

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

3 Stewart G. Molyneux ^{1*}, Aurélien Delabroye ^{2,3},
4 Reed Wicander ⁴ & Thomas Servais ²

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

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

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

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

14 *Corresponding author

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20 Abbreviated title: Palaeozoic phytoplankton biogeography

21
22 **Abstract:** Early to mid Palaeozoic marine phytoplankton are represented by
23 acritarchs and associated forms, which had a global distribution from the early
24 Cambrian to the early Carboniferous (Mississippian). Palaeozoic phytoplankton
25 assemblages show varying degrees of cosmopolitanism and endemism through time.
26 A high degree of cosmopolitanism was evidently characteristic of the Cambrian and
27 much of the Late Ordovician, Silurian and Devonian, but provincialism was more
28 marked in the Early Ordovician and Hirnantian (latest Ordovician), the latter at a time
29 of major palaeoenvironmental perturbations. Distribution patterns of Palaeozoic
30 phytoplankton are attributed to a number of interacting factors, including

31 palaeolatitude, palaeotemperature, oceanic circulation patterns, the disposition of
32 continents, differentiation between oceanic and more cratonic (distal–proximal)
33 assemblages, and sedimentary environments and facies. There are indications that
34 biogeographical ranges of taxa shift over time. Moving our understanding of
35 Palaeozoic phytoplankton biogeography forward requires targeted investigation of
36 regions and time periods for which no or little data exist, quantitative analysis of data
37 to investigate how similarity varies through time and how this might correlate with
38 other datasets such as carbon isotope stratigraphy or sea level, and rigorous
39 application of well-defined time slices to compare coeval assemblages, at least within
40 the limits of resolution. **(End of Abstract)**

41

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

52 Acritarchs and related phytoplanktonic forms had a global distribution from the early
53 Cambrian to the early Carboniferous (Mississippian), prior to the late Palaeozoic
54 ‘Phytoplankton Blackout’ (Riegel 2008). Under favourable palaeoenvironmental
55 conditions, they formed diverse and abundant assemblages. Changes in Palaeozoic
56 phytoplankton diversity and abundance from proximal to distal positions along
57 onshore–offshore gradients are well-documented (Jacobson 1979; Dorning 1981;
58 Vecoli 2000, 2004; Li *et al.* 2004; Molyneux 2009). The most diverse and abundant
59 assemblages are found in mid shelf depositional environments, with diversity and
60 abundance declining towards nearshore settings on the one hand and outer
61 shelf/basinal settings on the other.

62 In reviewing what was then known about the palaeobiogeography of mid Palaeozoic
63 organic-walled phytoplankton, Colbath (1990a) highlighted some of the
64 characteristics that made these organisms suitable for palaeobiogeographical studies.
65 They can be abundant (up to 10^5 specimens per gram under favourable
66 circumstances), and are generally independent of lithofacies. Furthermore, as their
67 motility is inferred to have been restricted, they were probably incapable of active
68 dispersal against even relatively weak ocean currents so their distribution largely
69 reflects physical processes. To explain why they were so little used in spite of these
70 characteristics, Colbath pointed to a lack of taxonomic consensus, poorly documented
71 biostratigraphical ranges, and sampling biases, both geographical and stratigraphical.

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

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

93 Maps used in this review for the Cambrian to Silurian (542 – 416 Ma) periods were
94 generated using BUGPLATES software (Torsvik & Cocks 2013). Those used for the

95 Devonian Period are based on other sources, as indicated in the relevant figure
96 captions.

97

98 **Cambrian phytoplankton**

99 *Early Cambrian*

100 Definitive evidence for acritarch provincialism in the early Cambrian is lacking.
101 Acritarch assemblages from Baltica, described in a series of papers by Moczyłowska
102 (1991, 1998, and references therein), comprise some of the best documented
103 phytoplankton assemblages of that age and have been used to define a succession of
104 lower Cambrian acritarch biozones. In upwards succession, the *Asteridium tornatum*–
105 *Comasphaeridium velvetum*, *Skiagia ornata*–*Fimbriaglomerella membranacea*,
106 *Heliosphaeridium dissimulare*–*Skiagia ciliosa* and *Volkovia dentifera*–*Liepaina plana*
107 biozones span the Terreneuvian Series and Series 2 of the revised standard for the
108 Cambrian System (Rushton & Molyneux 2011). Although our knowledge of early
109 Cambrian acritarch assemblages is restricted to relatively few areas, the biozones have
110 been identified widely within those areas, suggesting that biozonally diagnostic forms
111 have similarly wide distributions.

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

121 Acritarch assemblages of Terreneuvian age from other palaeogeographical areas are
122 not well known. Acritarchs recorded from basal Cambrian successions of South
123 China and Tarim (northwest China) constitute the *Asteridium*–*Heliosphaeridium*–
124 *Comasphaeridium* assemblage of Yao *et al.* 2005 (see also Dong *et al.* 2009), an
125 association of small, morphologically simple, *Micrhystridium*-like acanthomorph
126 acritarchs. Assemblages from China, New Brunswick and Baltica all contain the

127 genera *Asteridium* and *Comasphaeridium*, although only one species, *Asteridium*
128 *tornatum*, has a biogeographical range that encompasses all three regions. In detail,
129 however, there are also differences between the Chinese assemblages and those from
130 New Brunswick and Baltica. *Heliosphaeridium*, for example, is not known from this
131 level in New Brunswick or Baltica, where its First Appearance Datum (FAD) is
132 higher in the stratigraphy. In contrast, *Granomarginata* was not recorded from South
133 China or Tarim, although it is present at this level in both New Brunswick and Poland
134 (East European Platform, Baltica). Hence, potentially subtle biogeographical signals
135 emerge, but whether these signals are real or whether they are artefacts of sampling
136 deficiencies, of variations in the facies sampled in each area, or of differences in
137 taxonomic treatment is unclear.

