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

Stewart G. Molyneux [1]*, Aurélien Delabroye [2, 3],
Reed Wicander [4] & Thomas Servais [2]

[1] *British Geological Survey, Keyworth, Nottingham NG12 5GG, U.K. (e-mail: sgm@bgs.ac.uk)*

[2] *UMR 8217 Géosystèmes, CNRS-Université de Lille1, Cité Scientifique, 59655 Villeneuve d'Ascq Cedex, France (e-mail: thomas.servais@univ-lille1.fr)*

[3] *Ichron Limited, Century House, Gadbrook Business Centre, Northwich, Cheshire, CW9 7TL U.K. (email: aurelien.delabroye@ichron.com)*

[4] *Department of Geology, Central Michigan University, Mt. Pleasant, MI 48859, U.S.A. (e-mail: reed.wicander@cmich.edu)*

*Corresponding author

| | |
|---|---|
| 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 Zygnematophyceae (Colbath & Grenfell 1995; Grenfell 1995; Le Hérissé *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 (1990*a*) 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* [*Micrhystridium*] *lanatum*, *Asteridium* [*Micrhystridium*] *tornatum*, *Globosphaeridium* [*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, 1978*a*; Ribecai & Vanguestaine 1993; England and Wales: Downie 1984; Upper Silesia: Moczydłowska 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 *Fimbriaglomerella* 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 & Díez (1974*a*, *b*) distinguished an African Palynological Unit, otherwise termed the *Coryphidium bohemicum* Province (Cramer & Díez 1974*b*), and an American Palynological Unit, described as having a "profoundly different" acritarch assemblage from that of the *Coryphidium bohemicum* Province (Cramer & Díez 1974*b*, 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 20$^{th}$ 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. destombesii*. 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 (1982*a*) 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 (1982*a*, p. 38) argued that the Mediterranean Province should include eastern Newfoundland, England and Wales, Spain, France, Belgium, Bohemia, North Africa and northwest Argentina. Martin (1982*a*) 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 (1982*a*) 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

289 diacromorph acritarchs, on the grounds that none of these genera had been reported
290 from Baltic Province localities. In contrast, he noted that supposedly characteristic
291 Baltic taxa such as species of *Baltisphaeridium*, *Goniosphaeridium* and
292 *Peteinosphaeridium* had been reported from Mediterranean Province localities.

293 At about the same time, Albani (1989) noted that Arenig acritarch assemblages from
294 Sardinia showed clear affinities with Vavrdová's Mediterranean Province, but
295 commented that the term 'Perigondwanian Palaeoprovince' was more appropriate,
296 referring to Martin's (1982*a*, *in* Martin & Dean 1988) earlier observations. Like Li
297 (1989), Albani (1989) considered the genera *Arbusculidium*, *Coryphidium* and
298 *Striatotheca* to be characteristic of the province, but also added the diacromorph
299 genera *Acanthodiacrodium* and *Dasydiacrodium*.

300 The term 'Perigondwanian Palaeoprovince' and variants have been used by most
301 subsequent workers, although Vavrdová (1997) introduced the '*Coryphidium*
302 *bohemicum* acritarch bioprovince' to cover essentially the same area during the same
303 time period. Furthermore, use of the term 'Mediterranean' has persisted in some of
304 the literature. Playford *et al*. (1995), for example, used 'Mediterranean' to delineate a
305 subprovince of the Perigondwana Province, comprising the area originally specified
306 by Vavrdová (1974) with the additions of England and Wales, the Arabian peninsula,
307 eastern Newfoundland, southern Turkey and Karakorum (Pakistan). South America
308 and South China were identified as separate Perigondwanan subprovinces. Also, from
309 1998 onwards, Tongiorgi and his co-workers (Tongiorgi *et al.* 1998, 2003*a, b*;
310 Tongiorgi & Di Milia 1999) reverted to use of the term 'Mediterranean Province'. In
311 this paper, we use the term 'Perigondwana Province' to refer to the biogeographical
312 unit defined by the distribution of the genera indicated above, principally
313 *Arbusculidium*, *Coryphidium* and *Striatotheca*. As depicted in Figure 5, the
314 Perigondwana Province extended along the margin of Gondwana from North Africa
315 through southern Europe and the Middle East to Pakistan (Karakorum Terrane), and
316 included Avalonia, South China and northwest Argentina (see also Playford *et al*.
317 1995; Tongiorgi *et al.* 1995; Vecoli 1999, fig. 9).

318

319 *Baltic Province*

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*a*; 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*

386 [*Sacculidium*] *aduncum*, *Baltisphaeridium*? *coolibahense*, *Gorgonisphaeridium*
387 *pusillum*, *G. miculum*, *Loeblichia heterorhabda*, *Polyancystrodorus radiosus* and *P.*
388 *taleatus*). A smaller component (8.9%) comprised species with Baltic affinities such
389 as *Ampullula suetica*.

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

402 Tongiorgi *et al*.'s (1995) initial investigation was based on only one sample, but the
403 biogeographical affinities of phytoplankton from South China were subsequently
404 investigated further using more extensive datasets. Hence, Tongiorgi *et al*. (1998)
405 documented assemblages with different affinities from the Arenig of the Yangtze
406 Platform. Taxa that are characteristic of the Perigondwanan assemblage dominate
407 microfloras from the middle Arenig *Azygograptus suecicus* Biozone (lower part of the
408 Dawan Formation), accompanied by rare Baltic elements and a number of
409 cosmopolitan taxa (Tongiorgi *et al*. 1998, p. 186). In contrast, assemblages from the
410 upper Arenig *Undulograptus austrodentatus* Biozone contain taxa such as
411 *Liliosphaeridium kaljoi* and other Baltic species, with the Baltic component entirely
412 substituting the Perigondwanan taxa in the upper part of the section, near the top of
413 the Arenig (Tongiorgi *et al*. 1998, pp. 186, 187). Consequently, Tongiorgi *et al*.
414 (1998) concluded that inclusion of South China in the Perigondwana Province could
415 only be confirmed for the earlier Arenig.

416 The change in biogeographical affinity that Tongiorgi *et al*. (1998) observed up-
417 section, however, is not so apparent elsewhere in South China. Brocke *et al*. (2000),
418 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*. (2003*a*) 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*.? *spiraliculum* 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 2006*a*, *b*), Oman (Rickards *et al*. 2010), South China (Li 1990; Yan *et al*. 2011), and possibly Argentina (Achab *et al*. 2006) and Bohemia (Vavrdova 1990*a*), demonstrating that the genus had a wide biogeographical range across palaeolatitude.

*Factors controlling Early to Mid Ordovician acritarch provincialism*

Cramer & Díez's (1974*a*, *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 & Díez (1974*b*), 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*. (2003*a*), 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*. (2003*a*) 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

549 Sichuan and northern Guizhou sections (Brocke *et al.* 2000) was attributed to their
550 more distal locations so that more proximal shelf conditions never developed.

551 Tongiorgi *et al*.'s (2003*a*) explanation for the upward change from Perigondwanan to
552 Baltic microfloras on the Yangtze Platform introduces the problem of discriminating
553 between biogeographical and palaeoecological controls. Changes in the composition
554 of Palaeozoic phytoplankton assemblages along proximal–distal transects are well
555 documented (Jacobson 1979; Dorning 1981; Vecoli 2000, 2004; Li *et al*. 2004;
556 Molyneux 2009), so the change from Perigondwanan to Baltic microfloras recorded
557 by Tongiorgi *et al.* (2003*a*) might be influenced by ecological factors as much as
558 biogeography, or perhaps by a combination of ecological and biogeographical factors.
559 Reflecting on this to some extent, Tongiorgi *et al*. (2003*a*) stated that they were
560 inclined to abandon the terms 'Mediterranean Province' and 'Baltic Province', at least
561 for the Arenig, in favour of 'Mediterranean palynoflora' and 'Baltic palynoflora'.
562 The latter terms were considered to be more in keeping with a role for environmental
563 and ecological factors as controls on assemblage composition. The Mediterranean
564 palynoflora corresponded to the "...phytoplankton of the early Arenig transgressive
565 oceans ('Perigondwana Oceanic Realm' of Playford *et al*. 1995..." (Tongiorgi *et al*.
566 2003*a*, p. 44). The Baltic palynoflora, on the other hand, comprises assemblages that
567 developed during the late Arenig on mid to low palaeolatitude shelves, especially the
568 more proximal parts, in response to repeated regressive episodes (Tongiorgi *et al*.
569 2003*a*, p. 45).

570 In the context of this discussion, it is notable that coeval assemblages from Argentina
571 also contain genera and species with Baltic, South Chinese, Australian and more
572 characteristic Perigondwanan affinities (**Fig. 5**). A microflora of probable Darriwilian
573 age from the Capillas Formation of the Sierras Subandinas (Capillas River Section,
574 Sierra de Zapla), northwest Argentina, for example, contains *Ampullula*? sp. and
575 *Liliosphaeridium intermedium*, representing genera that are both more typical of
576 Baltica and South China than Perigondwana. Also present, however, are species of
577 the characteristic Perigondwanan genera *Arbusculidium*, *Arkonia* and *Striatotheca*
578 (Rubinstein *et al*. 2011). A further example is provided by the record of *Ammonidium*
579 sp. cf. *A.* [*Sacculidium*] *aduncum* in a Dapingian assemblage from the Famatina
580 region of northwest Argentina (Achab *et al.* 2006), where it is associated with
581 *Striatotheca* and other more typically Perigondwanan taxa such as *Vogtlandia*.

582 *Sacculidium aduncum* has been reported from Sweden (Ribecai *et al*. 2002) and from
583 the Canning Basin of Australia (Playford & Martin 1984; Quintavalle & Playford
584 2006*a*, *b*). *Ampullula* [*Stelomorpha*] *erchunensis*, which has been reported from
585 Norway (Tongiorgi *et al*. 2003*b*), Poland and Baltic Russia (Raevskaya *et al*. 2004),
586 South China (Yin 1994; Brocke *et al*. 1999, 2000; Tongiorgi *et al*. 1995, 2003*a*; Yan
587 *et al*. 2011) and Pakistan (Quintavalle *et al*. 2000), is also present in the Famatina
588 region, where it is associated with *Arbusculidium filamentosum* and *Striatotheca*.
589 These records indicate that such associations of Baltic and Perigondwanan forms are
590 not restricted to South China, but might be more widespread around the northern
591 promontory of Gondwana, around northern and eastern Australia (**Fig. 5**).
592 Palynological investigation of successions in south-eastern Australia, Tasmania and
593 New Zealand might provide data to test this supposition.

594

595 *Duration of Early to Mid Ordovician Provinces*

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

612

613 ***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.* 2008*a*), south Turkey (Le Hérissé *in* Paris *et al*. 2007) and Iran (Ghavidel-syooki *et al*. 2011*a*, *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*. 2011*a*; 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 caelamenicutis*], 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 evexa*, *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

678 Formation of Anticosti Island, Québec, Canada, although her work concentrated more
679 on the local Silurian strata. Later, Martin (1988), who reprepared some of the samples
680 from the Ellis Formation previously studied by Duffield (1982), observed that "a
681 preliminary selection of taxa from ... strata on Anticosti Island, Québec, eastern
682 Canada, indicates that the area has the most continuous palynological record from at
683 least the Ashgill to the late Llandovery, with the best potential for establishing
684 detailed acritarch systematics and interregional correlation".

685 More recent work on acritarch dynamics across the Ordovician–Silurian boundary at
686 low palaeolatitudes (Delabroye 2010; Delabroye *et al*. 2011*a*, *b*; Vecoli *et al*. 2011)
687 has confirmed Martin's (1988) observations. High-resolution investigation of
688 acritarch distributions across the Ordovician–Silurian boundary on Anticosti Island
689 (Laurentia) and at Valga, Estonia (Baltica) were complemented by literature reviews
690 of Hirnantian assemblages from the Gondwanan and Perigondwanan localities
691 mentioned above plus South China (Yin & He 2000), Sweden (Le Hérissé 1989*a*),
692 north Estonia (Uutela & Tynni 1991) and Poland (Kremer 2001; Masiak *et al*. 2003);
693 see Delabroye *et al*. (2011*a*, *b*). The more recent investigations show that the
694 tendency towards speciation during the Hirnantian observed by Vecoli & Le Hérissé
695 (2004) in Gondwana occurred also at low to mid palaeolatitudes during the
696 Hirnantian, but involved different morphotypes (see also Vecoli 2008).

697 New species common to Laurentia and Baltica that appeared during the Hirnantian are
698 *Ammonidium* sp. *in* Delabroye *et al*. (2011*b*), *Leiofusa granulicatis quincunx*, *Evittia*
699 sp. A *in* Delabroye *et al*. (2011*b*), *Helosphaeridium tongiorgii*, *Hoegklintia visbyensis*
700 and *Oppilatala* sp. *in* Delabroye *et al*. (2011*b*). These species occur together with
701 other taxa that were endemic to the two low to mid latitude palaeoplates, but which
702 appeared earlier during the Sandbian and the Katian, such as *Baltisphaeridium*
703 *curtatum*, *Buedingiisphaeridium balticum*, *Dilatisphaera wimanii*, *Likropalla*
704 *adiazeta* and *Peteinosphaeridium septuosum*. In contrast to Gondwanan successions,
705 Hirnantian successions in Laurentia and Baltica have yielded numerous large forms of
706 *Baltisphaeridium* spp., 'giant' acritarchs such as *Hoegklintia* spp. or *Estiastra* spp.
707 that are typical of low to mid palaeolatitude carbonate environments, several large
708 species of the *Goniosphaeridium-Stellechinatum-Polygonium* plexus, and
709 *Dilatisphaera wimanii*, a giant precursor of smaller *Dilatisphaera* species that evolved
710 during the Silurian (Delabroye *et al*. 2011*b*). As in Gondwana, however, the

711 Laurentian and Baltic Hirnantian assemblages also contain endemic species that
712 belong to genera of Silurian affinity, in this case including *Ammonidium*, *Evittia*,
713 *Hoegklintia*, *Oppilatala* and *Tylotopalla*.

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

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

735 Recent investigations of acritarch assemblages from the Hirnantian of Iran (Ghavidel-
736 syooki *et al.* 2011*a*, *b*) highlight some species of particular interest for our
737 understanding of the factors controlling their distribution, i.e. whether they are
738 latitudinally distributed and/or follow palaeocontinental margins. Iranian assemblages
739 of Hirnantian age share a high proportion of species in common with those of other
740 Gondwanan and Perigondwanan localities, but also share species in common with
741 latest Ordovician assemblages from Laurentia and Baltica (Ghavidel-syooki *et al.*
742 2011*a, b*). Of particular interest here is the species from the Eastern Alborz Range,
743 northern Iran figured as *Tylotopalla* sp. (Ghavidel-syooki *et al.* 2011*a*, pl. 5, figs 9–

744 10), and also found in the Zagros Mountains of southern Iran (Ghavidel-syooki *et al.,*
745 2011*b*, fig. 4B). This is morphologically close to *Tylotopalla heterobrachiifera*
746 nomen nudum from the Ellis Bay Formation of Anticosti (Delabroye 2010; Delabroye
747 *et al.* 2011*a*). *Cheleutochroa diaphorosa* from the Eastern Alborz Range (in
748 Ghavidel-syooki *et al.* 2011*a*, pl. 2, fig. 6, pl. 3, fig. 8) also resembles the *Oppilatala*
749 specimens found in the uppermost Ordovician of Anticosti and Estonia (Delabroye *et*
750 *al.* 2011*b*, pl. 11, figs 6–7; *Oppilatala anticostiana* nomen nudum in Delabroye et *al.*
751 2011*a*; Delabroye 2010) in having conspicuous plugs at base of the processes. These
752 two species have not been recovered from other Gondwanan or Perigondwanan
753 localities. During the latest Ordovician, the Alborz Terrane and Zagros Basin of Iran
754 were situated on the margin of Gondwana at low to mid southern palaeolatitudes,
755 comparable with the palaeolatitudes of Anticosti in Laurentia and Estonia in Baltica
756 (Torsvik & Cocks, 2013, figs 15, 16). Hence, these observations might show that the
757 composition of the Iranian assemblages was controlled by a mixture of factors,
758 including continental physiography (see Servais *et al.* 2003), i.e. following the
759 continental margin of Gondwana, to account for the Perigondwanan aspect, and a
760 restriction to low to mid southern palaeolatitudes to account for the elements in
761 common with Laurentia and Baltica.

762

763

764 **Silurian**

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

772

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

774 Cramer (1971) and Cramer & Díez (1972, 1974*a*, *b*) identified six acritarch
775 'biofacies' in a late Llandovery–Wenlock palynological province model, which they

776 termed (i) the Baltic palynofacies, (ii) the *Gloeocapsomorpha prisca* facies, (iii) the
777 *Deunffia eisenackii* facies, (iv) the *Domasia* facies, (v) the *Neoveryhachium carminae*
778 facies (subdivided into Iberian, Transitional and Brazilian-Libyan realms), and (vi)
779 the *Pulvinosphaeridium-Estiastra* facies. As with their interpretation of Ordovician
780 acritarch biogeography, they considered these units to be delineated by
781 palaeoisotherms, which they regarded as being parallel to palaeolatitude, and so
782 showed the boundaries of these units as also being parallel to palaeolatitude.
783 Cramer's (1971; Cramer & Díez (1972, 1974*a*, *b*) latitude-parallel model, however,
784 was at least partially dependent on the palaeogeographical reconstruction used as a
785 base map (Colbath 1990*a*). When plotted on a reconstruction of Llandovery
786 palaeogeography by Scotese (1986), data from Cramer (1971) show major deviations
787 from the palaeolatitude-parallel model, particularly with regard to the distribution of
788 the *Neoveryhachium carminae* biofacies and the combined *Deunffia-Domasia*
789 biofacies (Colbath 1990*a*).

790 The distribution of the four principal biofacies of Cramer's model, namely the
791 *Neoveryhachium carminae* facies, the *Deunffia* facies, the *Domasia* facies and the
792 *Pulvinosphaeridium-Estiastra* facies, was re-evaluated by Le Hérissé & Gourvennec
793 (1995). Their analysis of late Llandovery–Wenlock distribution patterns, which used
794 quantitative methods to supplement qualitative assessments, again questioned the
795 latitudinal controls advocated by Cramer (1971) and Cramer & Díez (1972, 1974*a*, *b*)
796 and reached different conclusions regarding controlling factors. Based on data from
797 eastern North America, South America, western Europe, Baltoscandia, Siberia, North
798 Africa and adjacent regions and China, Le Hérissé & Gourvennec (1995) concluded
799 that acritarch distribution resulted from the combined effects of continental
800 distribution, latitude, environment and oceanic circulation. They also concluded that
801 the main contributory factors influencing the distribution of *Gloeocapsomorpha*
802 *prisca* and *Deunffia eisenackii* blooms were related to local environmental factors
803 rather than palaeotemperature, in contrast to Cramer's model.

804

805 *The* Neoveryhachium carminae *biofacies*

806 In terms of the palaeogeographical reconstructions of Torsvik & Cocks (2013),
807 *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 & Díez (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 1989*b*; 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: Ghavidel-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*. 1974*c*) 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 1974*b*, 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 (1990*a*, 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 *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 *Deunffia-Domasia* association between the relatively homogeneous outer shelf environments of both continental margins.

Le Hérissé & Gourvennec (1995) noted that there were transitions from the *Neoveryhachium carminae* biofacies to the *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 (1990*a*) earlier observation of the same pattern.

Based on their analyses, Colbath (1990*a*) and Le Hérissé & Gourvennec (1995) concluded that depositional environment and facies exerted greater controls on the distribution of the *Neoveryhachium carminae* and *Deunffia-Domasia* biofacies than palaeolatitude. Le Hérissé & Gourvennec (1995) also concluded that the *Pulvinosphaeridium-Estiastra* biofacies, which they noted was also characterized by abundant *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 *Neoveryhachium carminae* and *Deunffia-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 *Dilatisphaera willieriae* 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 *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 Paranaíba 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*. 2008*a*; 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, 1974*a*, *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–Přídolí)***

Le Hérissé *et al*. (1997*a*) 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*. (1997*a*) 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*. (1997*a*) also pointed out that cluster analysis enabled delineation of a biogeographical

938 unit encompassing part of South America (Bolivia), the Gondwanan margin (Florida,
939 Algeria) and Perigondwana (Armorican Massif), comparable to the Malvinokaffric
940 Realm of invertebrate biogeography.

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

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

969 Le Hérissé *et al*. (1997*a*) also distinguished an outer, deep-water belt on the
970 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 (1990*a*), who examined the biogeographical distribution of Frasnian microfloras, and Le Hérissé *et al*. (1997*a*), 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*. (1997*a*) 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*. 1997*a*, 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*. (1997*a*) 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*. 1997*a*, 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*. 1997*a*, fig. 4). Le Hérissé *et al*. (1997*a*, 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*. 2008*b*, fig. 3 and Le Hérissé *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, Crozon 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 (Jardiné & Yapaudjian 1968; Jardiné *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*. 2008*b* 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*. 1997*b*), 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*. 1997*a*). 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 ampliatum, Nanocyclopia aspratilis, 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*. 2008*b*).

Those taxa that have a widespread geographical distribution, are restricted to the Lochkovian, and can be used for worldwide stratigraphic correlations (Rubinstein *et al*. 2008*b*), 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, *Evittia* 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*. 2008*b*, 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 stratigraphic control: Brito (1967, 1971, 1976; Lower–Upper Devonian, northern Brazil), Pöthe 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 (1990*b*) 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 angelae, D. tenuicingulata, Estiastra rhytidoa, Exochoderma arca, Hapsidopalla chela, H. exornata, Lophosphaeridium ochthos, Muraticavea munificus, Navifusa bacilla, Oppilatala sparsa, Ozotobrachion furcillatus, 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 *Diexallophasis 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 *Diexallophasis 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 (1990*b*) 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 *Diexallophasis remota, Exochoderma arca, Hapsidopalla exornata, Multiplicisphaeridium ramispinosum, Navifusa bacilla, Oppilatala sparsa, Stellinium micropolygonale, Tyligmasoma alargada* and *Veryhachium trispinosum* complex. 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 brasiliensis, 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.

