regions during the Mid Devonian, but migrated into lower palaeolatitudes during the Late Devonian as shown by their occurrences in North America, Portugal and Spain (Wood 1984; González et al. 2005; Pereira et al. 2008.). Other species of *Maranhites* and *Umbellasphaeridium* have been reported from these regions, but we only list the two common species of each genus.

It should be noted that González (2009) proposed a reassessment of *Maranhites*, suggesting that many of the previously named species were not distinct taxa, but represented different ontogenetic stages of *Maranhites mosesii*. To address the implications of this reassessment is beyond the scope of this paper, and we are following past convention by listing previously named species of this genus.

In summary, the acritarch flora during the Late Devonian can be characterized as having had a large cosmopolitan element, as indicated by the wide palaeogeographical distribution of numerous species that are either stratigraphically long-ranging or
restricted to the Late Devonian. In addition, there is strong evidence for warm-water, low to mid palæolatitude oceanic interchange between the Euramerican region, Australia, Iran and China. Endemic acritarch assemblages also existed during the Late Devonian as seen by the high palæolatitude occurrences of several genera within the Perigondwana region. However, some characteristic high palæolatitude Perigondwana species were dispersed into mid to low palæolatitude Euramerican areas, possibly by cold-water gyres.

Synopsis of Devonian phytoplankton biogeography

Much has changed since the early attempts at reconstructing Devonian acritarch palæobiogeographical distributions. Palæogeographical maps for the Early, Mid and Late Devonian (Figs 9–11) show a Gondwana continent and associated seas located predominately at mid to high southern palæolatitudes, a continued closing of the Rheic Ocean between Gondwana and Laurussia with Gondwana continuing to move northward and resulting in a very narrow seaway by the end of the Devonian, and the movement and collision of several microcontinents and blocks. We can therefore discuss the distribution of acritarchs during the Devonian in terms of those that are cosmopolitan, those from generally low to mid palæolatitudes, and those from a high palæolatitude province. The apparent provincialism, however, might reflect local conditions or lack of geographic coverage and adequately described palynofloras.

During the Early Devonian, a mid palæolatitude province was present in Laurentia and Armorica and extended across North Africa. Although each region appears to have had some endemic species, a number of other species are found throughout this latitudinal belt, and as more localities are studied, the apparent provincialism diminishes. The seemingly endemic nature of some assemblages is probably due, in part, to lack of described material from well-dated sections. Among taxa that were seemingly restricted to particular regions during the Early Devonian, Schizocystia spp. have only been reported from north and west Gondwana. Other species that have a stratigraphical range restricted to the Lower Devonian and a cosmopolitan distribution include Demorhethium lappaceum, Riculasphaera fissa and Thysanoprobolus polykion.
As the Rheic Ocean continued to close, bringing Gondwana and Laurussia closer together during the Mid Devonian, a reasonably high degree of cosmopolitanism developed among acritarch assemblages, as shown by the numerous acritarch species in common between Laurussia (North America), Gondwana (primarily Argentina, Ghana, Libya, Algeria, Western Australia) and western China (Junggar Basin). A number of species, however, seem to have been endemic to the higher southern Gondwana palaeolatitudes.

During the Late Devonian, a large number of both stratigraphically long ranging species and many species that were restricted to the Late Devonian can be characterized as cosmopolitan. There is strong evidence for oceanic connections within the low palaeolatitude areas of the Euramerican region, Australia, Iran and China. There are also a number of endemic acritarchs that occur within the high palaeolatitude Perigondwana region. In addition, it appears that oceanic circulation patterns provided the means for dispersal of some characteristic high palaeolatitude Perigondwana species into low paleolatitude Euramerican areas.

Discussion

The review of phytoplankton biogeography presented above shows that a lot of relevant data from the Cambrian to the Devonian has been published since Colbath’s (1990a) assessment, some of it in passing in publications dealing with other aspects of Palaeozoic palynology, and some in papers with a biogeographical focus. Yet, we still do not fully understand the pattern of Palaeozoic phytoplankton biogeography or many of the controls influencing its distribution. In part, this is due to incomplete spatial datasets for many time periods. Almost nothing is known of Early–Mid Ordovician phytoplankton from the Appalachian margin of Laurentia, for example, at a time when the Perigondwana Province was present along the margin of Gondwana and adjacent Perigondwanan terranes. Similarly, very little has been published on late Cambrian marine phytoplankton from Laurentia and other areas, such as Australia. In part, our understanding of the patterns and factors influencing them is also hindered by biases introduced by sampling (e.g. of different facies) or by different taxonomic treatment of material, and by the difficulties of unravelling the complex interactions.
of various controls on phytoplankton distribution. Nevertheless, some common themes have begun to emerge.