138 Above the Terreneuvian Series, lower Cambrian acritarch assemblages from
139 Gondwana (Stansbury and Arrowie basins of South Australia, South China, and the
140 Armorican and Avalonian margins), Baltica (Norway, Sweden, Poland), Laurentia
141 (northwest Scotland, Svalbard, Greenland) and Siberia (Anabar shelf) are reported to
142 be taxonomically comparable (Moczyłowska 1998, fig. 19; Moczyłowska & Zang
143 2006). In her review of Cambrian acritarch palaeobiogeography, Moczyłowska
144 (1998, p. 37) noted that lower Cambrian acritarch associations from South China and
145 Australia, located at that time in northern Gondwana at equatorial palaeolatitudes,
146 included cosmopolitan taxa that also occurred in successions deposited at higher
147 palaeolatitudes on the Armorican and Avalonian margins of Gondwana (Torsvik &
148 Cocks 2013, fig. 7) as well as on other palaeocontinents, including Siberia, Baltica
149 and the eastern extremity of Laurentia (northwest Scotland, Svalbard, Greenland).
150 She postulated that all of these areas might have been connected along their
151 continental shelves, thus aiding phytoplankton dispersal, and pointed out that the most
152 uniform global distribution of phytoplankton was during the later part of Stage 3
153 (*Holmia kjerulfi* Biozone of Scandinavia and equivalents), apparently coinciding with
154 a maximum flooding event. This level also coincides with the widespread distribution
155 of the acritarch genus *Skiagia*.

156 The FAD of *Skiagia*, at about the base of Series 2 and more or less coinciding with
157 the FAD of trilobites (Moczyłowska & Zang 2006), is a significant biostratigraphical
158 acritarch event in the lower Cambrian. The genus provides index species for two of
159 the acritarch zones first determined in Baltica, namely the *Skiagia ornata*–

160 *Fimbriaglomerella membranacea* and *Heliosphaeridium dissimulare*–*Skiagia ciliosa*
161 biozones, which together span Stage 3 and the lower part of Stage 4, both in Series 2
162 (Rushton & Molyneux 2011). The palaeogeographical reconstruction of Torsvik &
163 Cocks (2013) for the early Cambrian places those areas yielding *Skiagia* at low to
164 high palaeolatitudes in the southern hemisphere (**Fig. 1**), with their distribution
165 outlining two trends, one along the margin of Gondwana and the second diverging to
166 encircle the early Cambrian ocean bordered by Baltica and Laurentia.

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

186

187 ***Mid and late Cambrian***

188 The palaeobiogeography of acritarchs for the mid and late Cambrian (approximately
189 Series 3 and the Furongian Series in the revised global Cambrian chronostratigraphy;
190 Rushton 2011) was touched upon by Ghavidel-syooki & Vecoli (2008). These
191 authors compared middle and upper Cambrian acritarch assemblages from southern

192 Iran with coeval assemblages from Baltica (East European Platform: Volkova 1990;
193 northern Norway: Welsch 1986), the Avalonian margin of Gondwana (eastern
194 Newfoundland: Martin & Dean 1981, 1984, 1988; Belgium and northern France:
195 Vanguetaine 1973, 1978a; Ribecai & Vanguetaine 1993; England and Wales:
196 Downie 1984; Upper Silesia: Moczyłowska 1998), Gondwana (North Africa: Albani
197 *et al.* 1991; Vecoli 1996) and Laurentia (Missouri, Arkansas: Wood & Stephenson
198 1989). Most of these regions were at mid to high southern palaeolatitudes (**Fig. 3**),
199 the exception being Laurentia which straddled the palaeoequator. Cluster analysis
200 (**Fig. 4**) shows that a number of genera have widespread distributions, and that the
201 important late Cambrian genera *Timofeevia* and *Vulcanisphaera* are known from all,
202 or almost all, regions, including Laurentia. Laurentia and Kolguev Island (Baltica)
203 are least similar to most other regions (**Table 1**), lacking significant upper Cambrian
204 genera such as *Cristallinium*, *Cymatiogalea* and *Stelliferidium*, but including genera
205 not reported from other late Cambrian assemblages, for example *Fimbriaglomerella*
206 in the North American assemblage. The Laurentian assemblage also contains a
207 number of species recorded in open nomenclature. Ghavidel-syooki & Vecoli (2008)
208 acknowledged that the difference in composition between the Laurentian assemblage
209 and those from the Gondwanan margin, Avalonia and Baltica could be attributed to
210 sample bias, but noted also that the unusual taxonomic composition of the Laurentian
211 assemblage might be due to palaeogeographical factors, namely the wide
212 palaeolatitudinal and palaeogeographical separation between palaeocontinents.

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

222 At present, it is difficult to draw any general conclusions regarding Cambrian
223 phytoplankton biogeography. The distribution of the lower Cambrian *Skiagia*-bearing
224 assemblages and that of the upper Cambrian assemblages both suggest a degree of

225 cosmopolitanism. The distinction between the lower middle Cambrian assemblage
226 from the Amadeus Basin and putative correlative assemblages from Sweden and the
227 East European Platform does point to the possibility that there was more
228 biogeographical differentiation in the early mid Cambrian, however, perhaps in this
229 case between intracratonic settings, as in the Amadeus Basin, and more oceanic,
230 continental margin settings. The distinction noted by Ghavidel-syooki & Vecoli
231 (2008) between Laurentia on the one hand and Gondwana, Avalonia and Baltica on
232 the other might also signify biogeographical differentiation in the late Cambrian, as
233 too does the distinctive character of the late Cambrian assemblage described by
234 Rubinstein *et al.* (2003) from northwest Argentina.