In North America, studies of well-dated acritarch occurrences and assemblages include Staplin (1961; Frasnian, Alberta, Canada), Winslow (1962; Famennian, Ohio, U.S.A.), Bharadwaj *et al*. (1970; Famennian, Kentucky, U.S.A.), Wicander (1974, 1975; Famennian, Ohio, U.S.A.), Wicander & Loeblich (1977; Frasnian–Famennian, Indiana, U.S.A.), Reaugh (1978; Famennian, Tennessee, U.S.A.), Molyneux *et al*. (1984; Famennian, Ohio, U.S.A.), Wicander & Playford (1985; Frasnian, Iowa, U.S.A.), Turner (1986, 1991; Givetian–Frasnian, Alberta, Canada), Huysken *et al*. (1992; Givetian–Famennian, Kentucky, U.S.A.) and Playford & McGregor (1993; Famennian, southern Saskatchewan, Canada).

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, 1962*a*, *b*, 1966, 1967, 1969, 1974; Frasnian–Famennian, Belgium), Bain & Doubinger (1965; Famennian, France), Deunff (1965, 1981; Upper Devonian, France), Górka (1974*a*, *b*; Famennian, Poland), Vanguestaine (1978*b*; Famennian, Belgium), Deunff (1981; Givetian–Frasnian, France), Martin (1981, 1982*b*, 1985; Frasnian–Famennian, Belgium), Loboziak *et al*. (1983; Frasnian–Famennian, France),

Vanguestaine *et al*. (1983; Frasnian–Famennian, Belgium), Amirie (1984; Frasnian, Germany); Le Hérissé & Deunff (1988; Givetian–Frasnian, France), González *et al*. (2005; Famennian, Spain) and Pereira *et al*. (2008; Famennian, Portugal).

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 (1990*b*) 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*. (2002*a*) 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 (1990*a*) 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 *Umbellasphaeridium deflandrei* and *Umbellasphaeridium saharicum* from North America and South America, as well as from Africa. Vanguestaine (1986*b*) 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 *Umbellasphaeridium 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 (1986*b*), 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 *Chomotriletes vedugensis, Cymatiosphaera perimembrana, Daillydium pentaster, Dictyotidium litum, Diexallophasis remota, Gorgonisphaeridium ohioense, G. plerispinosum, Multiplicisphaeridium ramispinosum, Palacanthus ledanoisii, Polyedryxium pharaonis, Solisphaeridium 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 deminutum* 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 palaeolatitude oceanic interchange between the Euramerican region, Australia, Iran and China. Endemic acritarch assemblages also existed during the Late Devonian as seen by the high palaeolatitude occurrences of several genera within the Perigondwana region. However, some characteristic high palaeolatitude Perigondwana species were dispersed into mid to low palaeolatitude Euramerican areas, possibly by cold-water gyres.

***Synopsis of Devonian phytoplankton biogeography***

Much has changed since the early attempts at reconstructing Devonian acritarch palaeobiogeographical distributions. Palaeogeographical 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 palaeolatitudes, 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 palaeolatitudes, and those from a high palaeolatitude province. The apparent provincialism, however, might reflect local conditions or lack of geographic coverage and adequately described palynofloras.

During the Early Devonian, a mid palaeolatitude 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 (1990*a*) 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, 1974*a*, *b*) of Silurian phytoplankton distributions. Assemblages once regarded as being restricted to latitude-parallel climatic belts, such as Cramer's *Deunffia*, *Domasia* and *Neoveryhachium 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 palaeolatudinal 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, 2003*a*; Li *et al*. 2002*b*; 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 (1990*a*) 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 1986*a*) 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*. 1995; Tongiorgi *et al*. 1998, 2003*a*).

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 2006*a*, *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 2006*b*, 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*, *Cyclopospheridium*, *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 1990*a*, *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 (2006*a*, *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 (2006*b*) 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 2006*b*), 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*. 2003*a*; 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 cirritus* and *Striatotheca rarirrugulata* are present in South Chinese assemblages from the Floian or Dapingian onwards (Brocke *et al.* 2000; Tongiorgi *et al*. 1995, 2003*a*; 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 (2006*b*, text-fig. 6) correlate with the *Didymograptus artus* Graptolite Biozone of early Darriwilian (early Llanvirn) age, and the FADs of *Dasydorus cirritus* 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 & Díez (1974*b*) 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 (1974*b*, 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.* (2003*b*), 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 Perigondwanan markers are also present. If Tongiorgi *et al*.'s (2003*a*) 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, 2003*a*, *b*; Yan *et al*. 2011), and from South China and Australia (Canning Basin) in the Dapingian–lower Darriwilian (Brocke *et al*. 2000; Quintavalle & Playford 2006*a*, *b*; Tongiorgi *et al.* 2003*a*; 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 $CO_2$ 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 $CO_2$ 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 (1990*a*) 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 (1990*a*) 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 (1997*a*) 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 (1990*a*) 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 *Neoveryhachium 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 endemicity 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.

1791 **References**


1792 Achab, A., Rubinstein, C. V. & Astini, R. A. 2006. Chitinozoans and acritarchs from
1793 the Ordovician peri-Gondwana volcanic arc of the Famatina System,
1794 northwestern Argentina. *Review of Palaeobotany and Palynology*, **139**, 129–149.

1795 Al-Ameri, T. K. 2010. Palynostratigraphy and the assessment of gas and oil
1796 generation and accumulations in the Lower Paleozoic, Western Iraq. *Arabian*
1797 *Journal of Geosciences*, **3**, 155–179. doi: 10.1007/s12517-009-0060-2

1798 Albani, R. 1989. Ordovician (Arenigian) acritarchs from the Solanas Sandstone
1799 Formation, Central Sardinia, Italy. *Bollettino della Società Paleontologica*
1800 *Italiana*, **28**, (1), 3–37.

1801 Albani, R., Massa, D. & Tongiorgi, M. 1991. Palynostratigraphy (Acritarchs) of
1802 some Cambrian beds from the Rhadames (Ghadamis) Basin (Western Libya –
1803 Southern Tunisia). *Bollettino della Società Paleontologica Italiana*, **30**, (3), 255–
1804 280.

1805 Albani R., Bagnoli, G., Bernárdez, E., Gutíerrez-Marco, J. C. & Ribecai, C. 2006.
1806 Late Cambrian acritarchs from the "Túnel Ordovícico del Fabar", Cantabrian
1807 Zone, N Spain. *Review of Palaeobotany and Palynology*, **139**, 41–52.
1808 doi:10.1016/j.revpalbo.2005.07.005.

1809 Amirie, G. H. B. 1984. Phytoplankton aus dem Frasne des bergischen Landes,
1810 rheinisches Schiefergebirge. *Geologisches Institut der Universität zu Köln*
1811 *Sonderveröffentlichungen*, **49**, 1–99, pl. 1–16.

1812 Anan-Yorke, R. 1974. Devonian Chitinozoa and Acritarcha from exploratory oil
1813 wells on the shelf and coastal region of Ghana West Africa. *Ghana Geological*
1814 *Survey Bulletin*, **37**, 1–217.

1815 Bagnoli, G. & Ribecai, C. 2001. On the biostratigraphic significance of the
1816 Ordovician acritarch genus *Liliosphaeridium* on Öland, Sweden. *Review of*
1817 *Palaeobotany and Palynology*, **117**, 195–215. doi:10.1016/S0034-
1818 6667(01)00090-2.

1819 Bain, A. & Doubinger, J. 1965. Etude d'un microplancton (Acritarches) du
1820 Dévonien supérieur des Ardennes. *Bulletin du Service de la Carte Géologique*
1821 *d'Alsace et de Lorraine*, **18**, (1), 15–30.

1822 Barker, G.W. & Miller, M.A. 1989. Tremadocian (Lower Ordovician) acritarchs
1823 from the subsurface of West Texas. *Palynology*, **14**, 209.

1824 Barreda, V. D. 1986. Acritarcos Givetiano-Frasnianos de la Cuenca del Noroeste,
1825 Provincia de Salta, Argentina. *Revista Española de Micropaleontología*, **18**, (2),
1826 229–245.

1827 Bharadwaj, D. C., Tiwari, R. S. & Venkatachala, B. S. 1970. An Upper Devonian
1828 microflora from New Albany Shale, Kentucky, U. S. A. *The Paleobotanist*, **19**,
1829 29–40.

1830 Breuer, P. & Vanguestaine, M. 2004. The latest Tremadocian *messaoudensis-*
1831 *trifidum* acritarch assemblage from the upper part of the Lierneux Member (Salm
1832 Group, Stavelot Inlier, Belgium). *Review of Palaeobotany and Palynology*, **130**,
1833 41–58.

1834 Brito, I. 1967. Silurian and Devonian Acritarcha from Maranhão Basin, Brazil.
1835 *Micropaleontology*, **13**, 473–482.

1836 Brito, I. 1971. Contribuição ao conhecimento dos microfósseis silurianos e
1837 devonianos da Bacia do Maranhão. V - Acritarcha Herkomorphitae e
1838 Prismatomorphitae. *Simposio Brasileiro de Paleontologia, Anais da Academia*
1839 *Brasileira de Ciências*, Supplement, **43**, 201-208.

1840 Brito, I. 1976. Contribuição ao conhecimento dos microfósseis devonianos de
1841 Pernambuco. III Alguns acritarcha comuns aos do Devoniano do Saara. *Anais*
1842 *da Academia Brasileira de Ciências*, **48**, (4), 747–756.

1843 Brito, I. 1978. *Maranhites*, um importante fóssil índice do Devoniano Superior
1844 (Acritarcha Scutellomorphitae). *In*: Rösler, O. (ed.), *Advances in Palaeobotany*
1845 *and Allied Sciences in Brazil*. Boletim do Instituto de Geociências da
1846 Universidade de São Paulo, **9**, 80–85.

1847 Brocke, R., Fatka, O., Molyneux, S. G. & Servais, T. 1995. First appearance of
1848 selected Early Ordovician acritarch taxa from peri-Gondwana. *In*: Cooper, J. D.,
1849 Droser, M. L. & Finney, S. C. (eds) *Ordovician Odyssey: Short Papers for the*
1850 *7th International Symposium on the Ordovician System*. Pacific Section, SEPM,
1851 Society for Sedimentary Geology, No. **77**, 473–476.

1852 Brocke, R., Li, J. & Wang, Y. 1999. Preliminary results on upper "Arenigian" to
1853 lower "Llanvirnian" acritarchs from South China. *In*: Kraft, P. & Fatka, O. (eds)
1854 *Quo vadis Ordovician? Short papers of the 8th International Symposium on the*
1855 *Ordovician System (Prague, June 20–25, 1999)*. *Acta Universitatis Carolinae*,
1856 *Geologica*, **43**, (1-2), 259–261.

1857 Brocke, R., Li, J. & Wang, Y. 2000. Upper Arenigian to lower Llanvirnian acritarch
1858 assemblages from South China: a preliminary evaluation. *Review of*
1859 *Palaeobotany and Palynology*, **113**, 27–40.

1860 Bruton, D. L., Gabrielsen, R. H. & Larsen, B. T. 2010. The Caledonides of the Oslo
1861 Region, Norway - stratigraphy and structural elements. *Norwegian Journal of*
1862 *Geology*, **90**, 93–121.

1863 Bultynck, P. & Martin, F. 1982. Conodontes et acritarches de l'Ordovicien inférieur
1864 et acritarches du Silurien inférieur de la partie septentrional de la Cordillère
1865 Argentine. *Bulletin de l'Institut royal des Sciences naturelles de Belgique*,
1866 *Sciences de la Terre*, **53** (4), 1–21, pls I–II.

1867 Burmann, G. 1968. Diacrodien aus dem unteren Ordovizium. *Paläontologische*
1868 *Abhandlungen*, Abteilung B, **2**, 635–652.

1869 Burmann, G. 1970. Weitere organische Mikrofossilien aus dem unteren Ordovizium.
1870 *Paläontologische Abhandlungen*, Abteilung B, **3**, 289–332.

1871 Cermeño, P., de Vargas, C., Abrantes, F. & Falkowski, P.G. 2010. Phytoplankton
1872 biogeography and community stability in the ocean. *PLoS ONE*, **5**, e10037.
1873 doi:10.1371/journal.pone.0010037

1874 Chadwick, R. A., Jackson, D. I., Barnes, R. P., Kimbell, G. S., Johnson, H.,
1875 Chiverrell, R. C., Thomas, G. S. P., Jones, N. J., Riley, N. J., Pickett, E. A.,
1876 Young, B., Holliday, D. W., Ball, D. F., Molyneux, S. G., Long, D., Power, G.
1877 M. & Roberts, D. H. 2001. *Geology of the Isle of Man and its offshore area*.
1878 British Geological Survey Research Report, **RR/01/06**, Keyworth, Nottingham.

1879 Clayton, G., Wicander, R. & Pereira, Z. 2002. Palynological evidence concerning the
1880 relative positions of northern Gondwana and southern Laurussia in latest
1881 Devonian and Mississippian times. *In*: Wyse Jackson, P. N., Parkes, M. A. &
1882 Wood, R. (eds), *Studies in Palaeozoic palaeontology and biostratigraphy in*

*honour of Charles Hepworth Holland*. *Special Papers in Palaeontology*, **67**, 45–56.

Cocks, L. R. M. & Torsvik, T. H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society, London*, **159**, 631–644.

Colbath, G. K. 1990*a*. Palaeobiogeography of Middle Palaeozoic organic-walled phytoplankton. *In*: McKerrow, W. S. & Scotese, C. R. (eds), *Palaeozoic palaeogeography and biogeography*. Geological Society of London, Memoir, **12**, 207–213.

Colbath, G. K. 1990*b*. Devonian (Givetian–Frasnian) organic-walled phytoplankton from the Limestone Billy Hills reef complex, Canning Basin, Western Australia. *Palaeontographica*, Abteilung B, **217**, 87–145.

Colbath, G. K. & Grenfell, H. R. 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including 'acritarchs'). *Review of Palaeobotany and Palynology*, **86**, 287–314.

Cooper, A. H., Rushton, A. W. A., Molyneux, S. G., Hughes, R. A., Moore, R. M. & Webb, B. C. 1995. The stratigraphy, correlation, provenance, and palaeogeography of the Skiddaw Group (Ordovician) in the English Lake District. *Geological Magazine*, **132**, 185–211.

Cooper, A. H., Fortey, N. J., Hughes, R. A., Molyneux, S. G., Moore, R. M., Rushton, A. W. A. & Stone, P. 2004. *The Skiddaw Group of the English Lake District*. Memoir of the British Geological Survey, Keyworth, Nottingham.

Cramer, F. H. 1964. Some acritarchs of the San Pedro Formation (Gedinnien) of the Canabric mountains in Spain. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, **73**, 33–38.

Cramer, F. H. 1971. Distribution of selected Silurian acritarchs. *Revista Española Micropaleontología, Numero Extraordinario*, **1**, 1–203. [Imprinted 1970, issued 1971]

Cramer, F. H. & Díez, M. del C. R. 1972. North American Silurian palynofacies and their spatial arrangement: acritarchs. *Palaeontographica*, Abteilung B, **138**, 107–180.

1914 Cramer, F. H. & Díez, M. del C. R. 1974*a*. Early Paleozoic palynomorph provinces
1915 and paleoclimate. *In*: Ross, C. A. (ed.), *Paleogeographic Provinces and*
1916 *Provinciality*. Society of Economic Paleontologists and Mineralogists, U.S.A.,
1917 Special Publication, **21**, 177–188.

1918 Cramer, F. H. & Díez, M. del C. R. 1974*b*. Silurian acritarchs: distribution and
1919 trends. *Review of Palaeobotany and Palynology*, **18**, 137–154.

1920 Cramer, F. H. & Díez, M. del C. R. 1976. Seven new late Arenigian species of the
1921 acritarch Genus *Coryphidium*. *Paläontologische Zeitschrift*, **50**, 201–208.

1922 Cramer, F. H. & Díez, M. del C. R. 1977. Late Arenigian (Ordovician) acritarchs
1923 from Cis-Saharan Morocco. *Micropaleontology*, **23**, 339–360.

1924 Cramer, F. H., Allam, B., Kanes, W. H. & Díez, M. del C. R. 1974*a*. Upper
1925 Arenigian to lower Llanvirnian acritarchs from the subsurface of the Tadla Basin
1926 in Morocco. *Palaeontographica*, Abteilung B, **145**, 182–190.

1927 Cramer, F. H., Kanes, W. H., Díez, M. del C. R. & Christopher, R. A. 1974*b*. Early
1928 Ordovician acritarchs from the Tadla Basin of Morocco. *Palaeontographica*,
1929 Abteilung B, **146**, 57–64.

1930 Cramer, F. H., Díez, M. del C. R. & Cuerda, A. 1974*c*. Late Silurian chitinozoans
1931 and acritarchs from Cochabamba, Bolivia. *Neues Jahrbuch für Geologie und*
1932 *Paläontologie, Monatshefte*, **1974**, (1), 1–12.

1933 Daemon, R. F. 1974. Palinomorfos-guias do Devoniano Superior e Carbonífero
1934 Inferior das bacias do Amazonas e Parnaíba. *Anais da Academia Brasileira*
1935 *Ciências*, **46**, (3/4), 549–587.

1936 Daemon, R. F., Quadros, L. P. & da Silva, L. C. 1967. Devonian palynology and
1937 biostratigraphy of the Paraná Basin. *In*: Bigarella, J. J. (ed.), *Problems in*
1938 *Brazilian Devonian Geology*. *Boletim Paranaense de Geociências*, **21–22**, 99–
1939 132.

1940 Davies, J. R., Fletcher, C. J. N., Waters, R. A., Wilson, D., Woodhall, D. G. &
1941 Zalasiewicz, J. A. 1997. *Geology of the country around Llanilar and Rhayader*.
1942 Memoir of the British Geological Survey, Sheets 178 and 179 (England and
1943 Wales).

1944 Davies, J. R., Waters, R. A., Molyneux, S. G., Williams, M., Zalasiewicz, J. A.,
1945 Vandenbroucke, T. R. A. & Verniers, J. *in press*. A revised sedimentary and
1946 biostratigraphical architecture for the Type Llandovery area, Central Wales.
1947 *Geological Magazine*, **000**, 000–000.

1948 Dean, W. T. & Martin, F. 1978. Lower Ordovician acritarchs and trilobites from Bell
1949 Island, eastern Newfoundland. *Geological Survey of Canada*, *Bulletin*, **284**, 1–
1950 35.

1951 Dean, W. T. & Monod, O. 1990. Revised stratigraphy and relationships of Lower
1952 Palaeozoic rocks, eastern Taurus Mountains, south central Turkey. *Geological*
1953 *Magazine*, **127**, 333–347.

1954 Dean, W. T., Martin, F., Monod, O., Gül, M. A., Bozdo□an, N. & Özgül, N. 1993.
1955 Early Palaeozoic evolution of the Gondwanaland margin in the western and
1956 central Taurids, Turkey. *In*: Turgut, S. (ed.) *Tectonics and hydrocarbon potential*
1957 *of Anatolia and surrounding regions*. Ozan Sungurlu Symposium Proceedings,
1958 November 1991, Ankara, 262–273.

1959 Delabroye, A. 2010. *Dynamiques du phytoplancton à travers la limite Ordovicien-*
1960 *Silurien aux faibles paléolatitudes (Laurentia: Île d'Anticosti, Québec, Canada;*
1961 *Baltica: Valga, Estonie). Compléments aux données des hautes latitudes*
1962 *glaciaires du Gondwana*. Unpublished Ph.D. Thesis, Université de Lille 1,
1963 France, 464 pp.

1964 Delabroye, A. & Vecoli, M. 2010. The end-Ordovician glaciation and the Hirnantian
1965 Stage: a global review and questions about late Ordovician event stratigraphy.
1966 *Earth-Science Reviews*, **98**, 269–282.

1967 Delabroye, A., Munnecke, A., Vecoli, M., Copper, P., Tribovillard, N., Joachimski, M.
1968 M., Desrochers, A. & Servais, T. 2011*a*. Phytoplankton dynamics across the
1969 Ordovician/Silurian boundary at low palaeolatitudes: correlations with carbon
1970 isotopic and glacial events. *Palaeogeography, Palaeoclimatology,*
1971 *Palaeoecology*, **312**, 79–97.

1972 Delabroye, A., Vecoli, M., Hints, O. & Servais, T. 2011*b*. Acritarchs from the
1973 Ordovician-Silurian boundary beds of the Valga-10 drill core, southern Estonia

(Baltica), and their stratigraphic and palaeobiogeographic implications. *Palynology*, **35**, 4–45.

Deunff, J. 1954. Microorganismes planctoniques (Hystrichosphères) dans le Dévonien du Massif armoricain. *Compte rendu sommaire des séances de la Société géologique de France*, 1954, No. 11, 239–242.

Deunff, J. 1965. Acritarches du Dévonien supérieur de la presqu'île de Crozon. *Compte rendu sommaire des séances de la Société géologique de France*, 1965, Fascicule 5, 162–164.

Deunff, J. 1968. Sur une série à acritarches dans le Dévonien moyen du Finistère. *Bureau de recherches géologiques et minières, Mémoire*, **33**, 341–348.

Deunff, J. 1977. Un microplancton à Acritarches dans les schistes llanvirniens de l'Anti-Atlas (Zagora - Maroc). *Notes du Service géologique du Maroc*, **38**, 141–151.