**Latitude versus other controls**

Latitude is no longer seen as the primary factor influencing phytoplankton as it was, for example, in Cramer’s model (1971; Cramer & Díez 1972, 1974a, b) of Silurian phytoplankton distributions. Assemblages once regarded as being restricted to latitude-parallel climatic belts, such as Cramer’s *Deunffia*, *Domasia* and *Neovervychium carminae* biofacies, can now be shown, using more up-to-date palaeogeographical reconstructions, to occur along continental margins at both low and high palaeolatitudes, where their distribution is controlled by other factors. Besides latitude, factors that are now thought to have influenced the spatial distribution of Palaeozoic phytoplankton include depositional environments, differences between water masses of oceanic and cratonic settings, and oceanic circulation patterns. Oceanic circulation, for example, has been invoked by a number of authors to explain, at least in part, the distribution patterns that they discerned. Hence, Playford *et al.* (1995) and Tongiorgi *et al.* (1995, 1998) proposed that oceanic circulation was at least a partial control on spatial distribution patterns of genera and species in the Early–Mid Ordovician, and Le Hérissé & Gourvennec (1995) suggested the same to explain patterns in the mid Silurian (late Llandovery–Wenlock).

Nevertheless, the idea that phytoplankton distribution might, at least in part, reflect latitude has persisted, and Li & Servais (2002), for example, considered that some acritarch taxa might be restricted to certain palaeolatitudinal belts. They suggested that *Arbusculidium filamentosum* and the *Coryphidium-Vavrdovella* and *Arkonia-Striatotheca* generic complexes were most common at high southern palaeolatitudes during the Early to Mid Ordovician (essentially Arenig), from polar regions up to 60°S and more rarely up to 30°S. They also argued that although galeate and diacromorph acritarchs were to be found at high southern palaeolatitudes, they were more likely to be recorded from mid to low palaeolatitudes around 45–20°S. Furthermore, they noted that the acritarch genera *Aryballomorpha*, *Athabascaella* and *Lua*, which characterized Volkova’s (1997) warm-water assemblage, also occurred at low to mid palaeolatitudes.
Li & Servais (2002) were clear that their model was a first tentative attempt to identify climate-related latitudinal distributions among phytoplankton for the Early–Mid Ordovician and was subject to modification by subsequent reinterpretations of palaeogeography or further data on distributions. This has proved to be the case. Arbusculidium filamentosum and species of the Coryphidium-Vavrdovella and Striatotheca-Arkonia complexes are significant, if not always numerous constituents of Arenig assemblages from the Yangtze Platform (Li 1987, 1990; Brocke et al. 1999, 2000; Tongiorgi et al. 1995, 1998, 2003a; Li et al. 2002b; Yan et al. 2011), located at low palaeolatitudes in the reconstructions of Torsvik & Cocks (2013). On the other hand, Athabascaella has been recorded from lowest Ordovician (Tremadocian) successions deposited at high southern palaeolatitudes, from Belgium (uppermost Tremadocian, Avalonia, Breuer & Vanguestaine 2004) and Tunisia (lower Tremadocian, Gondwana, Vecoli 2004). One genus not included in Li & Servais’ (2002) analysis is Frankea, which Colbath (1990a) showed as being restricted to palaeolatitudes of about 60°S or higher. Frankea still appears to have had a spatial distribution that was restricted to relatively high palaeolatitudes during the Early–Mid Ordovician (Fig. 5). It is unreported from Baltica or low palaeolatitude Perigondwanan assemblages such as those from South China. The lowest palaeolatitude at which the genus occurred during the Arenig (Floian–early Darriwilian) was between about 45°S and 60°S in Avalonia (eastern Newfoundland: Dean & Martin 1978; the Isle of Man: Molyneux 1999; Chadwick et al. 2001; the English Lake District: Cooper et al. 1995, 2004; Molyneux 2009; Belgium: Martin 1977; Martin & Rickards 1979; Vanguestaine 1986a) and on the western margin of Gondwana (Saudi Arabia: Le Hérissé et al. 2007).