235

236 **Ordovician**

237 ***Early to Mid Ordovician***

238 The Early to Mid Ordovician has been a focus for biogeographical studies of early
239 Palaeozoic phytoplankton. Early attempts to model Ordovician acritarch
240 biogeography by Cramer & Díez (1974*a, b*) distinguished an African Palynological
241 Unit, otherwise termed the *Coryphidium bohemicum* Province (Cramer & Díez
242 1974*b*), and an American Palynological Unit, described as having a “profoundly
243 different” acritarch assemblage from that of the *Coryphidium bohemicum* Province
244 (Cramer & Díez 1974*b*, p.142). Much of the ensuing discussion, however, has taken
245 Vavrdová’s (1974) assessment of the biogeographical differentiation of Early
246 Ordovician acritarch provinces in Europe as its starting point. The development of
247 ideas on Early and Mid Ordovician acritarch biogeography in the latter part of the 20th
248 century was reviewed and synthesized by Servais *et al.* (2003).

249 Vavrdová’s (1974) analysis of biogeographical patterns among European Ordovician
250 acritarchs recognized two provinces, the Mediterranean Province encompassing
251 Belgium, France, Spain, North Africa, southern Germany, Bohemia and Bulgaria, and
252 the Baltic (or Boreal) Province incorporating northern Russia, Poland, Sweden and
253 north Germany. Among the key criteria used to characterize these provinces,
254 Vavrdová (1974) pointed to the prevalence of acanthomorph acritarchs in the Baltic
255 Province, represented by species of *Baltisphaeridium*, *Peteinosphaeridium*,
256 *Goniosphaeridium* and *Filisphaeridium*, and the occurrence of diacromorph acritarchs

257 such as species of *Arbusculidium* and *Acanthodiacrodium* in the Mediterranean
258 Province. This distinction is not always clear cut, however, and Vavrdová herself
259 pointed out that the Baltic Tremadocian species *Dasydiacrodium monstrorsum*
260 resembled the coeval Mediterranean species *Arbusculidium frondiferum* and *A.*
261 *destombesii*. Conversely, she reported the occurrence of *Baltisphaeridium klabavense*
262 and *Goniosphaeridium polygonale* in Arenig rocks of the Mediterranean Province.
263 She also highlighted, however, the occurrence of species of *Aureotesta*, *Coryphidium*,
264 *Frankea* and *Striatotheca* in the Arenig–Llanvirn Mediterranean Province. None of
265 these genera is known from the Lower Ordovician of the Baltic Province. The
266 Mediterranean Province and the Baltic Province have been the topics of much
267 subsequent work, the former now subsumed within a broader Perigondwana Province.

268

269 *From the Mediterranean Province to the Perigondwana Province*

270 Realization that Vavrdová's (1974) Mediterranean Province extended beyond Europe
271 came when Martin (1982a) commented on Tremadocian and Arenig acritarch
272 assemblages from southern Europe and eastern Newfoundland. Based on her analysis
273 of palynological data from the Tremadoc and Arenig series, Martin (1982a, p. 38)
274 argued that the Mediterranean Province should include eastern Newfoundland,
275 England and Wales, Spain, France, Belgium, Bohemia, North Africa and northwest
276 Argentina. Martin (1982a) further noted that eastern Newfoundland and the
277 Mediterranean area were located on the periphery of Gondwana at the beginning of
278 the Ordovician, based on palaeogeographical reconstructions available at the time,
279 and may have been the first to recognize the Mediterranean Province as a
280 Perigondwanan province, at least implicitly if not explicitly (see Tongiorgi *et al.*
281 1995).

282 Li's (1989) contribution to the debate, based on work on the Upper Yangtze region of
283 South China, was twofold. First, he augmented Martin's (1982a) observations by
284 demonstrating that Vavrdová's Mediterranean Province extended from eastern
285 Newfoundland through southern Europe and the Middle East to South China. Second,
286 he argued that affinity of acritarch assemblages to Vavrdová's Mediterranean
287 Province should be determined by the occurrence of the acritarch genera
288 *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 (1982a, 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, 2003a, 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*

320 In contrast to the Perigondwana Province, recognition of Vavrdová's (1974) Baltic
321 Province has remained problematical, mainly because, as Li (1989) pointed out, many
322 of the genera and species used in its original definition have much greater
323 biogeographical ranges. Tongiorgi & Di Milia (1999), for example, noted that
324 acanthomorph acritarch genera (*Baltisphaeridium*, *Liliosphaeridium*,
325 *Peteinosphaeridium*, *Polygonium*) constituted inadequate criteria to characterize
326 assemblages from the Baltic Province, given that acanthomorph acritarchs are also
327 abundant in coeval assemblages from the Perigondwana Province. Similarly, they
328 pointed out that the absence of diacromorph acritarchs as used by Vavrdova (1974) to
329 define the province could no longer be regarded as diagnostic, given the presence of
330 these forms in assemblages from Baltica (East European Platform, Baltoscandia).
331 Consequently, the Baltic Province came to be associated with the absence of taxa, and
332 principally the absence of those genera and species regarded as characteristic of upper
333 Tremadocian to lower Llanvirn (Darriwilian) Perigondwanan assemblages (Brocke *et*
334 *al.* 1995), namely *Arbusculidium filamentosum* and species of *Arkonia*, *Striatotheca*,
335 *Aureotesta*, *Coryphidium*, *Vavrdovella*, *Dicrodiacrodium* and *Frankea*. Servais &
336 Fatka (1997), for example, used these genera and species to delineate the Trans-
337 European Suture Zone, separating Perigondwanan terranes, including Avalonia and
338 Armorica, from Baltica.