Deunff, J. 1980. Le paléoplancton des Grès de Landévennec (Gedinnien de la Rade de Brest - Finistère) étude biostratigraphique. *Géobios*, **13**, 483–539.

Deunff, J. 1981. Observations preliminaries sur le paleophytoplancton de la coupe de Caffiers (Givétien–Frasnien du Boulonnais, France). *Annales de la Société géologique du Nord*, **100** (1980), 65–71.

Deunff, J. & Massa, D. 1975. Palynologie et stratigraphie du Cambro-Ordovicien (Libye nord-occidentale). *Comptes rendus de l'Académie des Sciences*, Paris, Série D, **281**, 21–24.

Díaz-Martínez, E., Vavrdová, M., Isaacson, P. E. & Grahn, C. Y. 2011. Early Silurian vs. Late Ordovician glaciation in South America. *In*: Gutiérrez-Marco, J.C., Rábano, I. & García-Bellido, D. (eds), *Ordovician of the World*. Cuadernos del Museo Geominero, **14**, Instituto Geológico y Minero de España, Madrid, 127–134.

Dino, R. & Rodrigues, M. A. C. 1995. Palinomorfos eodevonianos da Formação Furnas. *Anais da Academia Brasileira de Ciências*, **67**, 116–117.

Dong, L., Xiao, S., Shen, B., Zhou, C., Li, G. & Yao, J. 2009. Basal Cambrian microfossils from the Yangtze Gorges area (South China) and the Aksu area (Tarim Block, northwestern China). *Journal of Paleontology*, **83**, (1), 30–44.

2005 Dorning, K. J. 1981. Silurian acritarch distribution in the Ludlovian shelf sea of
2006 South Wales and the Welsh Borderland. *In*: Neale, J.W. & Brasier, M.D. (eds),
2007 *Microfossils from Recent and Fossil Shelf Seas*. Ellis Horwood Ltd., Chichester,
2008 31–36.

2009 Downie, C. 1984. *Acritarchs in British stratigraphy*. Geological Society, London,
2010 Special Report **17**, 1–26.

2011 Duffield, S.L. 1982. *Late Ordovician–Early Silurian acritarch biostratigraphy and*
2012 *taxonomy, Anticosti Island, Québec*. Unpublished Ph.D. thesis, University of
2013 Waterloo, Ontario, Canada, 296 p.

2014 Dufka P. & Fatka O. 1993. Chitinozoans and acritarchs from the Ordovician–
2015 Silurian boundary of the Prague Basin, Czech Republic. *Special Papers in*
2016 *Palaeontology*, **48**, 17–28.

2017 Dufka, P. & Pacltova, B. 1988. Upper Llandoverian acritarchs from Karlštejn,
2018 Barrandian area, Bohemian Massif. *Véstník Ústředního ústavu geologického*, **63**,
2019 11–22, pls I–IV.

2020 Eklund, C. 1990. Lower Cambrian acritarch stratigraphy of the Bårstad 2 core,
2021 Östergötland, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar,* **112**,
2022 19–44.

2023 Elaouad-Debbaj, Z. 1984. Acritarches et chitinozoaires de l'Arenig-Llanvirn de
2024 l'Anti-Atlas (Maroc). *Review of Palaeobotany and Palynology*, **43**, 67–88.

2025 Elaouad-Debbaj, Z. 1988. Acritarches de l'Ordovicien supérieur (Caradoc, Ashgill)
2026 de l'Anti-Atlas, Maroc. *Revue de Micropaléontologie*, **30**, 232–248.

2027 Fontaneto, D. 2011. *Biogeography of microscopic organisms: is everything small*
2028 *everywhere?* The Systematics Association Special Volume **79**. Cambridge
2029 University Press, Cambridge.

2030 Fontaneto, D. & Brodie, J. 2011. Why biogeography of microorganisms? In:
2031 Fontaneto, D. (ed.) *Biogeography of microscopic organisms: is everything small*
2032 *everywhere?* The Systematics Association Special Volume **79**. Cambridge
2033 University Press, Cambridge, 3–10.

2034 Gao Lianda. 1986. Late Devonian and Early Carboniferous acritarchs from Nyalam
2035 County, Xizang (Tibet), China. *Review of Palaeobotany and Palynology*, **47**, (1–
2036 2), 17–30.

2037 Ghavidel-syooki, M. 1994. Upper Devonian acritarchs and miospores from the
2038 Geirud Formation in Central Alborz Range, northern Iran. *Iranian Journal of*
2039 *Science*, **5**, (3), 103–122.

2040 Ghavidel-syooki, M. 1997. Acritarch biostratigraphy of the Palaeozoic rock units in
2041 the Zagros Basin, Southern Iran. *In*: Fatka, O. & Servais, T. (eds), *Acritarcha in*
2042 *Praha 1996.* Proceedings of International Meeting andWorkshop. *Acta*
2043 *Universitatis Carolinae*, *Geologica*, **40**, (3–4), 385–411. [For 1996]

2044 Ghavidel-syooki, M. 2001. Palynostratigraphy and paleogeography of the Late
2045 Devonian in northeastern Esfahan City, central Iran. *In:* Goodman, D.K. &
2046 Clarke, R. T. (eds), *Proceedings of the IX International Palynological Congress*,
2047 *Houston, Texas, U.S.A., 1996*. American Association of Stratigraphic
2048 Palynologists Foundation, 37–51.

2049 Ghavidel-syooki, M. 2003. Palynostratigraphy of Devonian sediments in the Zagros
2050 Basin, southern Iran. *Review of Palaeobotany and Palynology*, **127**, 241–268.

2051 Ghavidel-syooki, M. 2006. Palynostratigraphy and palaeogeography of the Cambro-
2052 Ordovician strata in southwest of Shahrud City (Kuh-e-Kharbash, near Deh-
2053 Molla), Central Alborz Range, northern Iran. *Review of Palaeobotany and*
2054 *Palynology*, **139**, 81–95.

2055 Ghavidel-syooki, M. & Owens, B. 2007. Palynostratigraphy and palaeogeography of
2056 the Padeha, Khoshyeilagh, and Mobarak formations in the eastern Alborz Range
2057 (Kopet-Dagh region), northeastern Iran. *Revue de micropaléontologie*, **50**, 129–
2058 144.

2059 Ghavidel-syooki, M. & Vecoli, M. 2008. Palynostratigraphy of Middle Cambrian to
2060 lowermost Ordovician stratal sequences in the High Zagros Mountains, southern
2061 Iran: regional stratigraphic implications, and palaeobiogeographic significance.
2062 *Review of Palaeobotany and Palynology*, **150**, 97–114.

2063 Ghavidel-syooki, M., Hassanzadeh, J. & Vecoli, M. 2011*a*. Palynology and isotope
2064 geochronology of the Upper Ordovician–Silurian successions (Ghelli and Soltan

Maidan formations) in the Khoshyeilagh area, eastern Alborz Range, northern Iran; stratigraphic and palaeogeographic implications. *Review of Palaeobotany and Palynology*, **164**, 251–271.

Ghavidel-syooki, M., Álvaro, J. J., Popov, L., Ghobadi Pour, M., Ehsani, M. E. & Suyarkova, A. 2011*b*. Stratigraphic evidence for the Hirnantian (latest Ordovician) glaciations in the Zagros Mountains, Iran. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **307**, 1–16.

Ghienne, J.-F., Le Heron, D., Moreau, J., Denis, M. & Deynoux, M. 2007. The Late Ordovician glacial sedimentary system of the North Gondwana platform. *In*: Hambrey, M., Christoffersen, P., Glasser, N., Janssen, P., Hubbard, B. & Siegert, M. (eds), *Glacial Sedimentary Processes and Products*. Special Publication, International Association of Sedimentologists, Blackwells, Oxford, 295–319.

González, F. 2009. Reappraisal of the organic-walled microphytoplankton genus *Maranhites*: morphology, excystment, and speciation. *Review of Palaeobotany and Palynology*, **154**, 6–21.

González, F., Playford, G. & Moreno, C. 2005. Upper Devonian biostratigraphy of the Iberian Pyrite Belt, southwest Spain Part Two: Organic-walled microphytoplankton. *Palaeontographica*, Abteilung B, **273**, 53–86.

Górka, H. 1974*a*. Quelques informations sur une association d'acritarches du Famennien de Pologne. *Review of Palaeobotany and Palynology*, **18**, 131–135.

Górka, H. 1974*b*. Les acritarches de concretions calcaires du Famennien supérieur de Lagów (Monts de Sainte Croix, Pologne). *Acta Palaeontologica Polonica*, **19**, 225–250.

Gray, J., Boucot, A. J., Grahn, Y. & Himes, G. 1992. A new record of early Silurian land plant spores from the Paraná Basin, Paraguay (Malvinokaffric Realm). *Geological Magazine*, **129**, 741–752. doi:10.1017/S0016756800008463

Grenfell, H. R. 1995. Probable fossil zygnematacean algal spore genera. *Review of Palaeobotany and Palynology*, **84**, 201–220.

Gueinn, K. J. & Rasul, S. M. 1986. A contribution to the biostratigraphy of the Palaeozoic of the Western desert, utilizing new palynological data from the

subsurface. *Proceedings VIII Petroleum Exploration Conference*, EGPC, Cairo, 85–96.

Hashemi, H. & Playford, G. 1998. Upper Devonian palynomorphs of the Shishtu Formation, Central Iran Basin, east-central Iran. *Palaeontographica*, Abteilung B, **246**, 115–212.

Heuse, T., Erdtmann, B.-D. & Kraft, P. 1994. Early Ordovician microfossils (acritarchs, chitinozoans) and graptolites from the Schwarzburg Anticline, Thuringia (Germany). *Veröffentlichungen Naturhistorisches Museum Schleusingen*, **9**, 41–68.

Hill, P. J. 1974. Stratigraphic palynology of acritarchs from the type area of the Llandovery and the Welsh Borderland. *Review of Palaeobotany and Palynology*, **18**, 11–23.

Hill, P. J. & Dorning, K. J. 1984. Appendix 1. Acritarchs. *In*: Cocks, L. R. M., Woodcock, N. H., Rickards, R. B., Temple, J. T. & Lane, P. D. The Llandovery Series of the type area. *Bulletin of the British Museum (Natural History)*, Geology Series, **38**,174–76.

Hill, P. J. & Molyneux, S. G. 1988. Biostratigraphy, palynofacies and provincialism of Late Ordovician-Early Silurian acritarchs from northeast Libya. *In*: El-Arnauti, A., Owens, B. & Thusu, B. (eds), *Subsurface Palynostratigraphy of Northeast Libya.* Garyounis University, Benghazi, Libya, 27–43.

Huang Fei, Zhang Zhongying & Xiao Chengxie. 1994. Acritarchs from the *Azygograptus suecicus* Zone of the Ningguo Stage in Yushan area, Jiangxi Province. *Journal of Nanjing University (Earth Sciences)*, **6**, (4), 402–411.

Huysken, K. T., Wicander, R. & Ettensohn, F. R. 1992. Palynology and biostratigraphy of selected Middle and Upper Devonian black-shale sections in Kentucky. *Michigan Academician*, **24**, 355–368.

Jachowicz, M. 2000. Acritarch assemblages from the Silurian Pomeranian Caledonides and their foreland. *Geological Quarterly*, **44**, (3), 317–331.

Jacobson, S. J. 1979. Acritarchs as paleoenvironmental indicators in Middle and Upper Ordovician rocks from Kentucky, Ohio and New York. *Journal of Paleontology*, **53**, 1197–1212.

2126 Jardiné, S. 1972. Microplancton (Acritarches) et limites stratigraphiques du Silurien
2127 terminal au Dévonien supérieur. *Septième Congrès International de Stratigraphie*
2128 *et de Géologie du Carbonifère, Krefeld (1971), Comptes Rendus*, **1**, 313–323.

2129 Jardiné, S. & Yapaudjian, L. 1968. Lithostratigraphie et palynologie du Dévonien–
2130 Gothlandien gréseux du Bassin de Polignac (Sahara). *Revue de l'Institut*
2131 *Français du Pétrole*, **23**, 439–469.

2132 Jardiné, S., Combaz, A., Magloire, L., Peniguel, G. & Vachey, G. 1972. Acritarches
2133 du Silurien terminal et du Dévonien du Sahara Algérien. *Septième Congrès*
2134 *International de Stratigraphie et de Géologie du Carbonifère, Krefeld (1971),*
2135 *Comptes Rendus*, **1**, 295–311.

2136 Jardiné, S., Combaz, A., Magloire, L., Peniguel, G. & Vachey, G. 1974. Distribution
2137 stratigraphique des acritarches dans le Paléozoïque du Sahara algérien. *Review of*
2138 *Palaeobotany and Palynology*, **18**, 99–129.

2139 Kaźmierczak, J. & Kremer, B. 2009. Spore-like bodies in some early Paleozoic
2140 acritarchs: clues to chlorococcalean affinities. *Acta Palaeontologica Polonica*, **54**
2141 (3), 541–551. doi: 10.4202/app.2008.0060

2142 Keegan, J. B., Rasul, S. M. & Shaheen, Y. 1990. Palynostratigraphy of the Lower
2143 Palaeozoic, Cambrian to Silurian, sediments of the Hashemite Kingdom of
2144 Jordan. *Review of Palaeobotany and Palynology*, **66**, 167–180.

2145 Kreft, H. & Jetz, W. 2010. A framework for delineating biogeographical regions
2146 based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.
2147 doi:10.1111/j.1365-2699.2010.02375.x

2148 Kremer, B. 2001. Acritarchs from the Upper Ordovician of southern Holy Cross
2149 Mountains, Poland. *Acta Palaeontologica Polonica*, **46**, 595–601.

2150 Lange, F. W. 1967. Biostratigraphic subdivision of the Devonian in the Paraná
2151 Basin. *In*: Bigarella, J. J. (ed.), *Problems in Brazilian Devonian Geology*.
2152 *Boletim Paranaense de Geociências*, **21–22**, 63–98.

2153 Le Hérissé, A. 1989*a*. *Acritarches et kystes d'algues prasinophycées de l'Ordovicien*
2154 *Supérieur et du Silurien de Gotland, Suède*. Unpublished Ph.D. thesis, Université
2155 de Bretagne Occidentale, Brest, France, 409 pp.

Le Hérissé, A. 1989*b*. Acritarches et kystes d'algues Prasinophycées du Silurien de Gotland, Suède. *Palaeontographia Italica*, **76**, 57–302.

Le Hérissé, A. 2000. Characteristics of the acritarch recovery in the Early Silurian of Saudi Arabia. *In*: Al-Hajri, S. & Owens, B. (eds) *Stratigraphic Palynology of the Palaeozoic of Saudi Arabia*. GeoArabia Special Publication, **1**, 57–81.

Le Hérissé, A. 2001. Evolution of Devonian phytoplanktonic assemblages in the Upper Ererê Formation and Curuá Group (Barreirinha and lower Curiri formations), Tapajós River area, Amazon Basin, northern Brazil. *In:* Melo, J. H. G. & Terra, G. J. S. (eds), *Correlação de Seqüências Paleózoicas Sul-Americanas. Seção: Exploração de Petróleo*, **20**, 117–124.

Le Hérissé, A. 2002. Paleoecology, biostratigraphy and biogeography of late Silurian to early Devonian acritarchs and prasinophycean phycomata in well A161, Western Libya, North Africa. *Review of Palaeobotany and Palynology*, **118**, 359–395.

Le Hérissé, A. & Deunff, J. 1988. Acritarches et prasinophycees (Givetian supérieur–Frasnian moyen) de Ferques (Boulonnias–France). *In*: Brice, D. (ed.), *Le Dévonien de Ferques. Bas-Boulonnais (N. France)*. Biostratigraphie du Paleozoique, Université de Bretagne Occidentale, **7**, 103–152.

Le Hérissé, A. & Gourvennec, R. 1995. Biogeography of upper Llandovery and Wenlock acritarchs. *Review of Palaeobotany and Palynology*, **86**, 111–113.

Le Hérissé, A., Al-Tayyar, H. & van der Eem, H. 1995. Stratigraphic and paleogeographical significance of Silurian acritarchs from Saudi Arabia. *Review of Palaeobotany and Palynology*, **89**, 49–74.

Le Hérissé, A., Gourvennec, R. & Wicander, R. 1997*a*. Biogeography of Late Silurian and Devonian acritarchs and prasinophytes. *Review of Palaeobotany and Palynology*, **98**, 105–124.

Le Hérissé, A., Rubinstein, C. & Steemans, P. 1997*b*. Lower Devonian palynomorphs from the Talacasto Formation, Cerro del Fuerte Section, San Juan Precordillera, Argentina. *In*: Fatka, O. & Servais, T. (eds), *Acritarcha in Praha 1996. Proceedings of the International Meeting and Workshop*. *Acta Universitatis Carolinae*, *Geologica*, **40**, 497–515. [For 1996]

2187 Le Hérissé, A., Servais, T. & Wicander, R. 2000. Devonian acritarchs and related
2188 forms. *Courier Forschungsinstitut Senckenberg*, **220**, 195–205.

2189 Le Hérissé, A., Perez-Leyton, M., Paris, F., Morales, R. & Racheboeuf, P. R. 2004.
2190 Marine palynomorphs from the Siluro-Devonian transition and Lower Devonian
2191 in the Boomerang area, Bolivia. XII International Palynological Conference,
2192 Session G3: Lower Paleozoic Palynology, CIMP Symposium, Granada, 4—9
2193 July 2004. *Polen*, **14**, 146.

2194 Le Hérissé, A., Al-Ruwaili, M., Miller, M. & Vecoli, M. 2007. Environmental
2195 changes reflected by palynomorphs in the early Middle Ordovician Hanadir
2196 Member of the Qasim Formation, Saudi Arabia. *Revue de micropaléontologie*,
2197 **50**, 3–16.

2198 Le Hérissé, A., Dorning, K. J., Mullins, G. L. & Wicander, R. 2009. Global patterns
2199 of organic-walled phytoplankton biodiversity during the Late Silurian to Earliest
2200 Devonian. *Palynology*, **33**, (1), 25–75.

2201 Legault, J. A. 1973. Chitinozoa and Acritarcha of the Hamilton Formation (Middle
2202 Devonian), Southwestern Ontario. *Geological Survey of Canada, Bulletin*, **221**,
2203 1–103.

2204 Li, J. 1987. Ordovician acritarchs from the Meitan Formation of Guizhou Province,
2205 south-west China. *Palaeontology*, **30**, 613–634.

2206 Li, J. 1989. Early Ordovician Mediterranean Province acritarchs from Upper
2207 Yangtze Region, China. *In*: *Developments in Geoscience: contributions to the*
2208 *28th International Geological Congress, 1989, Washington D.C.* Chinese
2209 Academy of Science, Beijing, 231–234.

2210 Li, J. 1990. Ordovician acritarchs from the Jiuxi Formation of Jishou, Hunan. *Acta*
2211 *Micropalaeontologica Sinica*, **7**, (2), 141–160, pls I–V.

2212 Li, J. & Servais, T. 2002. Ordovician acritarchs of China and their utility for global
2213 palaeobiogeography. *Bulletin de la Société géologique de France*, **173**, 399–406.

2214 Li, J., Servais, T. & Brocke, R. 2002*a*. Chinese Paleozoic acritarch research: review
2215 and perspectives. *Review of Palaeobotany and Palynology*, **118**, 181–193.

Li, J., Wang, Y., Servais, T. & Brocke, R. 2002*b*. Ordovician acritarchs from Meitan Formation of Huanghuachong, Guizhou, South China. *Acta Palaeontologica Sinica*, **41**, 96–104.

Li, J., Servais, T., Yan, K. & Zhu, H. 2004. A nearshore–offshore trend in the acritarch distribution of the Early–Middle Ordovician of the Yangtze Platform, South China. *Review of Palaeobotany and Palynology*, **130**, 141–161. doi:10.1016/j.revpalbo.2003.12.005

Loboziak, S., Streel, M. & Vanguestaine, M. 1983. Miospores et Acritarches de la formation d'Hydrequent (Frasnien supérieur à Famennien inférieur, Boulonnais, France). *Annales de la Société géologique de Belgique*, **106**, 173–183.

Loeblich, A. R. Jr. & Wicander, E. R. 1976. Organic-walled microplankton from the Lower Devonian (Late Gedinnian) Haragan and Bois d'Arc Formations of Oklahoma, USA, Part 1. *Palaeontographica*, Abteilung B, **159**, 1–139.

Lu Li-chang. 1987. Acritarchs from the Dawan Formation (Arenigian) of Huanghuachang in Yichang, western Hubei. *Acta Micropalaeontologica Sinica*, **4**, (1), 87–102, pls I–III.

Lu Li-chang & Wicander, R. 1988. Upper Devonian acritarchs and spores from the Hongguleleng Formation, Hefeng District in Xinjiang, China. *Revista Española de Micropaleontología*, **20**, (1), 109–148.

Mabillard, J. E. & Aldridge, R. J. 1985. Microfossil distribution across the base of the Wenlock Series in the type area. *Palaeontology*, **28**, 89–100.

Maletz, J. & Servais, T. 1993. Acritarchs and graptolites from the Early Llanvirn (Ordovician) of the Herscheider Schichten (Rheinisches Schiefergebirge, Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **190**, 125–142.

Martin, F. 1969. Les Acritarches de l'Ordovicien et du Silurien belges. Détermination et valeur stratigraphique. *Mémoires de l'Institut royal des Sciences naturelles de Belgique*, **160** [for 1968], 1–175.

Martin, F. 1974. Ordovicien supérieur et Silurien inférieur à Deerlijk (Belgique). Palynofacies et microfacies. *Mémoires de l'Institut royal des Sciences naturelles de Belgique*, **174** [for 1973], 1–71.