Distal versus proximal (oceanic versus cratonic) distribution patterns

One of the themes to have emerged from recent assessments of Palaeozoic phytoplankton biogeography is the spatial differentiation between assemblages from distal, oceanic settings and those from more proximal cratonic settings. Changes in the diversity of phytoplankton assemblages along onshore–offshore gradients are well documented. Assemblages from proximal and deep basinal settings are generally characterized by low diversity and the predominance of relatively simple forms such...
as leiospheres (sphaeromorph acritarchs). In contrast, the most diverse assemblages
with a range of often complex morphospecies are generally associated with fully
marine, shelf successions. The evidence to emerge from analysis of Palaeozoic
phytoplankton biogeography is that the taxonomic character of assemblages changes
along with diversity. Examples include the spatial differentiation of the
*Neoveryhachium carminae* and *Deunffia-Domasia* biofacies along the eastern margin
of Laurentia (Le Hérissé & Gourvennec 1995), and distinction between ocean-facing
assemblages with Perigondwanan characteristics and more proximal assemblages with
Baltic characteristics in the Lower–Middle Ordovician of South China (Playford *et al.*

A further example is provided by the distinction between Lower–Middle Ordovician
phytoplankton assemblages from the intracratonic Canning and Georgina basins of
north-western and central Australia (Playford & Martin 1984; Playford & Wicander
1988; Quintavalle & Playford 2006a, b) and those from the low palaeolatitude
Perigondwanan region of South China (*Fig. 5*). For the most part, assemblages from
the Canning and Georgina basins lack the key Perigondwanan Lower–Middle
Ordovician marker genera. The exception is *Striatotheca*, but even this genus is only
present in the middle to upper Darriwilian *Aremoricanium solaris* and *Dactylofusa
striatogranulata* biozones of the Canning Basin (Quintavalle & Playford 2006b, text-
figs 1, 6). In contrast, *Striatotheca* is present from the lower Floian upwards in South
China (Yan *et al.* 2011).

As well as the key Perigondwanan markers, *Arbusculidium, Coryphidium* and
*Striatotheca*, assemblages from South China include species of other genera that have
well-documented Perigondwanan and/or Baltic distributions. Among them are
species of diacromorph acritarch genera (*Acanthodiacrodium, Actinotodissus, 
Dicrodiacrodium*), galeate acritarchs (*Caldariola, Cymatiogalea, Stelliferidium*), and
species of *Adorfia, Arkonia, Aureotesta, Barakella, Cycloposphaeridium, Ferromia, 
Liliosphaeridium, Picostella, Stellechinatum, Tongzia, Tranvikium, Vavrdovella* and 
*Vogtlandia*. Altogether, 35 genera present in South Chinese assemblages, including
those listed above, have not been recorded from the Canning or Georgina basins
(Table 2).

In contrast, assemblages from the Coolibah Formation of the Georgina Basin, of Early
Ordovician age (Zhen *et al.* 2003, fig. 6), contain *Dictyodiscus, Pytinomorpha, 
*
Tunisphaeridium and Uncinisphaera (Playford & Wicander 1988). None of these genera have been recorded from South China (Table 2), although Uncinisphaera has been recorded from South Wales (Molyneux 1987) at about the same level and higher, and from late Floian to Darriwilian successions in Bohemia (Vavrdová 1990a, b), North Africa (Vecoli 1999), Saudi Arabia (Le Hérissé et al. 2007) and Oman (Molyneux et al. 2006; Rickards et al. 2010).

The succession studied by Quintavalle & Playford (2006a, b) in the Canning Basin comprises the Willara, Goldwyer and basal Nita formations, and covers a longer stratigraphical interval than that investigated in the Georgina Basin, extending from the middle Floian to the upper Darriwilian. Genera recorded from the Canning Basin that have not been recorded from South China are Dilatisphaera, Pylantios, Pytinomorpha, Sertulidium, Tribulidium, Tunisphaeridium and Uncinisphaera (Table 2). Of these, Pylantios, Pytinomorpha, Sertulidium and Tribulidium appear to have been endemic to the intracratonic Australian basins. Quintavalle & Playford (2006b) noted that assemblages from the Canning Basin differed from coeval suites of the Perigondwana Province in lacking diacromorph and trispinose veryhachid acritarchs, in having moderate to high frequencies of quadrate veryhachid and herkomorph acritarchs, and in yielding an abundance of forms with pylomes.