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

350 The criteria advanced by Playford *et al.* (1995) and Tongiorgi & Di Milia (1999) have
351 not been universally accepted, and Li & Servais (2002) presented a critique of the use
352 of species of *Peteinosphaeridium* as biogeographical markers. The latter authors

353 pointed particularly to the large amount of morphological variability often found
354 within acritarch species (morphospecies) and to the influence of environmental
355 conditions on the development of morphology among acritarchs in general. They
356 considered that the variability observed between morphospecies, such as that between
357 species of *Peteinosphaeridium*, could just as easily reflect local environmental
358 conditions as palaeogeographical differences. They argued that it was difficult to
359 justify the definition of a Baltic acritarch province based only on selected species of a
360 single genus. Li & Servais (2002) concluded that detailed investigations of the
361 variability of *Peteinosphaeridium* and related genera were needed to understand fully
362 the palaeoecological and palaeogeographical distribution of that acritarch plexus.

363

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

365 The ‘Mediterranean’ (i.e. Perigondwanan) affinity of acritarch assemblages from the
366 Lower to Middle Ordovician of South China had been recognized by Li (1987, 1989)
367 and was reaffirmed by later workers (Playford *et al.* 1995; Tongiorgi *et al.* 1995,
368 1998, 2003a; Tongiorgi & Di Milia 1999; Servais *et al.* 2003). But, although
369 Tongiorgi *et al.* (1995) supported Li’s (1989) conclusion that South China belonged
370 to the Perigondwana Province, they also indicated that the situation in South China
371 was more complicated than attribution to that province might imply. Working on
372 acritarchs from the Dawan Formation of Arenig age from the Yangtze Platform of
373 South China, Tongiorgi *et al.* (1995) noted that the assemblage had a predominantly
374 ‘Mediterranean’ character but also exhibited Australian and Baltic affinities. The
375 largest component of the assemblage was described at the time as an endemic South
376 Chinese component (42.2%), but this largely comprises endemic species assigned to
377 genera with much wider distributions, including *Baltisphaeridium*, *Barakella*,
378 *Cymatiogalea*, *Multiplicisphaeridium*, *Ordovicidium*, *Peteinosphaeridium*, *Pirea*,
379 *Striatotheca*, *Tongzia* and *Veryhachium*. Species with known Perigondwanan
380 affinities were identified as the second largest component of the assemblage (35.6%).
381 These include forms regarded as diagnostic of the Perigondwana Province such as
382 *Arbusculidium filamentosum*, *Coryphidium bohemicum*, *Striatotheca principalis*
383 *parva* and *Striatotheca rarirrugulata*, and other forms such as *Cymatiogalea*
384 *granulata* and *Petaloferidium florigerum*. The Australian component (13.3%)
385 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

419 assemblages from south-eastern Sichuan and northern Guizhou than was reported for
420 the sections studied by Tongiorgi *et al.* (1998). Subsequently, Tongiorgi *et al.*
421 (2003a) revisited the apparent change in biogeographical affinity from
422 Perigondwanan to Baltic among acritarch assemblages of the Yangtze Platform, and
423 proposed a model to explain why such changes might not be seen elsewhere (see
424 *Factors controlling Early to Mid Ordovician acritarch provincialism*).

425

426 *Other provinces*

427 Much of the discussion surrounding Early to Mid Ordovician acritarch biogeography
428 has focused on Perigondwana, Baltica and South China. Nevertheless, Playford *et al.*
429 (1995) recognized discrete North American and Australian provinces in addition to
430 Perigondwana and Baltica, making a total of seven acritarch biogeographical units
431 including their three Perigondwanan subprovinces (South America, Mediterranean,
432 South China). They also suggested that North China might be segregated from these
433 provinces, although it was virtually unexplored palynologically. They pointed out
434 that distinguishing a warm, subequatorial North China province from a more
435 temperate South China would be in accordance with other faunal, tectonic and
436 palaeomagnetic datasets (but note that the reconstruction from BUGPLATES used
437 here in **Figure 5** also places South China at equatorial palaeolatitudes). In common
438 with their Perigondwana and Baltica provinces, Playford *et al.* (1995) considered
439 species of *Peteinosphaeridium* and related genera to be characteristic elements of the
440 microfloras from each province. *Peteinosphaeridium? furcatum*, for example,
441 tentatively referred to that genus and reported to be from the Arenig of Western
442 Australia, was identified as being characteristic of the Australian Province, whereas
443 *Peteinosphaeridium? indianense* and *P.? spiraliculum* were considered to be
444 characteristic of the North American Province. Both of the latter species, however,
445 are from the Upper Ordovician, as Playford *et al.* (1995) acknowledged.

446 Volkova (1997) suggested that a separate warm-water (subequatorial) province could
447 be distinguished in the late Tremadocian (c. 480 Ma) based on co-occurrences of the
448 genera *Aryballomorpha*, *Athabascaella* and *Lua* and the absence of diacromorph
449 acritarchs. Upper Tremadocian assemblages with these characteristics were
450 documented from Laurentia (Alberta) by Martin (1984, 1992) and from North China

451 by Martin & Yin (1988), both areas situated at low subequatorial palaeolatitudes
452 during the late Tremadocian (Torsvik & Cocks 2013, fig. 11). A further Laurentian
453 occurrence, from Texas, was reported by Barker & Miller (1989) but not documented
454 in full. *Aryballomorpha* and *Athabascaella* have also been reported from the upper
455 Tremadocian of Baltica, however (Volkova 1995), which was situated at mid southern
456 palaeolatitudes in the Early Ordovician (Torsvik & Cocks 2013, figs 10–12), and
457 *Athabascaella* has been recorded from Perigondwanan successions that were at high
458 southern palaeolatitudes, including the lower Tremadocian of Tunisia (Vecoli 2004)
459 and the uppermost Tremadocian of Belgium (Breuer & Vanguestaine 2004). Other
460 Perigondwanan records of *Athabascaella* are from the Arenig of Australia
461 (Quintavalle & Playford 2006a, b), Oman (Rickards *et al.* 2010), South China (Li
462 1990; Yan *et al.* 2011), and possibly Argentina (Achab *et al.* 2006) and Bohemia
463 (Vavrdova 1990a), demonstrating that the genus had a wide biogeographical range
464 across palaeolatitude.