2247 Martin, F. 1977. Acritarches du Cambro-Ordovicien du Massif du Brabant,
2248 Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique*,
2249 *Sciences de la Terre,* **51** [for 1975], (1), 1–33.

2250 Martin, F. 1981. Acritarches du Famennien inférieur à Villers-sur-Lesse (Belgique).
2251 *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la*
2252 *Terre,* **52**, (2), 1–49.

2253 Martin, F. 1982*a*. Some aspects of late Cambrian and early Ordovician acritarchs.
2254 *In*: Bassett, M. G. & Dean, W. T. (eds), *The Cambrian-Ordovician Boundary:*
2255 *Sections, Fossil Distributions, and Correlations*. National Museum of Wales,
2256 Cardiff, Geological Series **3**, 29–40.

2257 Martin, F. 1982*b*. Acritarches et chitinozoires de la partie supérieure du Frasnian
2258 dans un affleurement au nord immediate de Frasnes (Belgique). *Bulletin de*
2259 *l'Institut royal des sciences naturelles Belgique, Sciences de la Terre,* **54**, (2), 1–
2260 17.

2261 Martin, F. 1984. New Ordovician (Tremadoc) acritarch taxa from the middle
2262 member of the Survey Peak Formation at Wilcox Pass, Southern Canadian Rocky
2263 Mountains, Alberta. *In*: Current Research, Part A, *Geological Survey of Canada,*
2264 *Paper,* **84–1A**, 441–448.

2265 Martin, F. 1985. Acritarches du Frasnien supérieur et du Famennien inférieur du
2266 bord meridional du Bassin de Dinant (Ardenne belge). *Bulletin de l'Institut royal*
2267 *des Sciences naturelles de Belgique, Sciences de la Terre,* **55**, (7), 1–57.

2268 Martin, F. 1988. Late Ordovician and Early Silurian acritarchs. *In*: Cocks, L. R. M.
2269 & Rickards, R. B. (eds) *A global analysis of the Ordovician–Silurian Boundary*.
2270 *Bulletin of the British Museum (Natural History)*, Geology Series, **43**, 299–309.

2271 Martin, F. 1989. Acritarchs. *In*: Holland, C. H. & Bassett, M. G. (eds) *A global*
2272 *standard for the Silurian System*. National Museum of Wales, Cardiff,
2273 Geological Series **9**, 207– 215.

2274 Martin, F. 1992. Uppermost Cambrian and Lower Ordovician acritarchs and Lower
2275 Ordovician chitinozoans from Wilcock Pass, Alberta. *Geological Survey of*
2276 *Canada, Bulletin*, **420**, 1–57.

2277 Martin, F. & Dean, W. T. 1981. Middle and Upper Cambrian and Lower Ordovician
2278 acritarchs from Random Island, eastern Newfoundland. *Geological Survey of*
2279 *Canada*, *Bulletin*, **343**, 1–43.

2280 Martin, F. & Dean, W. T. 1984. Middle Cambrian acritarchs from the Chamberlains
2281 Brook and Manuels River formations at Random Island, Eastern Newfoundland.
2282 *In*: Current Research, Part A, *Geological Survey of Canada, Paper,* **84–1A**, 429–
2283 440.

2284 Martin, F. & Dean, W. T. 1988. Middle and Upper Cambrian acritarch and trilobite
2285 zonation at Manuels River and Random Island, Eastern Newfoundland.
2286 *Geological Survey of Canada*, *Bulletin*, **381**, 1–91.

2287 Martin, F. & Rickards, R. B. 1979. Acritarches, chitinozoaires et graptolithes
2288 ordoviciens et siluriens de la Vallée de la Sennette (Massif du Brabant, Belgique).
2289 *Annales de la Société géologique de Belgique*, **102**, 189–197.

2290 Martin, F. & Yin, L.-M. 1988. Early Ordovician acritarchs from Southern Jilin
2291 Province, North-East China. *Palaeontology*, **31**, 109–127.

2292 Martin, R. E., Quigg, A. & Podkovyrov, V. 2008. Marine biodiversification in
2293 response to evolving phytoplankton stoichiometry. *Palaeogeography,*
2294 *Palaeoclimatology, Palaeoecology*, **258**, 277–291.

2295 Martínez Macchiavelo, J. C. 1968. Quelques acritarches d'une échantillon du
2296 Dévonien inférieur (Cordobés de Blanquillo, Département de Durazno, Uruguay).
2297 *Revue de Micropaléontologie*, **11**, 77–84.

2298 Masiak M., Podhalanska T. & Stempien-Salek M. 2003. Ordovician–Silurian
2299 boundary in the Bardo Syncline, Holy Cross Mountains, Poland – new data on
2300 fossil assemblages and sedimentary succession. *Geological Quarterly*, **47**, 311–
2301 330.

2302 Maziane-Serraj, N., Brück, P. M., Higgs, K. T., & Vanguestaine, M. 1999. Re-
2303 evaluation of proposed terranes in the Leinster Lower Palaeozoic Massif in
2304 Ireland using palynology: some preliminary results. *In*: Kraft, P. & Fatka, O.
2305 (eds) *Quo vadis Ordovician? Short papers of the 8th International Symposium*
2306 *on the Ordovician System (Prague, June 20–25, 1999)*. *Acta Universitatis*
2307 *Carolinae*, *Geologica*, **43**, (1–2), 241–242.

2308 Maziane-Serraj, N., Brück, P. M., Higgs, K. T., & Vanguestaine, M. 2000.
2309 Ordovician and Silurian acritarch assemblages from the west Leinster and
2310 Slievenamon areas of southeast Ireland. *Review of Palaeobotany and*
2311 *Palynology*, **113**, 57–71.

2312 Melendi, D. L. & Volkheimer, W. 1982. Datos palinológicos del límite Ordovícico-
2313 Silúrico de Talacasto, Provincia de san Juan. Parte I: Base del Silúrico. *Revista*
2314 *de la Asociación Geológica Argentina*, **37**, 221–236.

2315 Melendi, D. L. & Volkheimer, W. 1983. Datos palinológicos del límite Ordovícico-
2316 Silúrico de Talacasto (Provincia de San Juan). Parte II: La microflora de los
2317 estratos con *Climacograptus putillus* (Hall). *Revista Técnica YPF*, **9**, 157–163.

2318 Melo, J. H. G. 2000. Palynological evaluation and correlation of some Silurian-
2319 Devonian sections of southern Bolivia. *XIV Congreso Geológico Boliviano, La*
2320 *Paz*, 123–141.

2321 Melo, J. H. G. 2005. Palynostratigraphy of some Paleozoic rock units of Bolivia:
2322 additional results. *Proceedings of the 6th Hydrocarbon Exploration and*
2323 *Development Congress, Mar del Plata, CD-Rom*.

2324 Moczydłowska, M. 1991. Acritarch biostratigraphy of the Lower Cambrian and the
2325 Precambrian–Cambrian boundary in southeastern Poland. *Fossils and Strata*, **29**,
2326 1–127.

2327 Moczydłowska, M. 1998. Cambrian acritarchs from Upper Silesia, Poland –
2328 biochronology and tectonic implications. *Fossils and Strata*, **46**, 1–121.

2329 Moczydłowska, M. 2010. Life cycle of early Cambrian microalgae from the *Skiagia*-
2330 plexus acritarchs. *Journal of Paleontology*, **84**, (2), 216–230.

2331 Moczydłowska, M. & Stockfors, M. 2004. Acritarchs from the Cambrian–
2332 Ordovician boundary interval on Kolguev Island, Arctic Russia. *Palynology*, **28**,
2333 15–73.

2334 Moczydłowska, M. & Zang, W.-L. 2006. The Early Cambrian acritarch *Skiagia* and
2335 its significance for global correlation. *Palaeoworld*, **15**, 328–347.

2336 Molyneux, S. G. 1987. Acritarchs and chitinozoa from the Arenig Series of south-
2337 west Wales. *Bulletin of the British Museum (Natural History)*, Geology Series,
2338 **41**, 309–364.

2339 Molyneux, S. G. 1988. Late Ordovician acritarchs from northeast Libya. *In*: El-
2340 Arnauti, A., Owens, B. & Thusu, B. (eds) *Subsurface Palynostratigraphy of*
2341 *Northeast Libya*. Garyounis University, Benghazi, Libya, 45–59.

2342 Molyneux, S. G. 1990. Advances and problems in Ordovician palynology of
2343 England and Wales. *Journal of the Geological Society*, **147**, 615–618.
2344 doi:10.1144/gsjgs.147.4.0615

2345 Molyneux, S. G. 1999. A reassessment of Manx Group acritarchs, Isle of Man. *In*:
2346 Woodcock, N. H., Quirk, D. G., Fitches, W. R. & Barnes, R. P. (eds) *In sight of*
2347 *the suture: the Palaeozoic geology of the Isle of Man in its Iapetus Ocean context*.
2348 Geological Society of London, Special Publication **160**, 23–32.

2349 Molyneux, S. G. 2009. Acritarch (marine microphytoplankton) diversity in an Early
2350 Ordovician deep-water setting (the Skiddaw Group, northern England):
2351 implications for the relationship between sea-level change and phytoplankton
2352 diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **275**, 59–76.

2353 Molyneux, S. G. & Paris, F. 1985. Late Ordovician palynomorphs. *Journal of*
2354 *Micropalaeontology*, **4**, 11–26.

2355 Molyneux, S. G., Manger, W. L. & Owens, B. 1984. Preliminary account of Late
2356 Devonian palynomorph assemblages from the Bedford Shale and Berea
2357 Sandstone formations of central Ohio, U.S.A. *Journal of Micropaleontology*, **3**,
2358 41–51.

2359 Molyneux, S., Osterloff, P., Penney, R. & Spaak, P. 2006. Biostratigraphy of the
2360 Lower Palaeozoic Haima Supergroup, Oman; its application in sequence
2361 stratigraphy and hydrocarbon exploration. *GeoArabia*, **11**, (2), 17–48.

2362 Molyneux, S. G., Barron, H. F. & Smith, R. A. 2008. Upper Llandovery–Wenlock
2363 (Silurian) palynology of the Pentland Hills inliers, Midland Valley of Scotland.
2364 *Scottish Journal of Geology*, **44**, (2), 151–168.

2365 Moreau-Benoit, A. 1972. Palynologie stratigraphique du Silurien et du Dévonien
2366 dans le sud-est du Massif Armoricain (synclinoriums de Saint-Julien-de-
2367 Vouvantes et d'Ancenis). *Compte Rendu, Septième Congrès International de*
2368 *Stratigraphie et de Géologie du Carbonifère, Krefeld, August 1971*, **1**, 285–293

2369 Moreau-Benoit, A. 1974. Recherches de palynologie et de planctologie sur le
2370 Dévonien et quelques formations siluriennes dans le sud-est du Massif
2371 Armoricain. *Mémoires de la Société géologique et minéralogique de Bretagne,*
2372 **18**, 1–248.

2373 Moreau-Benoit, A. 1984. Acritarches et Chitinozoaires du Dévonien moyen et
2374 supérieur de Libye occidentale. *Review of Palaeobotany and Palynology*, **43**,
2375 187–216.

2376 Munnecke, A., Calner, M., Harper, D. A. T. & Servais, T. 2010. Ordovician and
2377 Silurian sea-water chemistry, sea level, and climate: a synopsis.
2378 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **296**, 389–413.

2379 Oliveira, S. F. & Burjack, M. I. A. 1997. *Petrovina connata* gen. n., sp. n.,
2380 provavelmente relacionado a Chlorophyta, da Formação Ponta Grossa
2381 (Neodevoniano), Bacia do Paraná, MT, Brasil. *Revista Universidade Guarulhos*
2382 *Geociências*, **1**, (3), 46–50.

2383 Ottone, E. 1996. Devonian palynomorphs from the Los Monos Formation, Tarija
2384 Basin, Argentina. *Palynology*, **20**, 105–155.

2385 Palacios T., Jensen, S., Barr, S. M. & White, C. E. 2009. Acritarchs from the
2386 MacLean Brook Formation, southeastern Cape Breton Island, Nova Scotia,
2387 Canada: new data on Middle Cambrian–Lower Furongian acritarch zonation.
2388 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **273**, 123–141.

2389 Palacios, T., Jensen, S., Barr, S. M., White, C. E. & Miller, R. F. 2011. New
2390 biostratigraphical constraints on the lower Cambrian Ratcliffe Brook Formation,
2391 southern New Brunswick, Canada, from organic-walled microfossils.
2392 *Stratigraphy*, **8**, (1), 45–60.

2393 Paris, F. 1988. New chitinozoans from the Late Ordovician-Late Devonian of
2394 northeast Libya. *In*: El-Arnauti, A., Owens, B. & Thusu, B. (eds) *Subsurface*
2395 *Palynostratigraphy of Northeast Libya*. Garyounis University, Benghazi, Libya,
2396 73–87.

2397 Paris, F., Richardson, J. B., Riegel, W., Streel, M. & Vanguestaine, M. 1985.
2398 Devonian (Emsian–Famennian) palynomorphs. *In*: Thusu, B. & Owens, B. (eds),

*Palynostratigraphy of North-East Libya*. *Journal of Micropalaeontology*, **4,** (1), 49–82.

Paris, F., Bourahrouh, A. & Le Hérissé, A. 2000. The effects of the final stages of the Late Ordovician glaciation on marine palynomorphs (chitinozoans, acritarchs, leiospheres) in well Nl-2 (NE Algerian Sahara). *Review of Palaeobotany and Palynology*, **113**, 87–104.

Paris, F., Le Hérissé, A., Monod, O., Kozlu, H., Ghienne, J.-F., Dean, W. T., Vecoli, M. & Günay, Y. 2007. Ordovician chitinozoans and acritarchs from southern and south eastern Turkey. *Revue de micropaléontologie*, **50**, 81–107.

Parsons, M. G. & Anderson, M. M. 2000. Acritarch microfloral succession from the Late Cambrian and Ordovician (early Tremadoc) of Random Island, eastern Newfoundland, and its comparison to coeval microfloras, particularly those of the East European Platform. *American Association of Stratigraphic Palynologists, Contribution Series*, **38**, 1–123.

Pereira, Z., Matos J., Fernandes, P. & Oliveira, J. T. 2008. Palynostratigraphy and systematic palynology of the Devonian and Carboniferous successions of the South Portuguese Zone, Portugal. *Memórias Geológicas do Instituto Nacional de Engenharia, Tecnologia e Inovação*, **34**, 1–181.

Playford, G. 1977. Lower to Middle Devonian acritarchs of the Moose River Basin, Ontario. *Geological Survey of Canada, Bulletin*, **279**, 1–87.

Playford, G. 1981. Late Devonian acritarchs from the Gneudna Formation in the Western Carnarvon Basin, Western Australia. *Géobios*, **14**, 145–171.

Playford, G. & Dring, R. S. 1981. Late Devonian acritarchs from the Carnarvon Basin, Western Australia. *Special Papers in Palaeontology*, **27**, 1–78.

Playford, G. & Martin, F. 1984. Ordovician acritarchs from the Canning Basin, Western Australia. *Alcheringa*, **8**, 187–223.

Playford, G. & McGregor, D. C. 1993. Miospores and organic-walled microphytoplankton of Devonian-Carboniferous boundary beds (Bakken Formation), southern Saskatchewan: a systematic and stratigraphic appraisal. *Geological Survey of Canada, Bulletin*, **445**, 1–107.

Playford, G. & Wicander, R. 1988. Acritarch palynoflora of the Coolibah Formation (Lower Ordovician), Georgina Basin, Queensland. *Memoirs of the Association of Australasian Palaeontologists*, **5**, 5–40.

Playford, G. & Wicander, R. 2006. Organic-walled microphytoplankton of the Sylvan Shale (Richmondian: Upper Ordovician), Arbuckle Mountains, Southern Oklahoma. U.S.A. *Oklahoma Geological Survey Bulletin*, **148**, 1–116.

Playford, G., Ribecai, C. & Tongiorgi, M. 1995. Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cyclopospha*eridium: morphology, taxonomy, biostratigraphy, and palaeogeographic significance. *Bollettino della Società Paleontologica Italiana*, **34**, 3–54.

Pöthe de Baldis, E. D. 1974. Microplancton adicional del Silúrico Superior de Santiago del Estero, República Argentina. *Ameghiniana*, **11**, 313–327.

Pöthe de Baldis, E. D. 1978. Paleomicroplancton adicional del Devonico Inferior de Uruguay. *Revista Española de Micropaleontología*, **9**, 235–250.

Pöthe de Baldis, E. D. 1979. Acritarcos y quitinozoos del Devonico superior de Paraguay. *Palinologia*, *número extraordinario*, **1**, 161–177.

Pöthe de Baldis, E. D. 1987. Microplancton del Llandoveriano superior-Wenlockiano inferior, asociación de *Deunffia-Domasia*, de la Formación La Chilca, Aguada de Los Azulejitos, San Juan, Argentina. *Actas X Congreso Geológico Argentino*, Tucumán, **3**, 89–94.

Quadros, L. P. 1982. Distribuição bioestratigráfica dos Chitinozoa e Acritarchae no Bacia do Parnaíba. *PETROBRÁS. Ciência–Técnica–Petróleo. Seção Exploraçao de Petróleo*, **12**, 1–76.

Quadros, L. P. 1988. Zoneamento bioestratigráfico do Paleozóico inferior e médio (seção marinha) da Bacia do Solimões. *Boletim de Geociências da PETROBRÁS*, **2**, 95–109.

Quadros, L. P. 1999. Novos acritarcos do Devoniano superior da Bacia do Amazonas. *Acta Geologica Leopoldensia*, **23**, 15–27.

Quintavalle, M. & Playford, G. 2006*a*. Palynostratigraphy of Ordovician strata, Canning Basin, Western Australia. Part One: acritarchs and prasinophytes. *Palaeontographica*, Abteilung B, **275**, 1–88.

2460 Quintavalle, M. & Playford, G. 2006*b*. Palynostratigraphy of Ordovician strata,
2461 Canning Basin, Western Australia. Part Two: chitinozoans and biostratigraphy.
2462 *Palaeontographica*, Abteilung B, **275**, 89–131.

2463 Quintavalle, M., Tongiorgi, M. & Gaetani, M. 2000. Lower to Middle Ordovician
2464 acritarchs and chitinozoans from Northern Karakorum Mountains, Pakistan.
2465 *Rivista Italiana di Paleontologia e Stratigrafia*, **106**, 3–18.

2466 Raevskaya, E. G. 1999. Early Arenig acritarchs from the Leetse Formation (St.
2467 Petersburg region, northwest Russia) and their palaeogeographic significance.
2468 *Bollettino della Società Paleontologica Italiana*, **38**, 247–256.

2469 Raevskaya, E. & Golubkova, E. 2006. Biostratigraphical implication of Middle–
2470 Upper Cambrian acritarchs from Severnaya Zemlya (high Arctic of Russia).
2471 *Review of Palaeobotany and Palynology*, **139**, 53–69.

2472 Raevskaya, E., Vecoli, M., Bednarczyk, W. & Tongiorgi, M. 2004. Billingen (Lower
2473 Arenig/Lower Ordovician) acritarchs from the East European Platform and their
2474 palaeobiogeographic significance. *Lethaia*, **37**, 97–111.

2475 Raevskaya, E. G., Volkova, N. A. & Sivertseva, I. A. 2006. The Darriwilian
2476 acritarch assemblage from Ordovician deposits of the Arkhangelsk Oblast, the
2477 northern Russian Plate. *Stratigraphy and Geological Correlation*, **14**, (4), 386–
2478 398.

2479 Rauscher, R. 1969. Présence d'une forme nouvelle d'Acritarches dans le Dévonien
2480 de Normandie. *Comptes rendus des séances de l'Académie des Sciences de*
2481 *Paris, série D*, **268**, 34–36.

2482 Reaugh, A. B. 1978. A new species of *Cymatiosphaera* (Acritarcha) with constant
2483 field tabulation, from the Devonian of Tennessee. *Palaeontology*, **2,** (4), 835–
2484 856.

2485 Ribecai, C. & Tongiorgi, M. 1995. Arenigian acritarchs from Horns Udde (Öland,
2486 Sweden): a preliminary report. *Review of Palaeobotany and Palynology*, **86**, 1–
2487 11.

2488 Ribecai, C. & Vanguestaine, M. 1993. Latest Middle-Late Cambrian acritarchs from
2489 Belgium and northern France. *Special Papers in Palaeontology*, **48**, 45–55.

2490 Ribecai, C., Bruton, D. L. & Tongiorgi, M. 1999. Acritarchs from the Ordovician of
2491 the Oslo Region, Norway. *Norsk Geologisk Tiddskrift*, **80**, 251–258.

2492 Ribecai, C., Raevskaya, E. & Tongiorgi, M. 2002. *Sacculidium* gen. nov.
2493 (Acritarcha), a new representative of the Ordovician *Stelomorpha–Tranvikium*
2494 plexus. *Review of Palaeobotany and Palynology*, **121**, 163–203.

2495 Richardson, J. B. & Ioannides, N. S. 1973. Silurian palynomorphs from the
2496 Tanezzuft and Acacus Formation, Tripolitania, North Africa. *Micropaleontology*,
2497 **19**, 257–307.

2498 Rickards, R. B., Booth, G. A., Paris, F. & Heward, A. P. 2010. Marine flooding
2499 events of the Early and Middle Ordovician of Oman and the United Arab
2500 Emirates and their graptolite, acritarch and chitinozoan associations. *GeoArabia*,
2501 **15**, (4), 81–120.

2502 Riegel, W. 1974. Phytoplankton from the Upper Emsian and Eifelian of the
2503 Rhineland, Germany. A preliminary account. *Review of Palaeobotany and*
2504 *Palynology*, **18**, 29–39.