Cluster analyses of genera and species in Dapingian–lower Darriwilian assemblages from the Canning Basin and adjacent regions of the western Perigondwanan margin highlight the distinctive nature of the Canning Basin microflora (Fig. 12). The composition of the acritarch assemblage from the Comasphaeridium setaricum Biozone of the Canning Basin, of late Dapingian–early Darriwilian age (Quintavalle & Playford 2006b), is compared with approximately coeval assemblages from the Saq Formation of Saudi Arabia (Le Hérissé et al. 2007), from the Taurus Range (Taurides Terrane) and Border Folds (Arabian Plate) of Turkey (Paris et al. 2007), from the Zard-Kuh Formation, Palynological Zones O3 and O4, of the Zagros Basin (Arabian Plate: Ghavidel-syooki 1997) and the Lashkarak Formation, zones III (upper) and IV, of the Central Alborz Range, Iran (Alborz Terrane: Ghavidel-syooki 2006), from Pakistan (Karakorum Terrane: Tongiorgi et al. 1994; Quintavalle et al. 2000) and from South China (Brocke et al. 1999, 2000; Tongiorgi et al. 2003a; Yan et al. 2011). In each case, the Canning Basin is clearly separated from and does not cluster with the Perigondwanan regions.
A further point to note in connection with acritarch records from the Canning Basin is that, whereas species such as *Pirea ornata*, *Dasydorus cirratus* and *Striatotheca rarirrugulata* are present in South Chinese assemblages from the Floian or Dapingian onwards (Brocke et al. 2000; Tongiorgi et al. 1995, 2003a; Yan et al. 2011), the FADs of these or similar forms in the Canning Basin are in the Darriwilian. The FAD of *Pirea cf. P. ornata* is in the *Sacculidium aduncum* Biozone, which Quintavalle & Playford (2006b, text-fig. 6) correlate with the *Didymograptus artus* Graptolite Biozone of early Darriwilian (early Llanvirn) age, and the FADs of *Dasydorus cirratus* and *Striatotheca rarirrugulata* are in the *Aremoricanium solaris* Biozone, of mid Darriwilian (mid Llanvirn) age and correlated with the upper *D. artus* to lower *Didymograptus murchisoni* biozones.

Although some biogeographical differentiation is apparent between South China and the intracratonic Australian basins, such differentiation between ocean margin and cratonic settings is not so evident elsewhere. The Silurian intracratonic basins of the South American part of Gondwana are a case in point. Assemblages from the Paranaíba and Paraná basins, for example, reviewed by Rubinstein (1997), comprise species that had widespread distributions during the late Llandovery–early Wenlock, including along the margins of Gondwana and in some cases in Laurentia. These basins might have had better connections to more oceanic settings than other intracratonic basins, and might have been connected directly to the basins of north and west Africa, as suggested by Rubinstein (1997), or to the ocean-facing Central Andean Basin (e.g. Díaz-Martínez et al. 2011, fig. 1).

**Continental margin distributions**

A further theme to emerge from recent work is that phytoplankton assemblages with particular characteristics can be traced along continental margins, often crossing palaeolatitude. One of the best examples is the Early to Mid Ordovician Perigondwana Province (Fig. 5), but other examples include the *Neoveryhachium carminae* and *Deunffia-Domasia* biofacies (Fig. 7).

As discussed above, taxa that are characteristic of the Perigondwana Province occur along the margin of Gondwana from high to low palaeolatitudes. Cramer & Diez (1974b) referred to this as the “*Coryphidium bohemicum* province”, but it is clear...
from their description of it as being Lower Ordovician and occurring in North Africa, Arabia, Bohemia and France, as well as the reference to Vavrdová’s (1965, 1966, 1972, 1974) papers and the inclusion of C. bohemicum in its name, that they were referring to the same biogeographical unit. Intriguingly, Cramer & Díez (1974b, p. 142) also referred to the C. bohemicum province as apparently being present in Victoria, Australia, on the north-eastern margin of the Gondwanan craton, although they provided no further information and cited no references. If so, the province might be truly Perigondwanan, extending around the northern promontory of Gondwana from South China in the west to Argentina in the east (Fig. 5). Data from Lower–Middle Ordovician successions in south-west Australia, Tasmania and/or New Zealand ought to provide information to test this suggestion.