465

466 *Factors controlling Early to Mid Ordovician acritarch provincialism*

467 Cramer & Díez's (1974a, b) cold African Palynological Unit and warm American
468 Palynological Unit were depicted as being parallel to palaeolatitude and following
469 climatic belts, but the palaeogeographical reconstructions on which they were based
470 have since been superseded. Acritarch biogeography is no longer regarded as having
471 a simple relationship with palaeolatitude or climate. More recent models, of greater
472 complexity, invoke a range of interacting factors as controls on biogeographical
473 distributions.

474 Nevertheless, the biogeographical ranges of some acritarch genera and species are still
475 regarded as being constrained by palaeolatitude. Latitude figured as a factor in the
476 tentative model put forward by Li & Servais (2002) to explain the distribution of
477 selected Lower to Middle Ordovician acritarch genera. Furthermore, Colbath's
478 (1990a) conclusion that the genus *Frankea* was restricted to relatively high
479 palaeolatitudes remains largely true for the palaeogeographical reconstructions of
480 Torsvik & Cocks (2013), as shown in **Figure 5** (see also Servais 1993). The most
481 northerly occurrences of *Frankea* in Arenig–Llanvirn (Floian–Darriwilian)
482 Perigondwanan successions, including Avalonia, are from mid southern

483 palaeolatitudes. Its most northerly record on the margin of Gondwana is from Saudi
484 Arabia, where it occurs in the Saq Formation and the Hanadir Member of the Qasim
485 Formation (Le Hérisse *et al.* 2007). It occurs at similar mid southern palaeolatitudes
486 in Avalonian successions of eastern Newfoundland (Dean & Martin 1978), Germany
487 (Burmam 1968, 1970; Maletz & Servais 1993; Servais 1994), Belgium (Servais &
488 Maletz 1992) and England and Wales (Downie 1984; Molyneux 1990, 2009). Even
489 so, there are no known records of the genus from Baltica, which is placed at
490 comparable mid southern palaeolatitudes as Avalonia and Saudi Arabia (**Fig. 5**).
491 Clearly, palaeolatitude cannot have been the only factor affecting the distribution of
492 this genus.

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

506 Tongiorgi *et al.* (1995) further considered the factors that were likely to affect
507 acritarch distributions. They noted that a simple model such as that proposed by
508 Cramer (1971) and Cramer & Díez (1974*b*), with biogeographical distributions
509 controlled essentially by palaeoisotherms parallel to palaeolatitude, did not sit easily
510 with the complex pattern of biogeographical affinities exhibited by the Yangtze
511 acritarchs (see above). They proposed a modification of the model, in which the
512 distribution of Arenig acritarch communities was indeed delimited by
513 palaeoisotherms, but that the distribution of palaeoisotherms was in turn influenced by
514 oceanic circulation. They postulated that: (1) a cold Perigondwanan current flowed
515 northwards from the subpolar margin of Gondwana to South China, carrying typical

516 Perigondwanan taxa from high to low palaeolatitudes; (2) that the cold current gave
517 rise to a warm current northwest of South China which then returned southwards
518 through Baltica, with some shared taxa such as *Ampullula* originating in South China
519 and being carried to Baltica; and (3) that differences between Arenig acritarch
520 assemblages of South China and Australia could be explained by the former being
521 influenced by the cold Perigondwanan current whereas coeval deposits of the latter
522 were deposited in an inter-tropical epicontinental sea.

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

536 This theme was developed further by Tongiorgi *et al.* (2003a), who re-investigated
537 the apparent changes in biogeographical affinities of acritarchs in their data in order to
538 explain why such changes were not apparent in other studies of South Chinese
539 acritarchs (e.g. Brocke *et al.* 2000). Tongiorgi *et al.* (2003a) again argued that more
540 distal, oceanic settings around South China were characterized by Perigondwanan
541 microfloras, whereas more proximal settings were associated with assemblages that
542 exhibited Baltic characteristics. Consequently, a change from a distal to a proximal
543 environmental setting, either vertically within a section or laterally between sections,
544 might be accompanied by a change in assemblage-type from Perigondwanan to Baltic.
545 Hence, the upward change from Perigondwanan to Baltic assemblages recorded by
546 Tongiorgi *et al.* (1998) was correlated with a protracted regression from the mid to
547 late Arenig (late Floian to early Darriwilian) and the consequent development of more
548 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 (2003a) 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.* (2003a) 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.* (2003a) 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 2003a, 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 2003a, 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*, *Arkonina* 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 2006a, b). *Ampullula* [*Stelomorpha*] *erchunensis*, which has been reported from
585 Norway (Tongiorgi *et al.* 2003b), Poland and Baltic Russia (Raevskaya *et al.* 2004),
586 South China (Yin 1994; Brocke *et al.* 1999, 2000; Tongiorgi *et al.* 1995, 2003a; 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. hymeniferum*, *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*