2505 Riegel, W. 2008. The Late Palaeozoic phytoplankton blackout — artefact or
2506 evidence of global change? *Review of Palaeobotany and Palynology*, **148**, 73–
2507 90.

2508 Rodriguez Gonzalez, R. M. 1983. Palinología de las Formaciones del Silúrico
2509 superior — Devónico inferior de la Cordillera Cantábrica. *Servicio de*
2510 *Publicaciones, Universidad de León, Spain*, 1–231.

2511 Rubinstein, C. 1997. Silurian acritarchs from South America: a review. *In*: Fatka, O.
2512 & Servais, T. (eds), *Acritarcha in Praha 1996. Proceedings of the International*
2513 *Meeting and Workshop*. *Acta Universitatis Carolinae*, *Geologica*, **40**, (3–4),
2514 603–629. [For 1996].

2515 Rubinstein, C. V. 1999. Primer registro palinológico de la Formación Punta Negra
2516 (Devónico Medio-Superior), de la Precordillera de San Juan, Argentina.
2517 *Ameghiniana, Tomo Especial 6. X Simposio Argentino de Paleobotánica y*
2518 *Palinología*, 13–18.

2519 Rubinstein, C. V. 2000. Middle Devonian palynomorphs from the San Juan
2520 Precordillera, Argentina: biostratigraphy and paleobiogeography. *I Congresso*

*Ibérico de Paleontologia/XVI Jornadas de la Sociedad Española de Paleontologia, VIII International Meeting of IGCP 421*, 274–275.

Rubinstein, C. V. 2001. Microflora y microplancton silúricos de la Precordillera Central de San Juan, Argentina. *In*: Fombella Blanco, M. A., Fernández González, D. & Valencia Barrera, R. M. (eds) *Palinología: Diversidad y Aplicaciones*. Secretariado de Publicaciones, Universidad de León, Spain, 45–54.

Rubinstein, C. V. 2003. Ordovician acritarchs from northwestern Argentina: new insights into the biostratigraphy and palaeoenvironmental aspects of the Central Andean Basin and Famatina. *In*: Albanesi, G. L., Beresi, M. S. & Peralta, S. H. (eds) *Ordovician from the Andes: Proceedings of the 9th International Symposium on the Ordovician System*. Tucumán: Serie Correlación Geológica, **17**, INSUGEO, 125–130.

Rubinstein, C. V. 2005. Ordovician to Lower Silurian palynomorphs from the Sierras subandinas (Subandean ranges), northwestern Argentina: a preliminary report. *In*: Steemans, P. & Javaux, E. (eds) *Pre-Cambrian to Palaeozoic Palaeopalynology and Palaeobotany*. *Carnets de Géologie*/*Notebooks on Geology*, Brest, Memoir **2005/02**, 51–56.

Rubinstein, C. V. & Brussa, E. D. 1999. A palynomorph and graptolite biostratigraphy of the Central Precordillera Silurian Basin, Argentina. *Bollettino della Società Paleontologica Italiana*, **38**, 257–266.

Rubinstein, C. V. & Muro, V. J. C. 2011. Silurian to Early Devonian organic-walled phytoplankton and miospores from Argentina: biostratigraphy and diversity trends. *Geological Journal* (published online: 14 November 2011). doi: 10.1002/gj.1327.

Rubinstein, C. V. & Steemans, P. 2007. New palynological data from the Devonian Villavicencio Formation, Precordillera of Mendoza, Argentina. *Ameghiniana*, **44**, 3–9.

Rubinstein, C. V. & Vaccari, N. E. 2004. Cryptospore assemblages from the Ordovician–Silurian boundary in the Puna Region, north-west Argentina. *Palaeontology*, **47**, 1037–1061.

Rubinstein, C. V., Mángano, M. G. & Buatois, L. A. 2003. Late Cambrian acritarchs from the Santa Rosita Formation: implications for the Cambrian-Ordovician boundary in the Eastern Cordillera, northwest Argentina. *Revista Brasileira de Paleontologia*, **6**, 43–48.

Rubinstein, C. V., de la Puente, G. S., Delabroye, A. & Astini, R. A. 2008*a*. New palynological record of the Ordovician/Silurian boundary in the Argentine Cordillera Oriental, Central Andean Basin. *Terra Nostra* 2008/2, IPC – XII / IOPC – VIII, Bonn, p. 239.

Rubinstein, C. V., Le Hérissé, A. & Steemans, P. 2008*b*. Lochkovian (Early Devonian) acritarchs and prasinophytes from the Solimões Basin, northwestern Brazil. *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen*, **249**, (2), 167–184.

Rubinstein, C. V., Vecoli, M. & Astini, R. A. 2011. Biostratigraphy and paleoenvironmental characterization of the Middle Ordovician from the Sierras Subandinas (NW Argentina) based on organic-walled microfossils and sequence stratigraphy. *Journal of South American Earth Sciences*, **31**, 124–138.

Rushton, A. W. A. 2011. Chronostratigraphical subdivisions of the Cambrian Period. *In*: Rushton, A.W.A., Brück, P.M., Molyneux, S.G., Williams, M. & Woodcock, N.H. *A Revised Correlation of the Cambrian Rocks in the British Isles*. Geological Society, London, Special Report **25**, 3–5.

Rushton, A. W. A. & Molyneux, S. G. 2011. Biostratigraphical divisions. *In*: Rushton, A.W.A., Brück, P.M., Molyneux, S.G., Williams, M. & Woodcock, N.H. *A Revised Correlation of the Cambrian Rocks in the British Isles*. Geological Society, London, Special Report **25**, 6–12.

Scotese, C. R. 1986. Phanerozoic reconstructions: a new look at the assembly of Asia. *University of Texas, Institute for Geophysics, Technical Report*, **66**, 54 pp.

Scotese, C. R. & McKerrow, W. S. 1990. Revised world maps and introduction. *In*: McKerrow, W. S. & Scotese, C. R. (eds), *Palaeozoic Palaeogeography and Biogeography*. Memoirs of the Geological Society of London, **12**, 1–21.

Servais, T. 1993. The Ordovician acritarch *Frankea*. *Special Papers in Palaeontology*, **48**, 79–95.

Servais, T. 1994. The Ordovician acritarchs from Rügen (NE-Germany): palaeobiogeographical evidence for the attribution to Eastern Avalonia. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1994**, (9), 566–580.

Servais, T. & Fatka, O. 1997. Recognition of the Trans-European Suture Zone (TESZ) by the palaeobiogeographical distribution pattern of early to middle Ordovician acritarchs. *Geological Magazine*, **134**, 617–625.

Servais, T. & Maletz, J. 1992. Lower Llanvirn (Ordovician) graptolites and acritarchs from the "Assise de Huy", Bande de Sambre-et-Meuse, Belgium. *Annales de la Société Géologique de Belgique*, **115**, 265–285.

Servais, T., Brocke, R., Fatka, O., Le Hérissé, A. & Molyneux, S. G. 1997. Value and meaning of the term acritarch. *In*: Fatka, O. & Servais, T. (eds), *Acritarcha in Praha 1996. Proceedings of the International Meeting and Workshop*. *Acta Universitatis Carolinae*, *Geologica*, **40**, 631–643. [For 1996]

Servais, T., Li, J., Molyneux, S & Raevskaya, E. 2003. Ordovician organic-walled microphytoplankton (acritarch) distribution: the global scenario. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 149–172.

Smelror, M. 1987. Early Silurian acritarchs and prasinophycean algae from the Ringerike District, Oslo Region (Norway). *Review of Palaeobotany and Palynology*, **52**, 137–159.

Smelror, M. 1989. Palynomorphs from the *Cyrtograptus centrifugus* graptolite zone (Early Wenlock, Silurian), Bornholm. *Bulletin of the Geological Society of Denmark*, **39**, 83–89.

Staplin, F. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology*, **4**, 392–424.

Stockmans, F. & Willière, Y. 1960. Hystrichosphères du Dévonien belge (Sondage de l'Asile d'aliénés à Tournai). *Senckenbergiana Lethaea*, **41**, 1–11.

Stockmans, F. & Willière, Y. 1962*a*. Hystrichosphères du Dévonien belge (Sondage de l'Asile d'aliénés à Tournai). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **71,** (1), 41–77.

Stockmans, F. & Willière, Y. 1962*b*. Hystrichosphères du Dévonien belge (Sondage de Wépion). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **71**, (1), 83–99.

Stockmans, F. & Willière, Y. 1966. Les Acritarches du Dinantien du sondage de l'Asile d'aliénés à Tournai. *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **74**, (2, 3), 462–477.

Stockmans, F. & Willière, Y. 1967. Les Acritarches du Dinantien du sondage de Vieux Leuze à Leuze (Hainaut, Belgique). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **75**, (2), 233–242.

Stockmans, F. & Willière, Y. 1969. Acritarches du Famennien inférieur. *Académie royale de Belgique, Classe des Sciences, Mémoires*, **38**, 1–63.

Stockmans, F. & Willière, Y. 1974. Acritarches de la "Tranchée de Sanzeille" (Frasnien supérieur et Famennien inférieur). *Académie royale de Belgique, Classe des Sciences, Mémoires*, **41**, 1–79.

Streel, M., Paris, F., Riegel, W. & Vanguestaine, M. 1988. Acritarch, chitinozoan and spore stratigraphy from the Middle and Late Devonian of northeast Libya. *In*: El-Arnauti, A., Owens, B. & Thusu, B. (eds) *Subsurface palynostratigraphy of northeast Libya*. Garyounis University Publication, Benghazi, Libya, 111–128.

Stricanne, L., Munnecke, A., Pross, J. & Servais, T. 2004. Acritarch distribution along an inshore–offshore transect in the Gorstian (lower Ludlow) of Gotland, Sweden. *Review of Palaeobotany and Palynology*, **130**, 195–216.

Tongiorgi, M. & Di Milia, A. 1999. Differentiation and spread of the Baltic Acritarch Province (Arenig-Llanvirn). *Bollettino della Società Paleontologica Italiana*, **38**, 297–312.

Tongiorgi, M., Albani, R. & Di Milia, A. 1984. The Solanas Sandstones of Central Sardinia: new paleontological data (Acritarchs) and an attempt of geological interpretation (a "post-sardinian" molasse?). *Bulletin de la Société géologique de France*, **26**, (4), 665–680.

2641 Tongiorgi, M., Di Milia, A., Le Fort, P. & Gaetani, M. 1994. Palynological dating
2642 (Arenig) of the sedimentary sequence overlying the Ishkarwaz Granite (upper
2643 Yarkhun valley, Chitral, Pakistan). *Terra Nova*, **6**, 595–607.

2644 Tongiorgi, M., Yin, L.-M. & Di Milia, A. 1995. Arenigian acritarchs from the
2645 Daping section (Yangtze Gorges area, Hubei Province, Southern China) and their
2646 palaeogeographic significance. *Review of Palaeobotany and Palynology*, **86**, 13–
2647 48.

2648 Tongiorgi, M., Yin, L.-M., Di Milia, A. & Ribecai, C. 1998. Changing
2649 paleogeographical affinities of the acritarch assemblages throughout the Dawan
2650 Formation (Arenig, Yichang Area, South China). *Palynology*, **22**, 181–196.

2651 Tongiorgi, M., Yin, L.-M. & Di Milia, A. 2003*a*. Lower Yushanian to lower
2652 Zhejiangian palynology of the Yangtze Gorges area (Daping and Huanghuachang
2653 sections), Hubei Province, South China. *Palaeontographica*, Abteilung B, **266**,
2654 1–160.

2655 Tongiorgi, M., Bruton, D. L. & Di Milia, A. 2003*b*. Taxonomic composition and
2656 palaeobiogeographic significance of the acritarch assemblages from the
2657 Tremadoc-Arenig (Hunneberg, Billingen, and lower Volkhov Stages) of the Oslo
2658 Region. *Bollettino della Società Paleontologica Italiana*, **42**, (3), 205–224.

2659 Torsvik, T. H. & Cocks, L. R. M. 2013. New global palaeogeographical
2660 reconstructions for the Lower Palaeozoic and their generation. *Memoir of the*
2661 *Geological Society of London*, **000**, 000–000. (This volume)

2662 Tropepi, R. & Ribecai, C. 2000. An unusual process structure in *Tresarcus*, a new
2663 acritarch genus from the Ordovician of Öland, Sweden. *Review of Palaeobotany*
2664 *and Palynology*, **111**, 103–109.

2665 Turner, R. E. 1986. New and revised acritarch taxa from the Upper Devonian
2666 (Frasnian) of Alberta, Canada. *Canadian Journal of Earth Sciences*, **23**, 599–
2667 607.

2668 Turner, R. E. 1991. New acritarch taxa from the Middle and Upper Devonian
2669 (Givetian–Frasnian) of western Canada. *Canadian Journal of Earth Sciences*, **28**,
2670 1471–1487.

2671 Uutela, A. & Tynni, R. 1991. Ordovician acritarchs from the Rapla borehole,
2672 Estonia. *Bulletin of the Geological Survey of Finland*, **353**, 1–135.

2673 Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Paris, F., Sabbe, K.,
2674 Zalasiewicz, J.A., Nõlvak, J. & Verniers, J. 2010*a*. Epipelagic chitinozoan
2675 biotopes map a steep latitudinal temperature gradient for earliest Late Ordovician
2676 seas: implications for a cooling Late Ordovician climate. *Palaeogeography,*
2677 *Palaeoclimatology, Palaeoecology*, **294**, 202–219.

2678 Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Paris, F., Zalasiewicz, J.A.,
2679 Sabbe, K., Challands, T.J., Verniers, J. & Servais, T. 2010*b*. Polar front shift and
2680 atmospheric $CO_2$ during the glacial maximum of the Early Paleozoic Icehouse.
2681 *PNAS*, **107**, 14983–14986.

2682 Vanguestaine, M. 1973. New acritarchs from the Upper Cambrian of Belgium.
2683 *Proceedings of the Third International Palynological Conference, Novosibirsk*
2684 *1971. Akademiya Nauk, SSSR, Geologicheskii Institut, Moskva*, 28–30.

2685 Vanguestaine, M. 1978*a*. Critères palynostratigraphiques conduisants à la
2686 reconnaissance d'un pli couché revinien dans le Sondage de Grand-Halleux.
2687 *Annales de la Société Géologique de Belgique*, **100**, 249–276.

2688 Vanguestaine, M. 1978*b*. Acritarches du Famennien supérieur du sondage de
2689 Tohogne (Belgique) et correlation biostratigraphique transcontinentale.
2690 *Palinologia, número extraordinario*, **1**, 481–489.

2691 Vanguestaine, M. 1986*a*. Progrès récents de la stratigraphie par Acritarches du
2692 Cambro-Ordovicien d'Ardenne, d'Irlande, d'Angleterre, du Pays de Galles et de
2693 Terre-Neuve orientale. *Annales de la Société géologique du Nord*, **105**, 65–76.

2694 Vanguestaine, M. 1986*b*. Late Devonian and Carboniferous acritarch stratigraphy
2695 and paleogeography. *Annales de la Société géologique de Belgique*, **109**, 93–102.

2696 Vanguestaine, M., Declairfayt, T., Rouhart, A. & Smeesters, A. 1983. Zonation par
2697 acritarches du Frasnien supérieur–Famennien inférieur dans les basins de Dinant,
2698 Namur, Herve et Campine (Dévonien supérieur de Belgique). *Annales de la*
2699 *Société géologique de Belgique*, **106**, 121–171.

2700 Vavrdová, M. 1965. Ordovician acritarchs from Central Bohemia. *Véstník*
2701 *Ústředního ústavu geologického*, **40**, 351–357, pls I–IV.

Vavrdová, M. 1966. Palaeozoic microplankton from Central Bohemia. *Časopis pro mineralogii a geologii*, **11**, 409–414, pls I–III.

Vavrdová, M. 1972. Acritarchs from Klabava Shales (Arenig). *Véstník Ústředního ústavu geologického*, **47**, 79–86, pls I–II.

Vavrdová, M. 1974. Geographical differentiation of Ordovician acritarch assemblages in Europe. *Review of Palaeobotany and Palynology*, **18**, 171–175.

Vavrdová, M. 1977. Acritarchs from the Šárka Formation (Llanvirnian). *Véstník Ústředního ústavu geologického*, **52**, 109–118, pls I–IV.

Vavrdová, M. 1986. New genera of acritarchs from the Bohemian Ordovician. *Časopis pro mineralogii a geologii*, **31**, 349–360, pls I–IV.

Vavrdová, M. 1990*a*. Early Ordovician acritarchs from the locality Myto near Rokycany (late Arenig, Czechoslovakia). *Časopis pro mineralogii a geologii*, **35**, 239–250.

Vavrdová, M. 1990*b*. Coenobial acritarchs and other palynomorphs from the Arenig/Llanvirn boundary, Prague basin. *Véstník Ústředního ústavu geologického*, **65**, 237–242, pls I–IV.

Vavrdová, M. 1993. Acritarch assemblages in the Arenig Series of the Prague Basin. *Special Papers in Palaeontology*, **48**, 125–139.

Vavrdová, M. 1997. Early Ordovician provincialism in acritarch distribution. *Review of Palaeobotany and Palynology*, **98**, 33–40.

Vavrdová, M. & Isaacson, P. 1997. Affinities of Late Devonian acritarchs from the Madre de Dios Basin, northern Bolivia. *In*: Fatka, O. & Servais, T. (eds), *Acritarcha in Praha 1996. Proceedings of the International Meeting and Workshop*. *Acta Universitatis Carolinae*, *Geologica*, **40**, 683–693. [For 1996]

Vavrdová, M. & Isaacson, P. 1999. Late Famennian phytogeographic provincialism: evidence for a limited separation of Gondwana and Laurentia. *In*: Feist, R., Talent, J. A. & Daurer, A. (eds), *North Gondwana: Mid-Paleozoic terranes, stratigraphy and biota*. *Abhandlungen der Geologischen Bundesanstalt*, **54**, 453–463.

2731 Vavrdová, M. & Isaacson, P. 2000. Palynology of selected Devonian strata, Western
2732 Gondwana. *Zentralblatt für Geologie und Paläontologie, Teil 1: Allgemeine,*
2733 *Angewandte, Regionale und Historische Geologie*, Jahrgang **1999**, (7/8), 799–
2734 821.

2735 Vavrdová, M., Bek, J., Dufka, P. & Isaacson, P. 1996. Palynology of the Devonian
2736 (Lochkovian to Tournaisian) sequence, Madre de Dios Basin, northern Bolivia.
2737 *Véstník Ceského geologického ústavu*, **71**, 333–349.

2738 Vecoli, M. 1996. Stratigraphic significance of acritarchs in Cambro-Ordovician
2739 boundary strata, Hassi-Rmel area, Algerian Sahara. *Bollettino della Società*
2740 *Paleontologica Italiana*, **35**, 3–58.

2741 Vecoli, M. 1999. Cambro-Ordovician palynostratigraphy (acritarchs and
2742 prasinophytes) of the Hassi-R'Mel area and northern Rhadames Basin, North
2743 Africa. *Palaeontographia Italica*, **86**, 1–112.

2744 Vecoli, M. 2000. Palaeoenvironmental interpretation of microphytoplankton
2745 diversity trends in the Cambrian–Ordovician of the northern Sahara Platform.
2746 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **160**, 329–346.

2747 Vecoli, M. 2004. Stratigraphic and palaeoenvironmental distribution of organic-
2748 walled microfossils in Cambrian-Ordovician transitional strata of borehole Bir
2749 Ben Tartar-1 (Tt-1; Ghadamis Basin, southern Tunisia). *Memoirs of the*
2750 *Association of Australasian Palaeontologists*, **29**, 13–30.

2751 Vecoli, M. 2008. Fossil microphytoplankton dynamics across the Ordovician-
2752 Silurian boundary. *Review of Palaeobotany and Palynology*, **148**, 91–107.

2753 Vecoli, M. & Le Hérissé, A. 2004. Biostratigraphy, taxonomic diversity, and
2754 patterns of morphological evolution of Ordovician acritarchs (organic-walled
2755 microphytoplankton) from the northern Gondwana margin in relation to
2756 palaeoclimatic and palaeogeographic changes. *Earth-Science Reviews*, **67**, 267–
2757 311.

2758 Vecoli, M. & Playford, G. 1997. Stratigraphically significant acritarchs in uppermost
2759 Cambrian to basal Ordovician strata of northwestern Algeria. *Grana*, **36**, 17–28.

2760 Vecoli, M., Delabroye, A., Spina, A. & Hints, O. 2011. Cryptospore assemblages
2761 from Upper Ordovician (Katian-Hirnatian) strata of Anticosti Island, Québec,

Canada, and Estonia: palaeophytogeographic and palaeoclimatic implications. *Review of Palaeobotany and Palynology*, **166**, 76–93.

Volkova, N. A. 1990. Middle and Upper Cambrian acritarchs in East European Platform. *Academy of Sciences, USSR, Geological Institute, Transactions*, **454**, 3–114 [in Russian].

Volkova, N. A. 1995. Acritarchs from the Cambrian–Ordovician boundary beds of the Baltic phytoplankton province [in Russian]. *Stratigraphy and Geological Correlation*, **3**, (4), 31–43.

Volkova, N. A. 1997. Paleogeography of phytoplankton at the Cambrian-Ordovician Boundary. *Paleontological Journal*, **31**, 135–140.

Welsch, M. 1986. Die Acritarchen der höheren Digermul-Gruppe, Mittelkambrium bis Tremadoc, Ost-Finnmark, Nord-Norwegen. *Palaeontographica*, Abteilung B, **201**, (1–4), 1–109, 9 pls., 27 figs.