The distribution of the Perigondwana Province, however, is not simply restricted to the continental margin. Key taxa used to define the province, namely species of Arbusculidium, Coryphidium and Striatotheca, also occur in terranes derived from Gondwana, notably Avalonia. This raises other questions. In the reconstructions by Torsvik & Cocks (2013, fig. 12), Avalonia had separated from Gondwana long before the late Dapingian (469 Ma) and had moved northwards so that by then it straddled the same mid southern palaeolatitudes as Baltica (Fig. 5). Yet none of the key Perigondwana Province markers are known from Baltica, not even from the pale grey and black silty shales of the Tøyen Formation, of latest Tremadoc–mid Arenig age, which were deposited on the continental slope that formed the western edge of the Baltic platform (Bruton et al. 2010). Tongiorgi et al. (2003b), for example, noted that acritarch assemblages from the Galgeberg Member, which comprises the upper part of the Tøyen Formation in the Oslo region and is of Billingen to early Volkhov age (late Floian to early Dapingian, or mid Arenig), lacked species of Arbusculidium, Aureotesta, Coryphidium and Striatotheca. On the other hand, all species identified in the Galgeberg Member were known from coeval levels on the Yangtze Platform of South China, where, of course, the key Perigondwana markers are also present. If Tongiorgi et al.’s (2003a) interpretation of Perigondwana-type assemblages as distal oceanic assemblages applies, Perigondwana-type assemblages might be expected to occur in the deep-water successions of Baltica, but as yet there is no evidence that they do. So why are Perigondwanan assemblages characteristic of Early–Mid Ordovician Avalonia but not known from Baltica, although these palaeocontinents are
interpreted as being at about the same palaeolatitude and deep-water facies have been sampled in Baltica? Did oceanic circulation mean that the distribution of Perigondwanan assemblages by-passed Baltica, or did other factors come into play? Did historical contingency and the original derivation of Avalonian assemblages from Gondwana have something to do with this, and if so what mechanisms maintained the Perigondwanan affinities of Avalonian microfloras?

Changes in biogeographical ranges through time

One thing that becomes apparent when Palaeozoic phytoplankton distributions are examined in detail is that biogeographical ranges change through time, or at least can appear to do so. The Ordovician acritarch *Loeblichia*, for example, has been recorded from Baltica in the lower–middle Floian (Raevskaya 1999), from Baltica, South China and Australia (Georgina Basin) in the upper Floian–lower Dapingian (Brocke et al. 2000; Playford & Wicander 1988; Raevskaya et al. 2004; Tongiorgi et al. 1995, 2003a, b; Yan et al. 2011), and from South China and Australia (Canning Basin) in the Dapingian–lower Darriwilian (Brocke et al. 2000; Quintavalle & Playford 2006a, b; Tongiorgi et al. 2003a; Yan et al. 2011). Hence, its biogeographical range seems to shift eastwards from the early Floian to the early Darriwilian, i.e. through the Arenig. A further example is provided by *Neoveryhachium carminae*, which was apparently endemic to Gondwana in the Late Ordovician (see Late Ordovician above), but had a more widespread distribution in the mid Silurian (*Fig. 7*).

These apparent shifts in biogeographical range might, of course, be artefacts, introduced, for example, by sample bias, but the possibility that ranges might expand and contract is not generally acknowledged in papers addressing Palaeozoic phytoplankton biogeography. From a practical standpoint, there are implications for defining provinces or other biogeographical units. If, for example, biogeographical units are based on time slices that are too broad, or even mixed as in the case of Li & Servais’ (2002) study, where data from Volkova’s (1997) late Tremadocian warm-water assemblage was combined with data from the Arenig Perigondwana Province to determine latitudinally restricted ranges, biogeographical signals might be lost.

Cosmopolitanism, endemism and community breakdown
Unsurprisingly perhaps, Palaeozoic phytoplankton assemblages usually exhibit a degree of both cosmopolitanism and endemism, with cosmopolitan species occurring alongside endemic forms, but the degree to which assemblages might be described as cosmopolitan or endemic varies. The review of Late Ordovician biogeography presented above suggests that assemblages with a high degree of cosmopolitanism in the Katian (late Caradoc to pre-Hirnantian Ashgill) were succeeded by assemblages showing a high degree of endemism in the Hirnantian (Fig. 6). However, very few attempts, if any, have been made to quantify the degree of endemism or to determine how it might change through time. Quantitative data on these aspects are vital for an understanding of how changes in Palaeozoic phytoplankton biogeography might respond to changes in environmental parameters.