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

621

622 *Sandbian and Katian*

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

630 In their studies on lower Richmondian (middle Katian) strata of the North American
631 Midcontinent (i.e. Sylvan Shale, Maquoketa Shale, Bill’s Creek Shale and Stonington
632 Formation), Wicander *et al.* (1999), Playford & Wicander (2006) and Wicander &
633 Playford (2008) compared their Laurentian acritarch assemblages with time-
634 equivalent assemblages from Baltica, Avalonia, Gondwana and Perigondwanan
635 terranes. They reported (Wicander & Playford 2008) that many of the constituent
636 taxa of the Laurentian assemblages were geographically widespread during the
637 Katian. The combined Bill’s Creek Shale and Stonington Formation acritarch
638 assemblage, for example, was reported to include many taxa known from Upper
639 Ordovician localities in Baltica, Avalonia, South China and Gondwana, “thus
640 evincing Late Ordovician cosmopolitanism among marine microphytoplankton
641 communities” (Wicander & Playford 2008, p. 62). Cosmopolitan species include
642 *Aremoricanium squarrosus*, *Baltisphaeridium aliquigranulum*, *B. perclarum*,
643 *Dactylofusa ctenista*, *Diexallophasis denticulata*, *D. platynetrella*, *Dorsennidium*
644 *hamii*, *Excultibrachium concinnum*, *Leiofusa fusiformis*, *L. litotes*,
645 *Lophosphaeuridium edenense*, *Micrhystridium prolixum*, *Multiplicisphaeridium*

646 *irregulare*, *Orthosphaeridium rectangulare*, *Polygonium gracile*, *Veryhachium*
647 *europaeum*, *V. oklahomense* and *Villosacapsula setosapellicula*.

648

649 *Hirnantian*

650 Until recently, little was known about acritarch palaeobiogeography during the latest
651 Ordovician Hirnantian Stage. Most investigations of acritarchs from Hirnantian strata
652 have focused on Gondwanan or Perigondwanan successions in Morocco (Elaoud-
653 Debbaj 1988), northeast Libya (Molyneux & Paris 1985; Hill & Molyneux 1988;
654 Molyneux 1988; Paris 1988), northeast Algeria (Vecoli 1999; Le Hérissé *in Paris et*
655 *al.*, 2000), the Prague Basin (Dufka & Fatka 1993), Argentina (Rubinstein & Vaccari
656 2004; Rubinstein *et al.* 2008a), south Turkey (Le Hérissé *in Paris et al.* 2007) and Iran
657 (Ghavidel-syooki *et al.* 2011a, b). There, preservation, reworking and dilution linked
658 to the several advances and retreats of ice in local palaeovalleys during the Hirnantian
659 glacial phases (e.g. Ghienne *et al.* 2007) can make it difficult to analyse and interpret
660 palynological signals (Vecoli & Le Hérissé 2004; Vecoli 2008; Delabroye & Vecoli
661 2010). However, Vecoli & Le Hérissé (2004), in their extensive analysis of acritarch
662 diversity patterns throughout the Ordovician of the periglacial Gondwanan margin,
663 showed that standing diversity increased through the glacial interval with “new
664 speciations [...] of morphologically distinctive [...] species [...] such as *Beromia*
665 *clipeata*, *Eupoikilofusa* [= *Poikilofusa*] *ctenista*, and *Saharidia munfarida*”. A burst
666 of new netromorph species seems also to have occurred at that time (Vecoli & Le
667 Hérissé 2004, fig. 6). Many of these new taxa were endemic to Gondwana
668 (Delabroye 2010; Delabroye *et al.* 2011a; see below). In post-glacial Hirnantian
669 strata, they co-occur with “new distinct [and endemic] morphotypes of Silurian
670 ‘affinity’ such as *Cymbosphaeridium* spp., *Tylotopalla* spp. [e.g. *Tylotopalla*
671 *caelamenicutis*], and *Visbysphaera* spp.” (Vecoli & Le Hérissé 2004). All of these
672 species that appeared during the Hirnantian also occur with other species that were
673 endemic to Gondwana at this level and which had their first appearances during the
674 Sandbian and the Katian. The latter include *Leprotolypa evexa*, *Neoveryhachium*
675 *carminae*, *Striatotheca* sp. of Molyneux (1988) and *Veryhachium subglobosum*.

676 A few Hirnantian localities at low palaeolatitudes have been studied for
677 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 *Hoegkintia*, *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 biogeography 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, 1974a, b) latitude-parallel model, however,
784 was at least partially dependent on the palaeogeographical reconstruction used as a
785 base map (Colbath 1990a). 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 1990a).

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, 1974a, 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

808 Laurentia and the adjacent continental masses of Avalonia and Baltica (**Fig. 7**). In
809 addition to the rare occurrences in the south-eastern United States (Alabama, Georgia
810 and Virginia) reported by Cramer & Díez (1972), *Neoveryhachium carminae* has been
811 recorded from the Llandovery Series of Belgium (Avalonia: Martin 1969, 1974, 1989)
812 and the upper Wenlock and Ludlow series of Gotland (Baltica: Le Hérisse 1989b;
813 Stricanne *et al.* 2004).