Whelan, G.M. 1988. Preliminary acritarch and chitinozoan distributions across the Ordovician-Silurian boundary stratotype at Dob's Linn, Scotland. *In*: Cocks, L. R. M. & Rickards, R. B. (eds) *A global analysis of the Ordovician–Silurian Boundary*. *Bulletin of the British Museum (Natural History)*, Geology Series, **43**, 4–44.

White, D. E., Barron, H. F., Barnes, R. P. & Lintern, B. C. 1991. Biostratigraphy of late Llandovery (Telychian) and Wenlock turbiditic sequences in the SW Southern Uplands, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **82**, 297–322. doi:10.1017/S0263593300004181

Wicander, E. R. 1974. Upper Devonian–Lower Mississippian acritarchs and prasinophycean algae from Ohio, U.S.A. *Palaeontographica*, Abteilung B, **148**, 9–43.

Wicander, E. R. 1975. Fluctuations in a Late Devonian – Early Mississippian phytoplankton flora of Ohio, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **17**, 89–108.

Wicander, E. R. & Loeblich, A. R. Jr. 1977. Organic-walled microphytoplankton and its stratigraphic significance from the Upper Devonian Antrim Shale, Indiana, U.S.A. *Palaeontographica*, Abteilung B, **160**, 129–165.

2793 Wicander, R. 1986. Lower Devonian (Gedinnian) acritarchs from the Haragan
2794 Formation, Oklahoma, USA. *Review of Palaeobotany and Palynology*, **47**, 327–
2795 365.

2796 Wicander, R. 2004. A review of Ordovician Laurentian acritarch assemblages and
2797 their relevance to palaeogeographic and biodiversification trends. *Memoirs of the*
2798 *Association of Australian Palaeontologists*, **29**, 245–251.

2799 Wicander, R. & Playford, G. 1985. Acritarchs and spores from the Upper Devonian
2800 Lime Creek Formation, Iowa, USA. *Micropaleontology*, **31**, 97–138.

2801 Wicander, R. & Playford, G. 2008. Upper Ordovician microphytoplankton of the
2802 Bill's Creek Shale and Stonington Formation, Upper Peninsula of Michigan,
2803 U.S.A.: biostratigraphy and paleogeographic significance. *Revue de*
2804 *micropaléontologie*, **51**, 39–66.

2805 Wicander, R. & Wood, G. D. 1981. Systematics and biostratigraphy of the organic-
2806 walled microphytoplankton from the Middle Devonian (Givetian) Silica
2807 Formation, Ohio, U.S.A. *American Association of Stratigraphic Palynologists,*
2808 *Contributions Series*, **8**, 1–137.

2809 Wicander, R. & Wood, G. D. 1997. The use of microphytoplankton and chitinozoans
2810 for interpreting transgressive/regressive cycles in the Rapid Member of the Cedar
2811 Valley Formation (Middle Devonian), Iowa, U.S.A. *Review of Palaeobotany and*
2812 *Palynology*, **98**, 125–152.

2813 Wicander, R. & Wright, R. P. 1983. Organic-walled microphytoplankton abundance
2814 and stratigraphic distribution from the Middle Devonian Columbus and Delaware
2815 Limestones of the Hamilton Quarry, Marion County, Ohio. *Ohio Journal of*
2816 *Science*, **83**, (1), 2–13.

2817 Wicander, R., Playford, G. & Robertson, E. B. 1999. Stratigraphic and
2818 paleogeographic significance of an Upper Ordovician acritarch flora from the
2819 Maquoketa Shale, Northeastern Missouri, U.S.A. Paleontological Society,
2820 Memoir **51**. *Journal of Paleontology*, **73**, Supplement No. 6, 1–38.

2821 Wicander, R., Clayton, G., Marshall, J. E. A., Troth, I. & Racey, A. 2011. Was the
2822 latest Devonian glaciation a multiple event? New palynological evidence from
2823 Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **305**, 75–83.

2824 Winslow, M. R. 1962. Plant spores and other microfossils from Upper Devonian and
2825 Lower Mississippian rocks of Ohio. *United States Geological Survey,*
2826 *Professional Paper*, **364**, 1–93.

2827 Wood, G. D. 1984. A stratigraphic, palaeoecologic, and palaeobiogeographic review
2828 of the acritarchs *Umbellasphaeridium deflandrei* and *Umbellasphaeridium*
2829 *saharicum*. *Compte Rendu, Neuvième Congrès International de Stratigraphie et*
2830 *de Géologie du Carbonifère, Washington/Champaign-Urbana, May 1979*, **2**,
2831 199–211.

2832 Wood, G. D. 1995. The Gondwanan acritarch *Bimerga bensonii* gen. et sp. nov.:
2833 paleogeographic and biostratigraphic importance in the Devonian Malvinokaffric
2834 realm. *Palynology*, **19**, 221–231.

2835 Wood, G. D. & Clendening, J. A. 1985. Organic-walled microphytoplankton and
2836 chitinozoans from the Middle Devonian (Givetian) Boyle Dolomite of Kentucky,
2837 U.S.A. *Palynology*, **9**, 133–145.

2838 Wood, G. D. & Miller, M. A. 1991. Distinctive Silurian chitinozoans from the
2839 Itacurubí Group (Vargas Peña Shale), Chaco Basin, Paraguay. *Palynology*, **15**,
2840 181–192.

2841 Wood, G. D. & Stephenson, J. T. 1989. Cambrian palynomorphs from the
2842 warmwater provincial realm, Bonneterre and Davis formations of Missouri and
2843 Arkansas (Reelfoot rift area): biostratigraphy, paleoecology and thermal maturity.
2844 *In*: Gregg, J.M., Palmer, J.R. & Kurtz, V.E. (eds), *Field Guide to the Upper*
2845 *Cambrian of South Eastern Missouri: Stratigraphy, Sedimentology and Economic*
2846 *Geology*. Department of Geology and Geophysics, University of Missouri
2847 (Rolla), Geological Society of America Field Trip (Annual Meeting), 84–102.

2848 Wood, G. D. & Tekbali, A. O. 1987. A unique new genus of Acritarcha (organic-
2849 walled microphytoplankton) from the Tanezzuft Formation (Silurian) of Libya.
2850 *Palynology*, **11**, 107–112.

2851 Yan, K., Servais, T. & Li, J. 2010. Revision of the Ordovician acritarch genus
2852 *Ampullula* Righi 1991. *Review of Palaeobotany and Palynology*, **163**, 11–25.

2853 Yan, K., Servais, T., Li, J., Wu, R. & Tang, P. 2011. Biodiversity patterns of Early–
2854 Middle Ordovician marine microphytoplankton in South China.
2855 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **299**, 318–334.

2856 Yao, J., Xiao, S., Yin, L., Li, G. & Yuan, X. 2005. Basal Cambrian microfossils
2857 from the Yurtus and Xishanblaq formations (Tarim, north-west China):
2858 systematic revision and biostratigraphic correlation of *Micrhystridium*-like
2859 acritarchs. *Palaeontology*, **48**, 687–708.

2860 Yin, L.-M. 1994. New forms of acritarchs from early Ordovician sediments in
2861 Yichang, Hubei, China. *Acta Micropalaeontologica Sinica*, **11**, (1), 41–53, pls I–
2862 II.

2863 Yin, L.-M. & He, S. 2000. Palynomorphs from the transitional sequences between
2864 Ordovician and Sillurian of northwestern Zhejiang, South China. Palynofloras
2865 and palynomorphs of China. Hefei: Press of University of Science and
2866 Technology of China. p. 186–202.

2867 Young, T, Martin, F., Dean, W. T. & Rushton, A. W. A. 1994. Cambrian
2868 stratigraphy of St Tudwal's Peninsula, Gwynedd, northwest Wales. *Geological*
2869 *Magazine*, **131**, 335–360.

2870 Zang, W.-L. & Walter, M. R. 1992. Late Proterozoic and Cambrian microfossils and
2871 biostratigraphy, Amadeus Basin, central Australia. *Memoirs of the Association of*
2872 *Australasian Palaeontologists*, **12**, 1–132.

2873 Zhen, Y.Y., Percival, I.G. & Webby, B.D. 2003. Early Ordovician conodonts from
2874 far western New South Wales, Australia. *Records of the Australian Museum*, **55**,
2875 169–220.

2876 Zhu, H., Wicander, R., & Marshall, J. E. A. 2008. Biostratigraphic and
2877 paleogeographic significance of a palynological assemblage from the middle
2878 Devonian Ulusubasite Formation, eastern Junggar Basin, Xinjiang, China.
2879 *Review of Palaeobotany and Palynology*, **152**, 141–157.

2880

**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 3.** Late Cambrian acritarch localities plotted on a palaeogeographical reconstruction for the mid Furongian (Stage 9, 495 Ma). **1.** Missouri, Arkansas (Wood & Stephenson 1989). **2.** Severnaya Zemlya (Raevskaya & Golubkova 2006). **3.** Northern Norway (Welsch 1986). **4.** Kolguev Island (Moczydłowska & Stockfors 2004). **5.** East European Platform (Volkova 1990). **6.** Nova Scotia (Palacios *et al*. 2009). **7.** Eastern Newfoundland (Martin & Dean 1981, 1988; Parsons & Anderson 2000). **8**. England and Wales (Downie 1984; Young *et al*. 1994). **9.** Belgium (Ribecai & Vanguestaine 1993). **10.** Algeria (Vecoli 1996; Vecoli & Playford 1997). **11.** Spain (Albani *et al*. 2006). **12.** Tunisia (Albani *et al*. 1991). **13.** High Zagros Mountains, Iran (Ghavidel-syooki & Vecoli 2008). 14. Eastern Cordillera, Northwest Argentina (Rubinstein *et al*. 2003). Map from BUGPLATES, Galls Projection.

**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 reconstructio 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). **Avalonia. 1.** Eastern Newfoundland (Dean & Martin 1978); **2.** Southern Ireland (Maziane-Serraj *et al*. 1999, 2000); **3.** Isle of Man (Molyneux 1999; Chadwick *et al*. 2001); **4.** English Lake District (Cooper *et al*. 1995, 2004; Molyneux 2009); **5.** South Wales (Molyneux 1987); **6.** Belgium (Martin 1977, 1982*a*; Martin & Rickards 1979; Vanguestaine 1986*a*). **Baltica. 7.** Norway (Ribecai *et al*. 1999, 2002; Tongiorgi *et al*. 2003*b*); **8.** Sweden (Bagnoli & Ribecai 2001; Ribecai & Tongiorgi 1995; Ribecai *et al*. 2002; Tropepi & Ribecai 2000); **9.** Estonia (Uutela & Tynni 1991); **10.** Baltic Russia (Ribecai *et al*. 2002); **11.** Arctic Russia (Raevskaya *et al*. 2006). **Gondwana/Perigondwana. 12.** North Africa (Cramer & Díez 1976, 1977; Cramer *et al*. 1974*a*, *b*; Deunff 1977; Elaouad Debbaj 1984; Vecoli 1999); **13.** Saxo-Thuringia (Burmann 1968, 1970; Heuse *et al*. 1994); **14.** Sardinia (Albani 1989; Tongiorgi *et al*. 1984); **15.** Bohemia (Vavrdová 1977, 1986, 1993); **16.** Turkey – Taurides Terrane (Paris *et al*. 2007); **17.** Turkey – Border Folds, Arabian Plate (Paris *et al*. 2007); **18.** Iran – Alborz Terrane (Ghavidel-syooki 2006); **19.** Iran – Zagros (Ghavidel-syooki 1997); **20.** Saudi Arabia (Le Herisse *et al*. 2007); **21.** Pakistan – Karakorum Terrane (Tongiorgi *et al*. 1994; Quintavalle *et al*. 2000); **22.** South China (Brocke *et al*. 1999, 2000; Tongiorgi *et al*. 2003*a*; Yan *et al*. 2011); **23.** Canning Basin (Playford & Martin 1984; Quintavalle & Playford 2006*a*, *b*); **24.** Northwest Argentina (Achab *et al*. 2006; Rubinstein 2003; Rubinstein *et al*. 2011). Map from BUGPLATES, Galls Projection.

**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*. 2011*a*, 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 willieriae* based on Le Hérissé & Gourvennec (1995, fig. 2). Data sources. **Laurussia. 1, 2.** SE USA, NE USA, Canada: Cramer 1971, Cramer & Díez 1972. **3.** England and Wales: Davies *et al*. 1997, in press; Dorning 1981; Hill 1974; Hill & Dorning 1984; Mabillard & Aldridge 1985. **4.** Scotland: Molyneux *et al*. 2008; White *et al*. 1991. **5.** Norway: Smelror 1987. **6.** Sweden: Le Hérissé 1989*b*. **7.** Denmark: Smelror 1989. **8.** Belgium: Martin 1969, 1974, 1989. **Gondwana/Perigondwana. 9, 10.** Bolivia, Peru: Díaz-Martínez *et al*. 2011. **11.** Algeria: Jardiné & Yapaudjian 1968; Jardiné *et al*. 1974. **12.** Libya: Deunff & Massa 1975; Hill & Molyneux 1988. **13.** Jordan: Keegan *et al*. 1990. **14.** Turkey (Taurides): Dean & Monod 1990; Dean *et al*. 1993. **15.** Bohemia: Dufka & Pacltova 1988. **16.** Iraq: Al-Ameri 2010. **17.** Saudi Arabia: Le Hérissé *et al.* 1995; Le Hérissé 2000. **18.** Iran (Zagros): Ghavidel-syooki 1997. **19.** Argentina (Precordillera): Melendi & Volkheimer 1982, 1983; Pöthe de Baldis 1987; Rubinstein 1997, 2001; Rubinstein & Brussa 1999. **20.** Argentina (Central Andean Basin): Bultynck & Martin 1982; Rubinstein 2005; Rubinstein *et al*. 2008*a*; Rubinstein & Muro 2011. **21.** Argentina (Chaco-paranense Basin): Pöthe de Baldis 1974. **22.** Paraguay (Paraná Basin): Wood & Miller 1991; Gray *et al*. 1992. **23.** Brazil (Parnaíba Basin): Brito 1967; Quadros 1982; Rubinstein 1997.

**Figure 8.** Late Silurian acritarch biogeography plotted on a palaeogeographical reconstruction for the late Ludlow (419 Ma). After Le Hérissé *et al.* (1997*a*, fig. 1), with additional records of *Visbysphaera bonita* and *V. jardinei* from the Central Andean Basin, Bolivia (Cramer *et al.* 1974*c*), 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*. (2008*b*), 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.

**Table 2.** Occurrence of genera in Lower–Middle Ordovician phytoplankton assemblages from South China (Perigondwana) and the intracratonic Gondwanan Canning and Georgina basins of north-western and central Australia. Stratigraphic intervals and data sources are as follows. **South China:** lower Floian–lower Darriwilian, *Tetragraptus approximatus–Undulugraptus austrodentatus* graptolite biozones; Brocke *et al*. 1999, 2000; Huang *et al*. 1994; Li 1987, 1990; Li *et al*. 2002*b*; Lu 1987; Tongiorgi *et al*. 1995, 1998, 2003*a*; Yan *et al*. 2011; Yin 1994. **Canning Basin:** Willara, Goldwyer and Nita formations, middle Floian–upper Darriwilian, *Athabascaella rossii* to *Dactylofusa striatogranulata* acritarch biozones; Playford & Martin 1984; Quintavalle & Playford 2006*a*, *b*. **Georgina Basin:** Coolibah Formation, middle–upper Floian (upper Bendigonian–lower Chewtonian, Zhen *et al*. 2003, fig. 6); Playford & Wicander 1988.

Molyneux, Delabroye, Wicander & Servais: Table 1

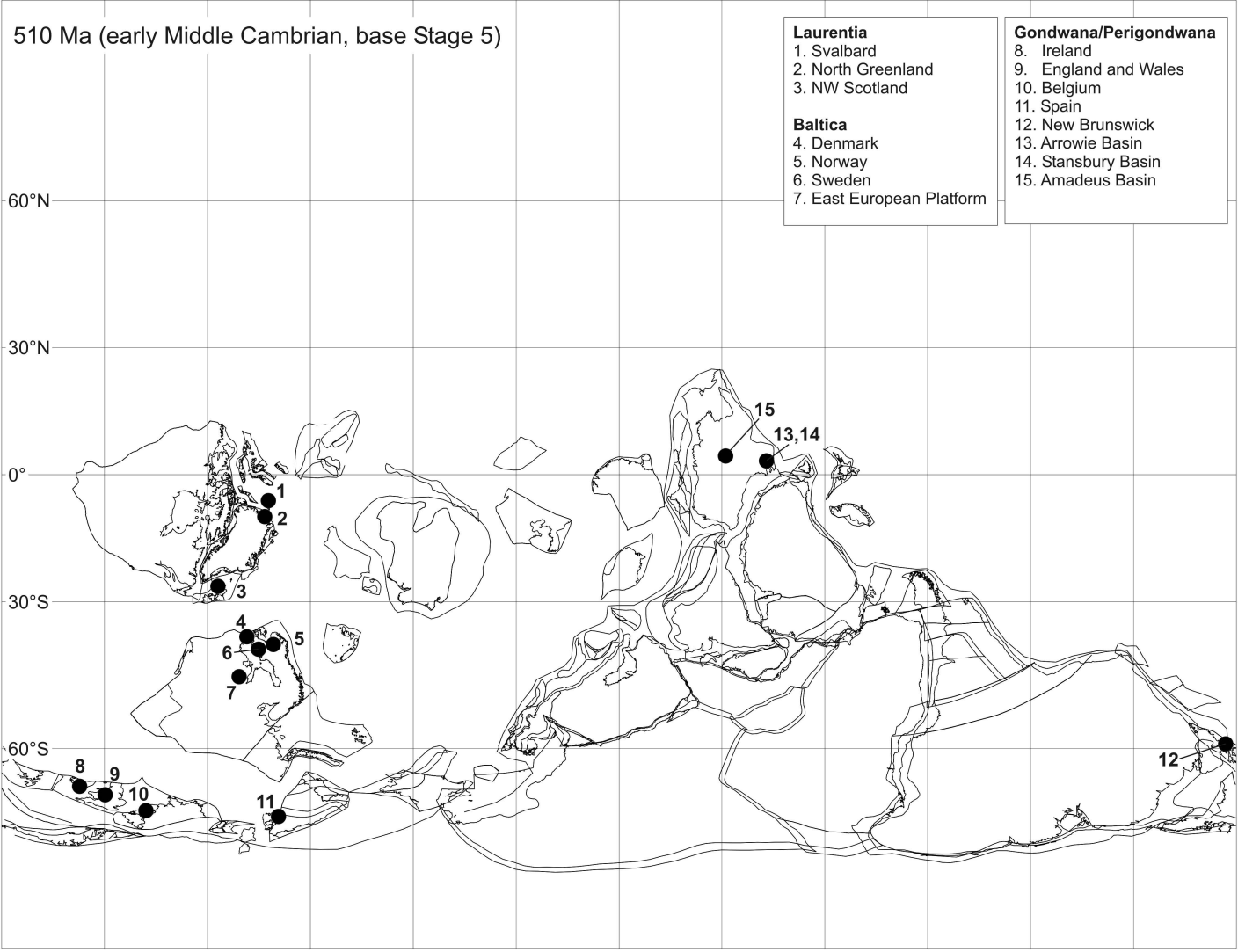
| | Missouri/Arkansas | East European Platform | Norway | Belgium | England & Wales | Tunisia | Algeria | Iran | Spain | E. Newfoundland | Nova Scotia | Severnaya Zemlya | Kolguev Island |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| East European Platform | **0.051282** | 1 | | | | | | | | | | | |
| Norway | 0.13333 | 0.25714 | 1 | | | | | | | | | | |
| Belgium | 0.10526 | 0.41176 | 0.41176 | 1 | | | | | | | | | |
| England & Wales | 0.125 | 0.42105 | 0.36364 | 0.47826 | 1 | | | | | | | | |
| Tunisia | 0.36364 | 0.13514 | 0.28571 | 0.22222 | 0.27273 | 1 | | | | | | | |
| Algeria | **0.090909** | 0.41667 | 0.28571 | 0.40909 | 0.37037 | 0.25 | 1 | | | | | | |
| Iran | **0.10526** | 0.33333 | 0.33333 | 0.75 | 0.41667 | 0.22222 | 0.34783 | 1 | | | | | |
| Spain | **0.15789** | 0.36111 | 0.31579 | 0.52632 | 0.45833 | 0.27778 | 0.45455 | 0.45 | 1 | | | | |
| E. Newfoundland | **0.088235** | 0.64103 | 0.29032 | 0.41935 | 0.51515 | 0.22581 | 0.46875 | 0.41935 | 0.36364 | 1 | | | |
| Nova Scotia | 0.23077 | 0.16216 | 0.26667 | 0.27778 | 0.20833 | 0.41667 | 0.18182 | 0.21053 | 0.2 | 0.14706 | 1 | | |
| Severnaya Zemlya | 0.13636 | 0.40541 | 0.27273 | 0.52381 | 0.58333 | 0.3 | 0.4 | 0.45455 | 0.65 | 0.37143 | 0.28571 | 1 | |
| Kolguev Island | 0.1 | 0.16667 | **0.086957** | 0.16 | 0.2069 | **0.095238** | 0.23077 | 0.20833 | 0.25 | 0.18421 | **0.043478** | 0.22222 | 1 |
| NW Argentina | 0.23077 | 0.075 | 0.11765 | **0.095238** | **0.11538** | 0.21429 | 0.13043 | 0.15 | 0.2 | 0.14706 | **0.058824** | **0.125** | 0.2 |