In a study of the response of marine diatom communities to climate change during the past 250 kyr, Cermeño et al. (2010, fig. 4) showed cycles in which community similarity, calculated using the Jaccard and Bray-Curtis indices, decreased and then recovered coincident with changes in atmospheric CO2 concentration and atmosphere/ocean physical forcing. In two out of the three localities that they studied, community breakdown, indicated by a decrease in similarity indices, showed a clear coincidence with reductions in atmospheric CO2 concentration, and community recovery with its increase. The questions this raises are whether other phytoplankton groups show similar community dynamics in response to climatic perturbations, and if so whether this also applies throughout geological time and at different timescales. Is the apparent increase in phytoplankton endemism in the Hirnantian part of a similar community response to the climatic perturbations of the time? Does community departure from similarity, i.e. increased biogeographical differentiation, correlate with other environmental perturbations such as changes in sea level, and if so is there a link between the magnitude of the disturbance and extinction, as opposed to increased endemism? Addressing these questions will require a more quantitative approach to Palaeozoic phytoplankton biogeography than has been the case up till now.

One of the conclusions reached by Colbath (1990a) was that progress in the analysis of the Palaeozoic phytoplankton biogeography would require the application of numerical methods, but few studies have undertaken quantitative analysis of distribution patterns. The most notable exceptions are Colbath’s (1990a) own analysis of Frasnian distributions, which used weighted average pair-group clustering...
based on the Simpson index of similarity, Le Hérissé & Gourvennec’s (1995) analysis of late Llandovery–Wenlock distributions and Le Hérissé et al.’s (1997a) analysis of late Silurian and Devonian distributions, which both used cluster analysis based on the Jaccard index.

In a paper dealing with the methods used to delineate present-day biogeographical regions, Kreft & Jetz (2010) noted that, historically, such regions had been based on qualitative assessments of criteria such as levels of endemism, but that this had set constraints on their utility and replicability and had introduced inconsistencies and confusion. They observed (p. 2031) that “...different schools and traditions in biogeography – as well as varying extent, grain and quality of data – have left the biogeographical regions of the world ambiguously defined...”. They also noted that multivariate methods overcame some of these difficulties, a particular strength being their ability to produce replicable results, and explored the relative usefulness of ordination and clustering methods, recommending the use of non-metric multidimensional scaling (NMDS) as an ordination method and UPGMA (unweighted pair-group method using arithmetic averages) clustering. Some of the criticisms levelled by Kreft & Jetz (2010) at traditional methods of delineating present-day biogeographical regions could also be levelled at approaches to Palaeozoic phytoplankton biogeography, with the inference that the routine application of numerical methods might at least provide a transparent, reproducible means of addressing biogeographical questions.

Conclusions

Since Colbath’s (1990a) assessment of Palaeozoic phytoplankton was published, more data have become available on spatial distributions and we have reached a better understanding of both phytoplankton distribution patterns and the factors that might influence them. We perhaps appreciate better the fact that distribution patterns are the result of many interacting factors, including palaeolatitude and therefore presumably palaeotemperature, oceanic circulation patterns, the disposition of continents, differentiation between oceanic and more cratonic (or distal and proximal) assemblages, and sedimentary environments and facies, the last, for example, in the case of the mid Silurian Neovervachium carminae and Deunffia-Domasia biofacies.
There are also indications that biogeographical ranges of taxa might shift over time, so defining biogeographical units requires an appreciation of this. Even so, many uncertainties remain. Some of these factors, for example oceanic circulation, are themselves interpretations and introduce the danger of circularity into the argument if they cannot be tested independently. How, for example, do we explain the absence of key Perigondwanan taxa from Early–Mid Ordovician deep-water settings around Baltica, in contrast to their contemporaneous presence in Avalonia at similar palaeolatitudes and from lower palaeolatitudes around Gondwana? Do we invoke an oceanic circulation that somehow by-passed Baltica to explain this pattern, and if so is there independent evidence to substantiate this?

Moving our understanding of Palaeozoic phytoplankton biogeography forward will require: (i) targeted investigation of regions and time periods for which no or little data exist, for example the Cambrian of Laurentia or Lower–Middle Ordovician deep-water successions in Australia; (ii) quantitative analysis of data to investigate, for example, how similarity varies through time and how this might correlate with other datasets such as carbon isotope stratigraphy or sea level; (iii) rigorous application of well-defined time slices to investigations so that we are comparing coeval assemblages, at least within the limits of resolution. Applying these principles might enable us to discern more biogeographical patterns, and perhaps more importantly, might also enable us to investigate linkages between environmental parameters and phytoplankton dynamics, including endemism and the development of provincialism, decreases in community similarity and its recovery, and the turnover, origination and extinction of genera and species.