814 The biogeographical range of *Neoveryhachium carminae* also extended along the
815 facing margin of Gondwana, where it occurs in rocks of Llandovery to early Wenlock
816 age from Bolivia and Peru (Díaz-Martínez *et al.* 2011) through North Africa (Libya:
817 Deunff & Massa 1975; Hill & Molyneux 1988) to Turkey (western Taurides: Dean &
818 Monod 1990; Dean *et al.* 1993), Iran (Zagros Basin: Ghavidel-syooki 1997) and Saudi
819 Arabia (Le Hérisse *et al.* 1995; Le Hérisse 2000). Other records are from Silurian
820 successions in Algeria (Argiles à Graptolites, Formation de Medarba, Formation de
821 l'Oued Tifist: Jardiné & Yapaudjian 1968; Jardiné *et al.* 1974), Jordan (Khushsha
822 Formation: Keegan *et al.* 1990), Egypt (Gueinn & Rasul 1986) and Iraq (Akkas
823 Formation: Al-Ameri 2010), and from rocks dated as late Silurian (upper Wenlock–
824 Ludlow series) in Libya (Richardson & Ioannides 1973; Wood & Tekbali 1987).
825 *Neoveryhachium carminae* has also been recorded from rocks of mid Llandovery to
826 early Wenlock age in the intracratonic Paranaíba and Paraná basins of Brazil and
827 Paraguay respectively (Brito 1967; Quadros 1982; Wood & Miller 1991; Rubinstein
828 1997), and from rocks of Ludlow age in Bolivia (Cramer *et al.* 1974c) and the
829 Precordillera Basin of Argentina (Rubinstein 2001).

830 Le Hérisse & Gourvenec (1995, p. 116) noted that *Neoveryhachium carminae* was
831 found preferentially at high palaeolatitudes. However, they also reported evidence for
832 facies control, with a tendency for the species to occur in turbid environments and
833 clastic sedimentary regimes of shallow shelf seas. Furthermore, they noted that the
834 species was found in environments with similar sedimentary conditions in Laurentian
835 North America and on Gotland. They pointed out that facies control to account for
836 the species' distribution had been advocated by Cramer (1971) but not considered
837 subsequently, and concluded that a correspondence could be established between the
838 distribution of the species and platform mudstones and fine-grained clastic sediments
839 deposited in shelf environments. Rubinstein (1997), however, questioned whether
840 this interpretation of facies control could be used to explain the distribution of

841 *Neoveryhachium carminae* in South American basins, arguing that there were no
842 marked differences in depositional environments between basins to explain the
843 presence or absence of the species. She suggested that the distribution of *N. carminae*
844 there might be related to conditions in each basin, citing in particular connection to or
845 isolation from other basins or an oceanic environment.

846

847 *The Deunffia-Domasia biofacies*

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

868 Based on this distribution pattern, Le Hérissé & Gourvenec (1995, p.121) argued for
869 dispersal of taxa belonging to the *Deunffia-Domasia* association between low and
870 high palaeolatitudes, and an increase in diversity from high to low palaeolatitudes.
871 They also noted, however, that although there were differences in diversity between
872 the Laurentian and Gondwanan margins, there was no real evidence for provincialism

873 within the group. They observed that the spatial distribution of the combined
874 *Deunffia-Domasia* biofacies was more closely related to depositional environment
875 than palaeolatitude, with better representation of the biofacies in outer shelf
876 environments on both the Laurentian and Gondwanan margins. Le Hérissé &
877 Gourvennec (1995) concluded that the wide distribution of the biofacies was likely to
878 have been influenced by oceanic circulation patterns that transported the *Deunffia-*
879 *Domasia* association between the relatively homogeneous outer shelf environments of
880 both continental margins.

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

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

896 Although they had demonstrated that the *Neoveryhachium carminae* and *Deunffia-*
897 *Domasia* biofacies had widespread distributions on the Laurentian and Gondwanan
898 margins of the Rheic Ocean, Le Hérissé & Gourvennec (1995) argued that other taxa
899 might have more restricted biogeographical distributions. They cited, in particular,
900 the apparent restriction of *Dilatisphaera williereae* in the late Llandovery–Wenlock to
901 a subtropical zone that encompassed the Brabant Massif of Belgium, Gotland, the
902 Llandovery type area of Wales, western Ireland, and the Gaspé Peninsula and
903 Anticosti Island of eastern Canada (**Fig. 7**). They also noted that the distribution of
904 *Dilatisphaera* was subsequently modified in time and space, with dispersal from low
905 to high palaeolatitudes. Among other taxa identified as having potential

906 biogeographical significance, Le Hérissé & Gourvennec (1995) suggested that
907 *Gracilisphaeridium* might be used in addition to other taxa to define a “Euramerican”
908 (i.e. Laurentian/Avalonian/Baltic) province at the Llandovery–Wenlock boundary,
909 and that other distinctive taxa, notably *Dactylofusa maranhensis* and *Tyrannus*
910 *giganteus* might be restricted to Gondwana (**Fig. 7**). *Dactylofusa maranhensis*, for
911 example, is widespread in Gondwanan successions, where it occurs in the
912 intracratonic Paranaíba and Paraná basins of Brazil and Paraguay (Brito 1967;
913 Quadros 1982; Gray *et al.* 1992; Rubinstein 1997) and in the Central Andean Basin of
914 northwest Argentina (Rubinstein 2005; Rubinstein *et al.* 2008a; Rubinstein & Muro
915 2011) as well as along the margin of Gondwana as depicted by Le Hérissé &
916 Gourvennec (1995, fig. 2).

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

926

927 ***Late Silurian (Ludlow–Přídolí)***

928 Le Hérissé *et al.* (1997a) used methods similar to those employed by Le Hérissé &
929 Gourvennec (1995) to investigate the biogeography of late Silurian phytoplankton in
930 the context of the base maps published by Scotese & McKerrow (1990). Their
931 analysis highlights some of the complexities introduced by the interplay of different
932 factors affecting biogeographical distributions of Palaeozoic phytoplankton. On the
933 one hand, Le Hérissé *et al.* (1997a) referred to the apparent homogeneity of late
934 Silurian assemblages from southern Baltica and the Gondwanan margin. However,
935 they also referred to the degree of endemism that was evident among late Silurian
936 phytoplankton assemblages from either side of the Rheic Ocean. Le Hérissé *et al.*
937 (1997a) 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.* (1997a) 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 Příklad 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.* (1997a) 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.* (1997a) 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.* (1997a) 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.* (1997a) also distinguished an outer, deep-water belt on the
970 Perigondwanan margin of the Rheic Ocean (**Fig. 8**), characterized by a low diversity

971 assemblage with *Cymbosphaeridium* or *Evittia*, cysts of prasinophycean algae
972 (*Cymatiosphaera*, *Dictyotidium*) and mazuelloids. This assemblage was documented
973 from Bohemia, with other possible examples from the Carnic Alps, Sardinia, the
974 Vendée (southern Brittany, Aquitaine) and Spain.