**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.

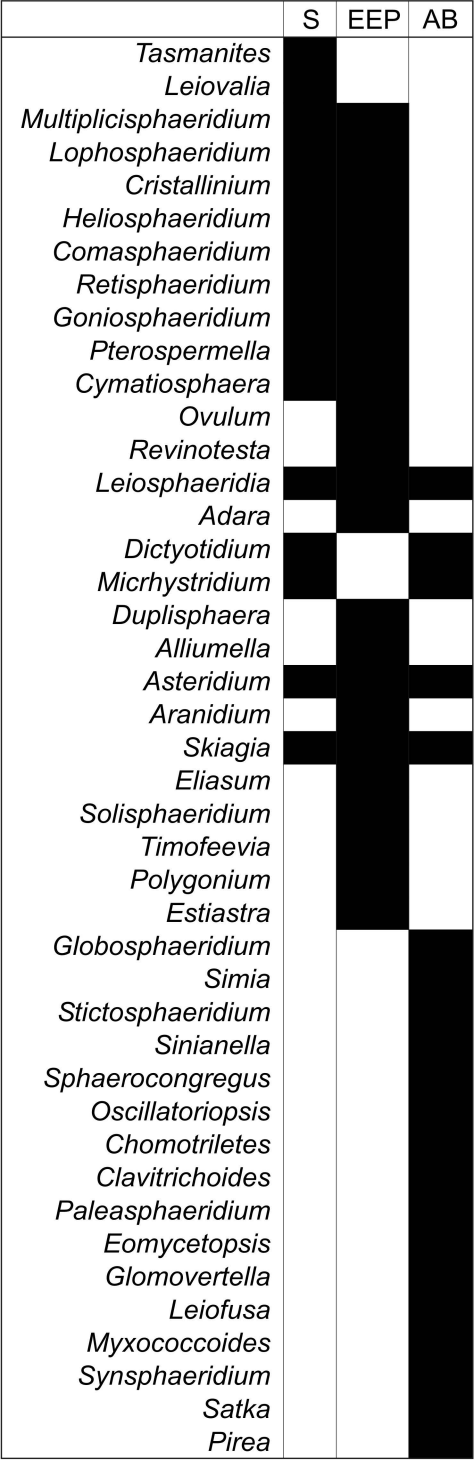
| | South China | Australia: Canning Basin | Australia: Georgina Basin | |
|---|---|---|---|---|
| *Acanthodiacrodium* | 1 | | | South China (35) |
| *Actinotodissus* | 1 | | | |
| *Adorfia* | 1 | | | |
| *Arbusculidium* | 1 | | | |
| *Arkonia* | 1 | | | |
| *Aureotesta* | 1 | | | |
| *Barakella* | 1 | | | |
| *Caldariola* | 1 | | | |
| *Coryphidium* | 1 | | | |
| *Cristallinum* | 1 | | | |
| *Cycloposphaeridium* | 1 | | | |
| *Cymatiogalea* | 1 | | | |
| *Dicrodiacrodium* | 1 | | | |
| *Ferromia* | 1 | | | |
| *Leiofusa* | 1 | | | |
| *Leprotolypa* | 1 | | | |
| *Liliosphaeridium* | 1 | | | |
| *Macroptycha* | 1 | | | |
| *Multiplicisphaeridium* | 1 | | | |
| *Ordovicidium* | 1 | | | |
| *Palaiosphaeridium* | 1 | | | |
| *Papilliferum* | 1 | | | |
| *Passalosphaera* | 1 | | | |
| *Picostella* | 1 | | | |
| *Poikilofusa* | 1 | | | |
| *Schizodiacrodium* | 1 | | | |
| *Solisphaeridium* | 1 | | | |
| *Stellechinatum* | 1 | | | |
| *Stelliferidium* | 1 | | | |
| *Synsphaeridium* | 1 | | | |
| *Tectitheca* | 1 | | | |
| *Tongzia* | 1 | | | |
| *Tranvikium* | 1 | | | |
| *Vavrdovella* | 1 | | | |
| *Vogtlandia* | 1 | | | |
| *Ammonidium* | 1 | 1 | | South China, Canning Basin (24) |
| *Ampullula* | 1 | 1 | | |
| *Aremoricanium* | 1 | 1 | | |
| *Athabascaella* | 1 | 1 | | |
| *Buedingiisphaeridium* | 1 | 1 | | |
| *Comasphaeridium* | 1 | 1 | | |
| *Cymatiosphaera* | 1 | 1 | | |
| *Dactylofusa* | 1 | 1 | | |
| *Dasydorus* | 1 | 1 | | |
| *Dorsennidium* | 1 | 1 | | |
| *Goniosphaeridium* | 1 | 1 | | |
| *Gorgonisphaeridium* | 1 | 1 | | |
| *Leiosphaeridia* | 1 | 1 | | |
| *Loeblichia* | 1 | 1 | | |

| | | | | |
|---|---|---|---|---|
| *Lophosphaeridium* | 1 | 1 | | |
| *Orthosphaeridium* | 1 | 1 | | |
| *Pachysphaeridium* | 1 | 1 | | |
| *Petaloferidium* | 1 | 1 | | |
| *Peteinosphaeridium* | 1 | 1 | | |
| *Pirea* | 1 | 1 | | |
| *Pterospermella* | 1 | 1 | | |
| *Sacculidium* | 1 | 1 | | |
| *Striatotheca* | 1 | 1 | | |
| *Veryhachium* | 1 | 1 | | |
| *Baltisphaeridium* | 1 | 1 | 1 | South China, Canning Basin, Georgina Basin (6) |
| *Dictyotidium* | 1 | 1 | 1 | |
| *Micrhystridium* | 1 | 1 | 1 | |
| *Polyancistrodorus* | 1 | 1 | 1 | |
| *Polygonium* | 1 | 1 | 1 | |
| *Rhopaliophora* | 1 | 1 | 1 | |
| *Baltisphaerosum* | 1 | | 1 | South China, Georgina Basin |
| *Tenuirica*? | 1 | | 1 | |
| *Tunisphaeridium* | | 1 | 1 | Canning Basin, Georgina Basin |
| *Uncinisphaera* | | 1 | 1 | |
| *Dilatisphaera* | | 1 | | Canning Basin |
| *Pylantios* | | 1 | | |
| *Sertulidium* | | 1 | | |
| *Tribulidium* | | 1 | | |
| *Dictyodiscus* | | | 1 | Georgina Basin |
| *Eomerismopedia* | | | 1 | |
| *Pytinomorpha* | | | 1 | |
| Total Genera | 67 | 36 | 13 | |

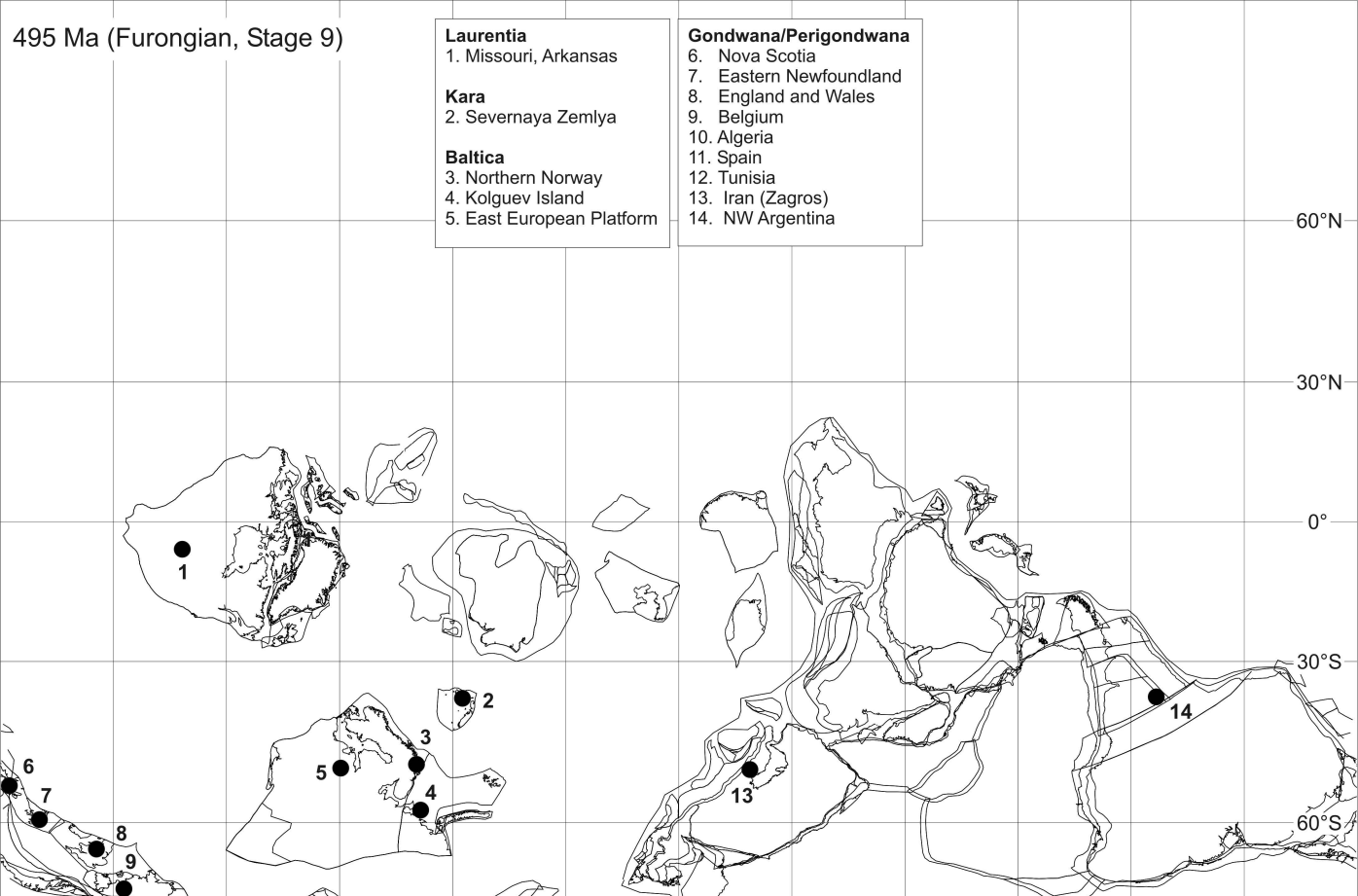
Table 2.