Finally, there is much current interest in the biogeography of extant microbial organisms, and, in particular, whether the processes that determine the biogeographical distributions of organisms with a body size of about 2 mm or less differ fundamentally from those that influence the biogeography of larger organisms (Fontaneto 2011). At the heart of this debate is the question of whether the biogeography of microorganisms conforms to the ubiquity hypothesis (also known as EiE, from the paradigm that ‘everything is everywhere, but the environment selects’) or whether some other hypothesis such as the ‘moderate endemcity model’ applies (Fontaneto & Brodie 2011). Such questions might well inform our approach towards phytoplankton biogeography in the Palaeozoic. At the same time, this raises a further
question of whether we can use the fossil record of phytoplankton to investigate their biogeography under conditions that differ from those of the present day and at timescales beyond those of direct human observation, and thereby reach some understanding of fundamental biogeographical and macroecological processes and principles affecting these organisms.

We thank Jeremy M. Conner, Central Michigan University, for drafting Figures 9–11, and Paul Strother and Claudia Rubinstein for their reviews of the manuscript. Figures 1, 3, 5, 7 and 8 were produced using BUGPLATES software downloaded from http://www.geodynamics.no/Web/Content/Software/; Figures 2, 4, 6 and 12 were produced using PAST software downloaded from http://folk.uio.no/ohammer/past/. Stewart Molyneux publishes by permission of the Executive Director, British Geological Survey, Natural Environment Research Council.
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Figure and Table captions

**Figure 1.** Distribution of *Skiagia*-bearing assemblages plotted on a palaeogeographical reconstruction at about the base of Stage 5 (510 Ma). Localities plotted from Moczydłowska & Zang (2006, figs 1, 2), with the addition of New Brunswick (Palacios *et al.* 2011) and the Amadeus Basin, central Australia (Zang & Walter 1992). Map from BUGPLATES, Galls Projection.

**Figure 2.** Seriation of acritarch genera from the Tempe Formation of the Amadeus Basin (AB), central Australia, dated as early mid Cambrian (Zang & Walter 1992), and from *Skiagia*-bearing assemblages of equivalent age from Baltica (S: Sweden, Eklund 1990, Assemblage D - top Lingulid Sandstone, Glauconite Sandstone, *oelandicus* Mudstone; EEP: East European Platform, Moczydłowska 1998, *oelandicus* Superzone, *insularis* and *praecurrens* zones).


**Figure 4.** Two-way Q- and R-mode cluster analysis (UPGMA algorithm, Jaccard Index) of Upper Cambrian (Furongian) acritarch genera. Localities and data sources as for Figure 4.
**Figure 5.** Early–Mid Ordovician acritarch localities and the distribution of the Perigondwana and Baltic phytoplankton provinces plotted on a palaeogeographical reconstruction for the late Dapingian (late Arenig, 469 Ma). Assemblages from South China (22) and northwest Argentina (24) contain taxa with Perigondwanan affinities as well as those with Baltic affinities. Coeval assemblages from the Canning Basin (23) are distinct from the Perigondwanan and Baltic microfloras (see Discussion and Fig. 12).


**Figure 6.** Pairwise comparisons of taxonomic similarity for latest Katian and Hirnantian acritarch assemblages from Anticosti Island, Estonia and Gondwana, based on ranges shown in Delabroye et al. 2011a, figs 5, 6, 7 and 8, and showing decreasing similarity through the Hirnantian glaciation.
Figure 7. Distribution of *Neoveryhachium carminae*, *Domasia* and *Deunffia* in the mid Silurian (late Llandovery – early Wenlock) plotted on a late Llandovery (430 Ma) palaeogeographical reconstruction. Distributions of *Dactylofusa maranhensis*, the *Estiastra–Hoegklintia–Pulvinosphaeridium* association and *Dilatisphaera williereae* based on Le Hérissé & Gourvennec (1995, fig. 2). Data sources. 


Figure 8. Late Silurian acritarch biogeography plotted on a palaeogeographical reconstruction for the late Ludlow (419 Ma). After Le Hérissé *et al.* (1997a, fig. 1), with additional records of *Visbysphaera bonita* and *V. jardinei* from the Central Andean Basin, Bolivia (Cramer *et al.* 1974c), and the Pomeranian Caledonides, Poland (Jachowicz 2000; Le Hérissé 2002).