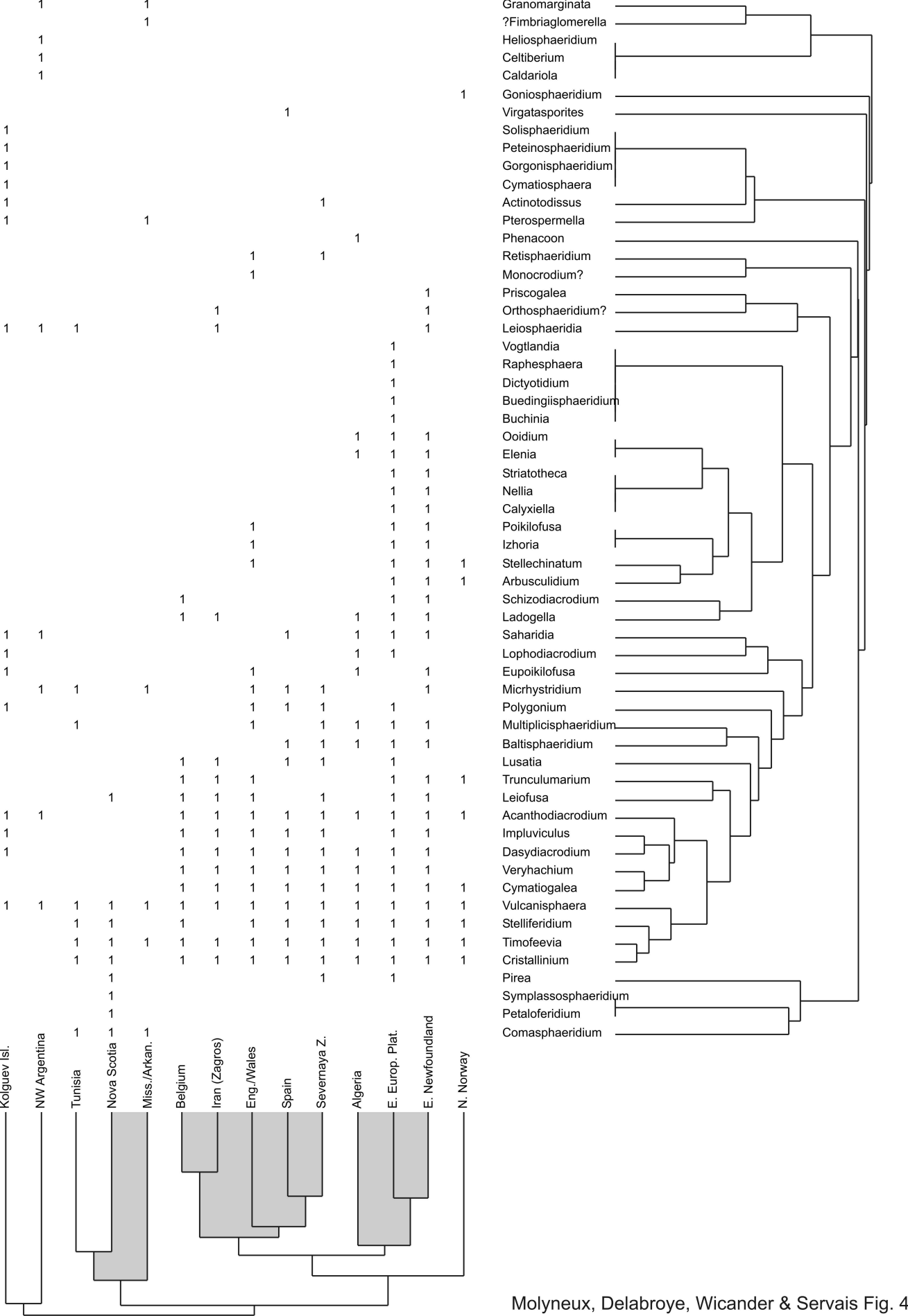

Molyneux, Delabroye, Wicander & Servais Fig. 1



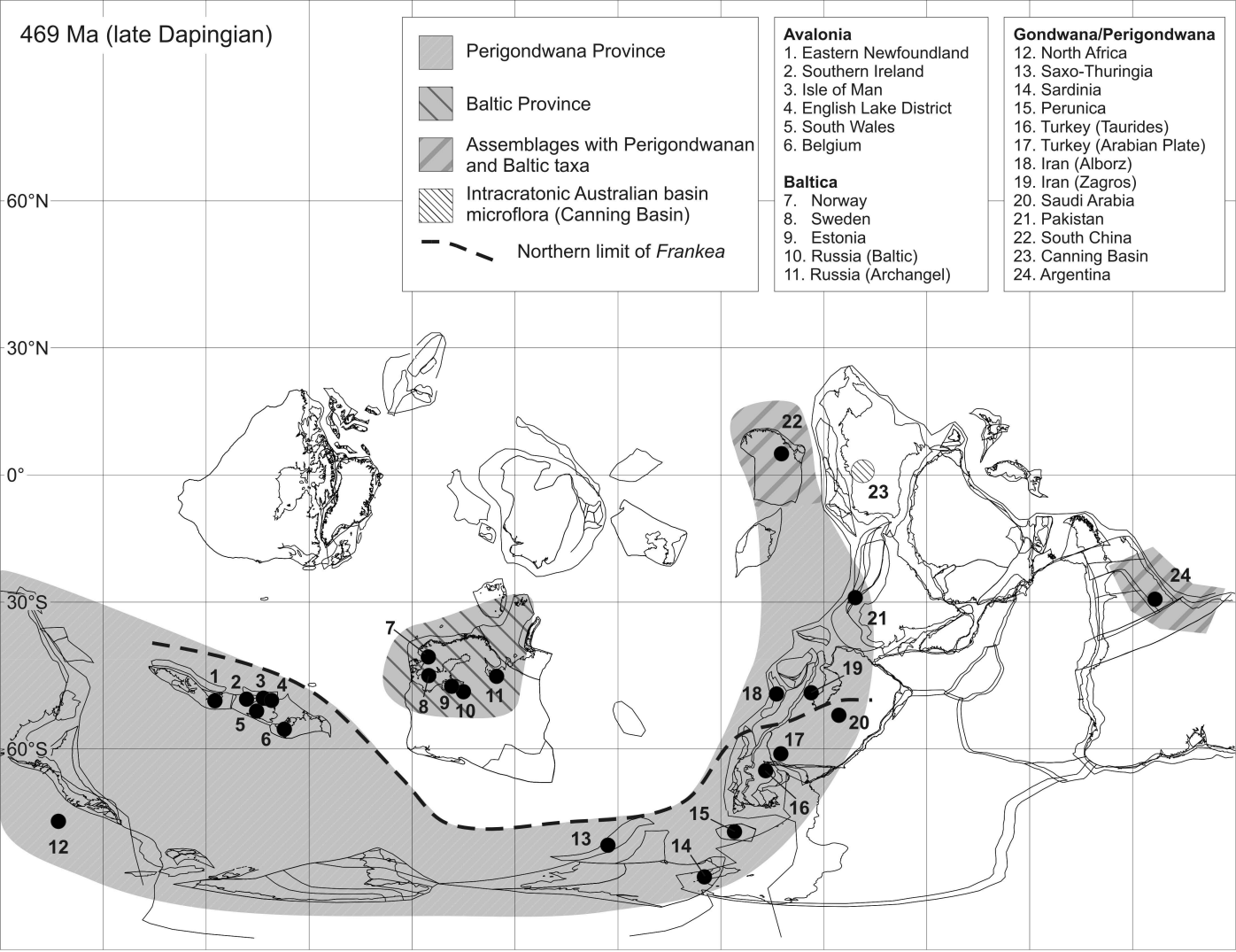

Molyneux, Delabroye, Wicander & Servais Fig. 2



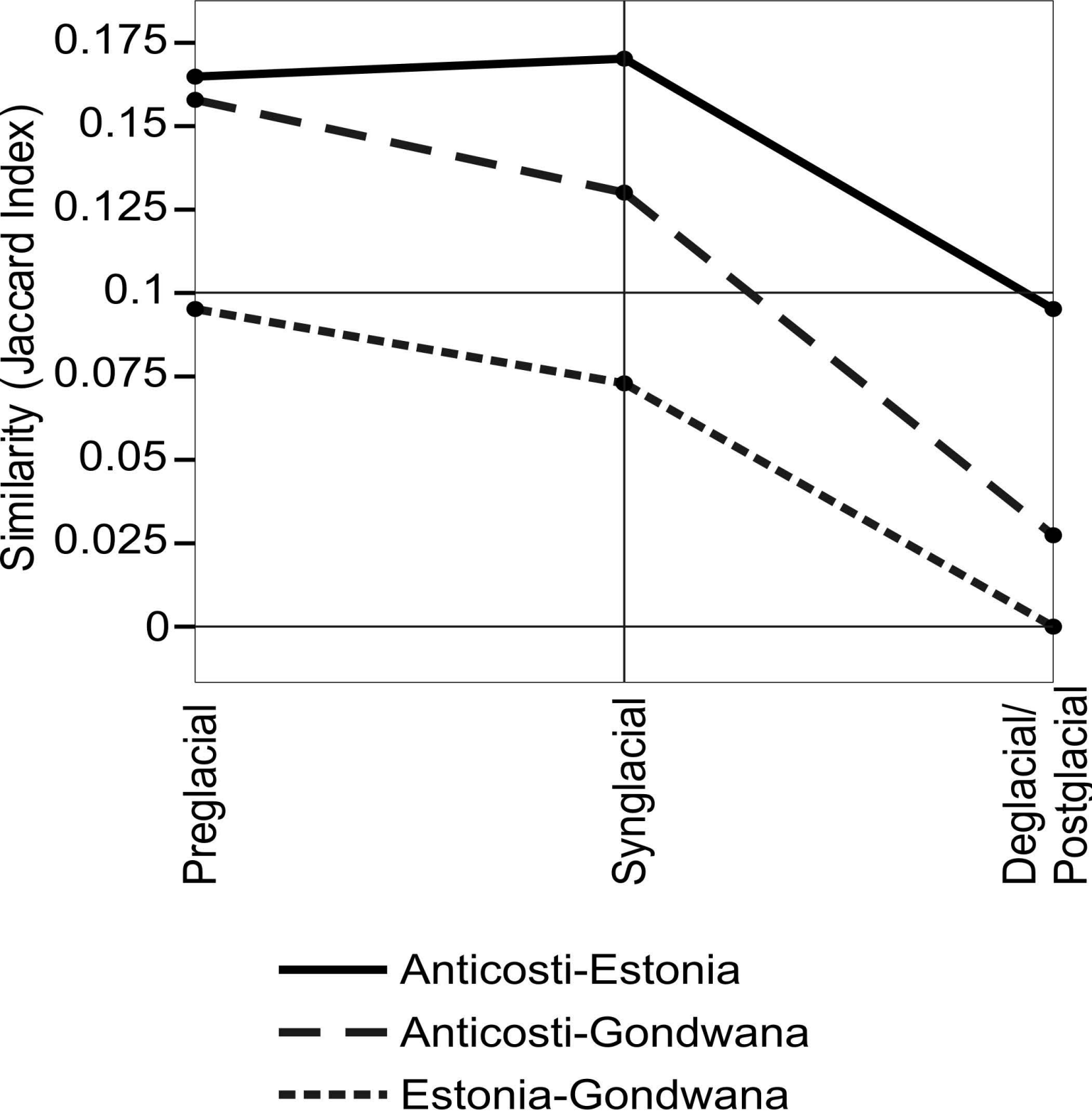

Molyneux, Delabroye, Wicander & Servais Fig. 3



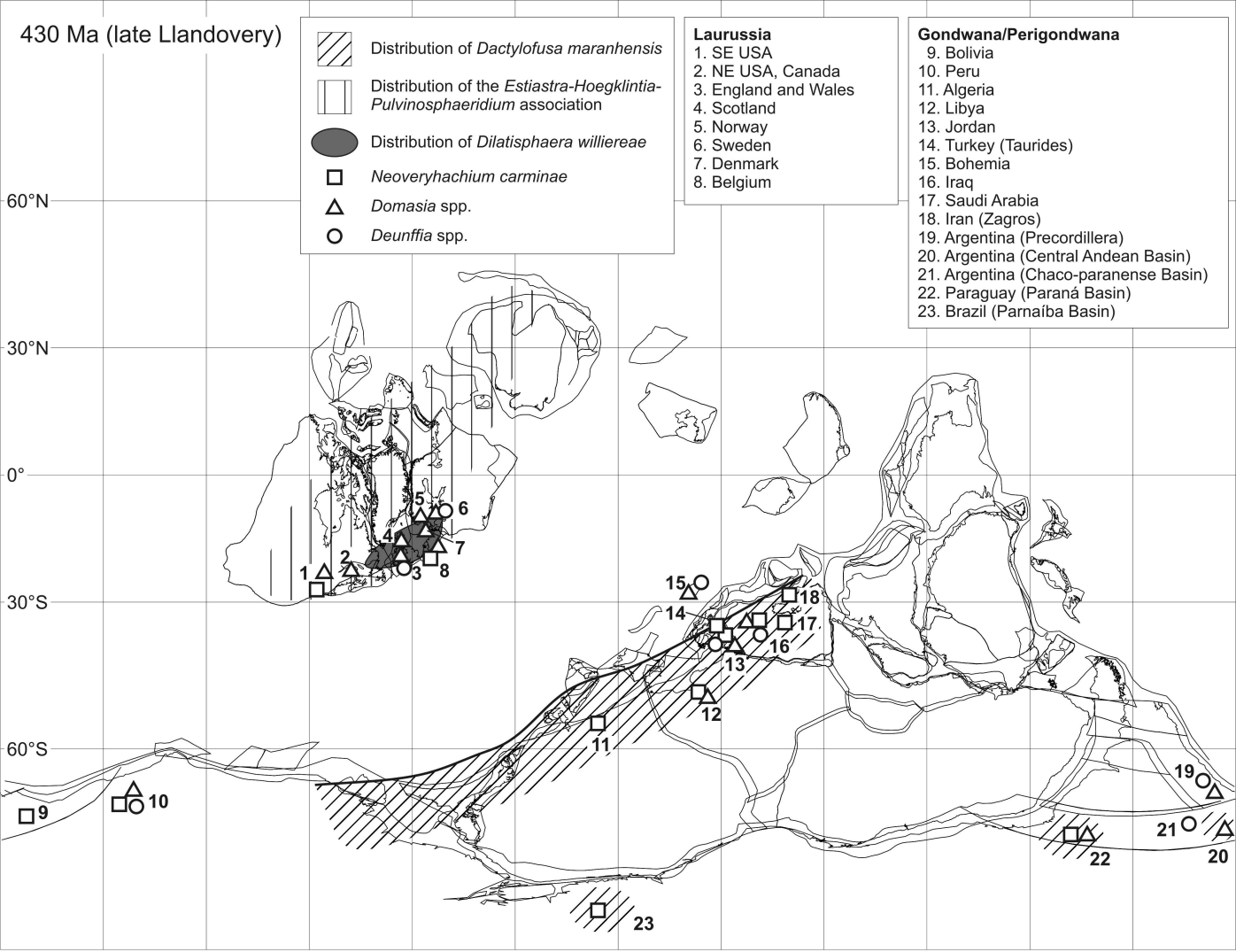

Molyneux, Delabroye, Wicander & Servais Fig. 4



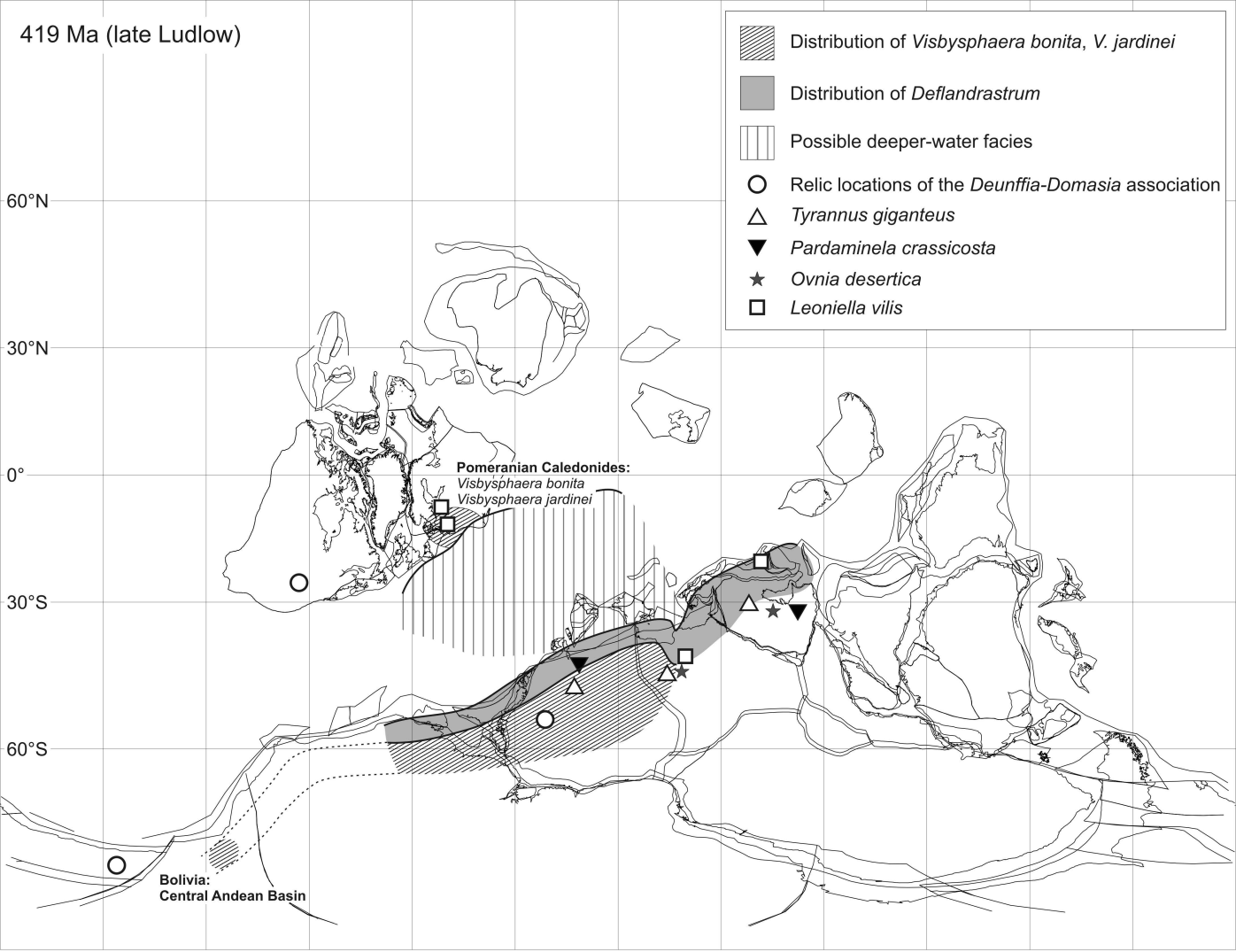

Molyneux, Delabroye, Wicander & Servais Fig. 5



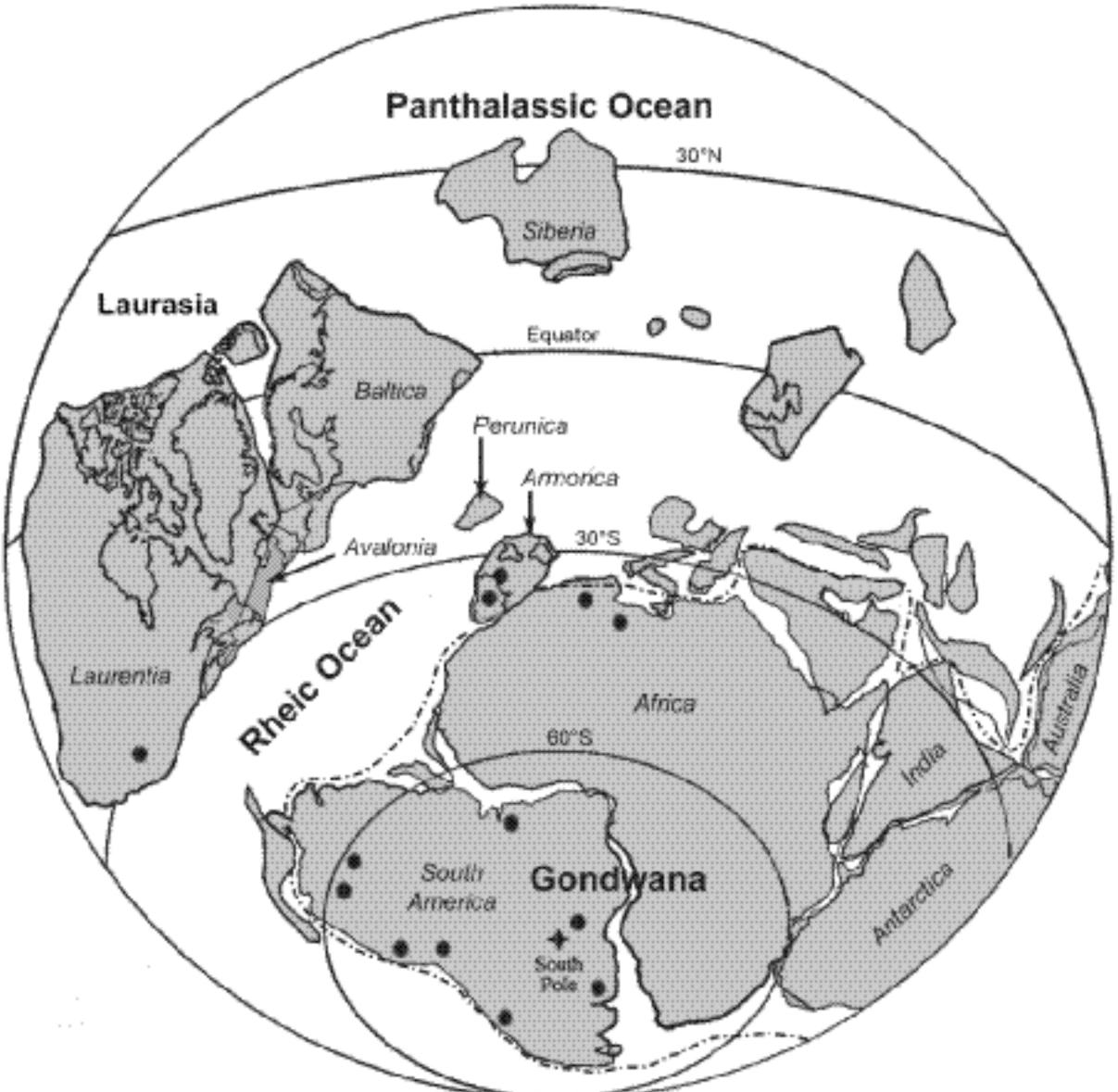

Molyneux, Delabroye, Wicander & Servais Fig. 6



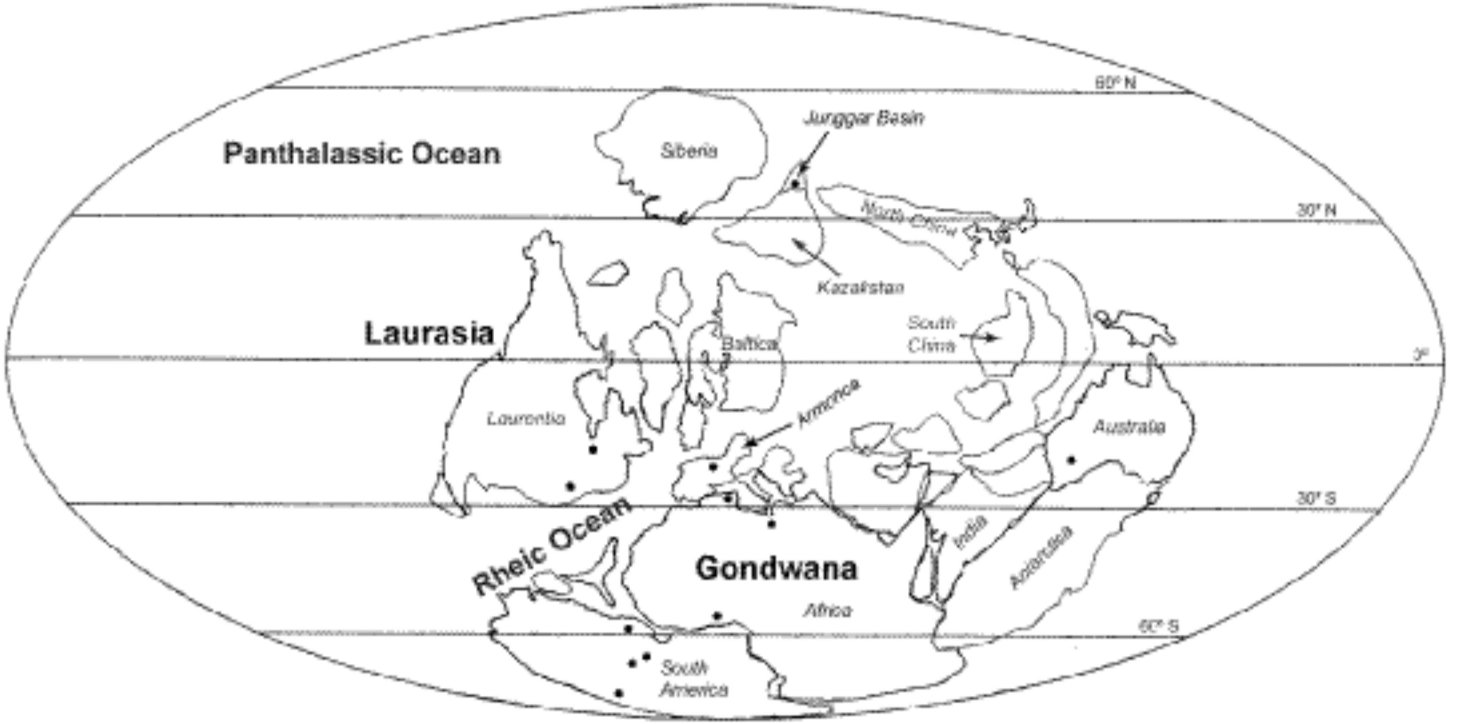

Molyneux, Delabroye, Wicander & Servais Fig. 7



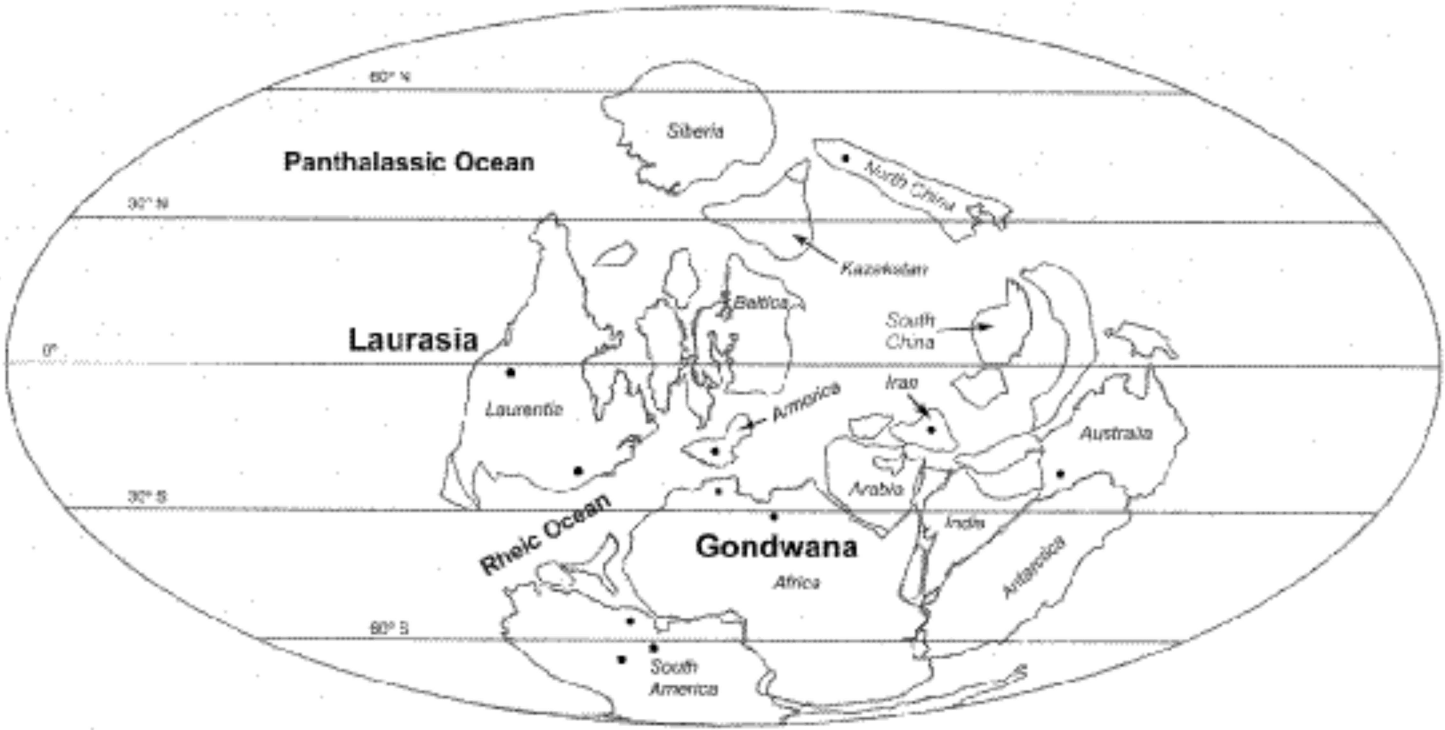

Molyneux, Delabroye, Wicander & Servais Fig. 8



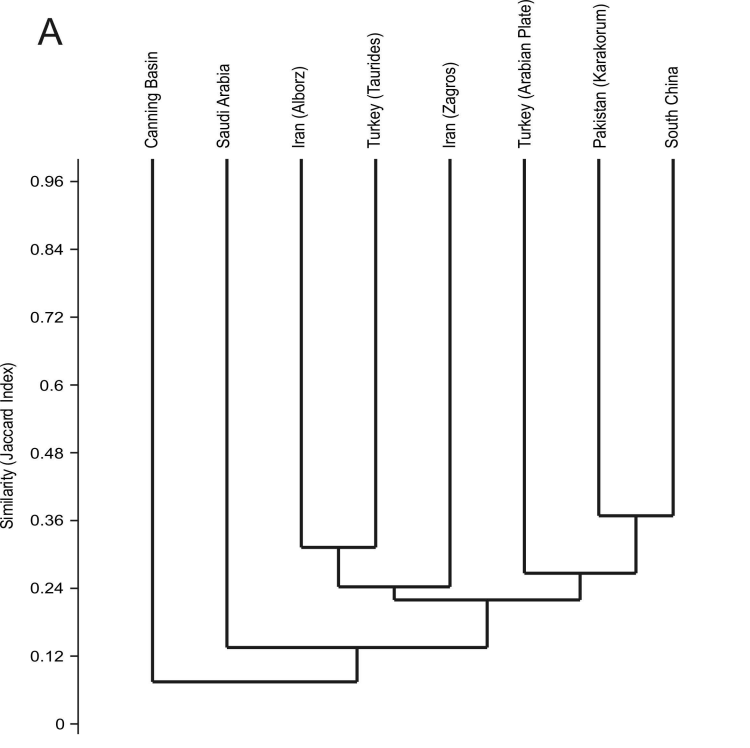

Molyneux, Delabroye, Wicander & Servais Fig. 9

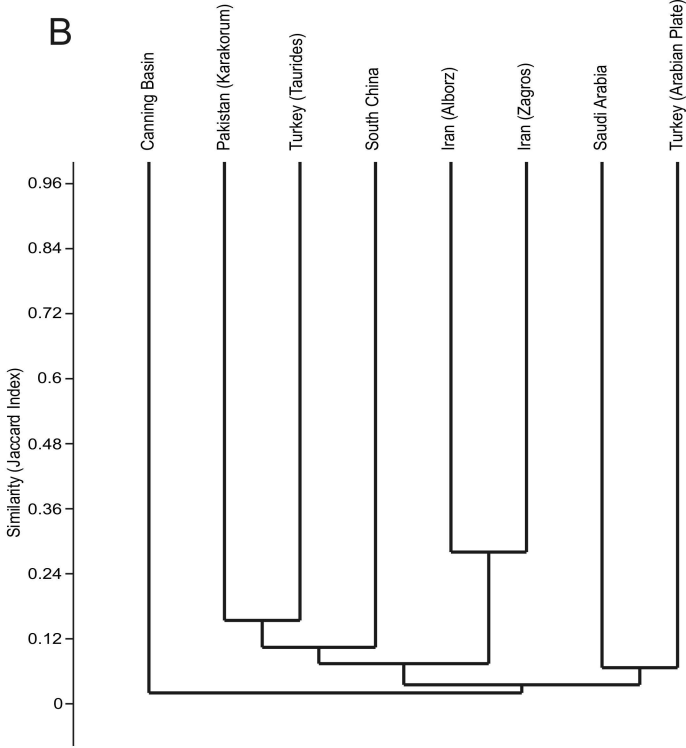



Molyneux, Delabroye, Wicander & Servais Fig. 10




Molyneux, Delabroye, Wicander & Servais Fig. 11




Molyneux, Delabroye, Wicander & Servais Fig. 12