Figure 9. Early Devonian palaeogeography, modified from Le Hérissé *et al.* (2009) and Rubinstein *et al.* (2008b), and based on the reconstruction of Cocks & Torsvik (2002, fig. 8). The solid circles indicate the major Lochkovian localities from which well-preserved and diverse acritarch assemblages have been published and are
discussed in the text. These include Laurentia: Oklahoma, U.S.A.; Armorica: Crozon peninsula of France, and northern Spain; Gondwana: Algerian Sahara and western Libya, Africa; Argentina, Bolivia, Brazil, and Uruguay, South America.

Figure 10. Mid Devonian (Givetian) palaeogeography, modified from Scotese & McKerrow (1990, fig. 15). The solid circles indicate the major Middle Devonian (Eifelian, Givetian) localities from which well-preserved and diverse acritarch assemblages have been published and are discussed in the text. These include Laurentia: Iowa, Kentucky, Ohio, U.S.A., and Ontario, Canada; Junggar Terrane: Junggar Basin, western China; Armorica: France and Germany; Gondwana: Canning Basin, Western Australia; Algeria, Libya, and Ghana, Africa; Argentina, Bolivia, Brazil, and Paraguay, South America.

Figure 11. Late Devonian (Famennian) palaeogeography, modified from Scotese & McKerrow (1990, fig. 16). The solid circles indicate the major Late Devonian (Frasnian, Famennian) localities from which well-preserved and diverse acritarch assemblages have been published and are discussed in the text. These include Laurentia: Indiana, Iowa, Kentucky, Ohio, Tennessee, U.S.A., Alberta, Saskatchewan, Canada; North China: Xinjiang, China; Armorica: Belgium, France, Germany, Poland, and Spain; Gondwana: Canning Basin, Western Australia; Algeria, Iran, and Libya, Africa and the Middle East; Bolivia, Brazil, and Paraguay, South America.

Figure 12. Cluster analysis (UPGMA algorithm, Jaccard Index) comparing the acritarch assemblage from the late Dapingian – early Darriwilian *Comasphaeridium setaricum* Biozone of the intracratonic Canning Basin of Australia, with coeval assemblages from the western margin of Gondwana and adjacent Perigondwanan terranes. A. Genera; B. Species. See text for data sources and discussion.

Table 1. Jaccard similarity coefficients for Upper Cambrian data used in cluster analysis (Fig. 4). Lowest values (least similarity) are indicated by grey-filled cells. In
all cases, either Missouri/Arkansas (Laurentia), Kolguev Island (Baltica) or NW Argentina is least similar to other regions.

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Table 1. Jaccard similarity coefficients for Upper Cambrian data used in cluster analysis (Fig. 4). Lowest values (least similarity) are indicated by grey-filled cells. In all cases, either Missouri/Arkansas (Laurentia), Kolguev Island (Baltica) or NW Argentina is least similar to other regions.
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510 Ma (early Middle Cambrian, base Stage 5)

Laurentia
1. Svalbard
2. North Greenland
3. NW Scotland

Baltica
4. Denmark
5. Norway
6. Sweden
7. East European Platform

Gondwana/Perigondwana
8. Ireland
9. England and Wales
10. Belgium
11. Spain
12. New Brunswick
13. Arrowie Basin
14. Stansbury Basin
15. Amadeus Basin

Molyneux, Delabroye, Wicander & Servais Fig. 1
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Molyneux, Delabroye, Wicander & Servais Fig. 2
469 Ma (late Dapingian)

- Perigondwana Province
- Baltic Province
- Assemblages with Perigondwanan and Baltic taxa
- Intracratonic Australian basin microflora (Canning Basin)

Northern limit of Frankea

Avalonia
1. Eastern Newfoundland
2. Southern Ireland
3. Isle of Man
4. English Lake District
5. South Wales
6. Belgium

Baltica
7. Norway
8. Sweden
9. Estonia
10. Russia (Baltic)
11. Russia (Archangel)

Gondwana/Perigondwana
12. North Africa
13. Saxo-Thuringia
14. Sardinia
15. Perunica
16. Turkey (Taurides)
17. Turkey (Arabian Plate)
18. Iran (Alborz)
19. Iran (Zagros)
20. Saudi Arabia
21. Pakistan
22. South China
23. Canning Basin
24. Argentina

Molyneux, Delabroye, Wicander & Servais Fig. 5