975

976 **Devonian**

977 Notable papers dealing with Devonian phytoplankton biogeography include those by
978 Colbath (1990a), who examined the biogeographical distribution of Frasnian
979 microfloras, and Le Hérissé *et al.* (1997a), who analysed the biogeography of Early
980 Devonian acritarchs and prasinophytes. These studies made use of quantitative
981 methods, principally cluster analysis, as well as more qualitative assessments, but
982 were subject to the limitations imposed by the available data. As Le Hérissé *et al.*
983 (1997a) noted, there were, at that time, relatively few publications on Lower
984 Devonian (Lochkovian and equivalent ‘Gedinnian’) acritarch assemblages, and that
985 they were also geographically limited.

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

993 Only those Devonian acritarch papers germane to the discussion of Devonian
994 acritarch palaeobiogeography were used for this review. Papers dealing with
995 Devonian acritarchs and prasinophytes that contain poorly preserved assemblages,
996 those representing environments generally unfavourable to diverse assemblages (both
997 preservational and morphological), those in which assemblages are not illustrated, and
998 those that describe only one or several new taxa are not included. Many of the papers
999 cited do, however, contain extensive bibliographies that include papers not referenced
1000 here.

1001 Lastly, Le Hérissé *et al.* (2000) reviewed the biostratigraphical, palaeoecological and
1002 palaeogeographical status of Devonian acritarchs in general, as well as plotting the

1003 stratigraphical range and geographical distribution of some 180 selected acritarch
1004 species. These species were classified as being Cosmopolitan, Gondwanan, European
1005 (primarily from Belgium), North American, South American or Australian.

1006

1007 *Early Devonian*

1008 In their pioneering investigation of the Early Devonian biogeography of acritarchs and
1009 prasinophytes, Le Hérissé *et al.* (1997a) applied cluster analysis to assemblages from
1010 eastern North America (single location, Oklahoma), Bolivia, North Africa (Algeria,
1011 Libya, Tunisia), the Armorican Massif, north-west Spain, the Moesian platform
1012 (Romania), and the Estonian and Podolian block (Le Hérissé *et al.* 1997a, fig. 6).

1013 Their analysis distinguished three groups of assemblages. One cluster comprised
1014 Podolia and Romania. A second cluster consisted of north-west Spain, the Armorican
1015 Massif and North Africa, with Bolivia linked at lower similarity values. The third
1016 cluster, eastern North America, was clearly isolated from the other two groups (Le
1017 Hérissé *et al.* 1997a, fig. 4). Le Hérissé *et al.* (1997a, p. 120) concluded that eastern
1018 North America and Gondwana were characterized by distinctive acritarch
1019 assemblages during the Early Devonian. They went on to write “Taking into account
1020 more recent palaeogeographic reconstructions, it seems that this provincialism was
1021 not controlled by water temperature differences, but rather influenced by physical
1022 barriers (e.g. emergent land) between these areas, preventing seaway connections and
1023 the dispersal of acritarchs. In spite of the limited data available, particularly from
1024 northern Europe, close similarities exist between this region and the North
1025 Gondwanan margin. This linkage reflects the low latitudinal positioning of this
1026 region and the narrowing of the Rheic Ocean during the Early Devonian.” As shown
1027 below, this conclusion has had to be modified as more sections became available.

1028 Studies of Lower Devonian acritarchs still remain relatively sparse. Le Hérissé *et al.*
1029 (2009) examined phytoplankton biodiversity changes for the late Silurian to earliest
1030 Devonian (Lochkovian) based on published and unpublished data from key
1031 stratigraphic sections where independent age control was firmly established. Regional
1032 biodiversity for Lochkovian phytoplankton communities was determined for
1033 Laurentia (Oklahoma, western Newfoundland), Armorica (Crozon Peninsula and
1034 Normandy, France; northern Spain) and Gondwana (Libya, Bolivia). Le Hérissé *et al.*

1035 (2009) concluded that there was an initial radiation of new acritarch taxa during the
1036 Lochkovian and an increase in cosmopolitan species in both hemispheres.

1037 When plotted on the Early Devonian palaeogeographical map of Cocks & Torsvik
1038 (2002, fig. 8; see also Rubinstein *et al.* 2008*b*, fig. 3 and Le Hérissé *et al.* 2009, text-
1039 fig. 3), published acritarch records form two distinct groups. One group comprises
1040 records from mid palaeolatitudes, about 30°–40°S, from Laurentia, Armorica and
1041 northern Gondwana (North Africa). The second group consists of assemblages from
1042 high palaeolatitudes (>60°S) and mainly from South America (**Fig. 9**).

1043 At mid palaeolatitudes, well-preserved and diverse Lochkovian acritarch assemblages
1044 from Laurentia are known from the Haragan and Bois d’Arc formations of Oklahoma
1045 (Loeblich & Wicander 1976; Wicander 1986). Similarly well-preserved and diverse
1046 Lochkovian acritarch assemblages have been recorded from the Landévennec
1047 Formation, Crozon Peninsula, Brittany (Deunff 1980) and the San Pedro Formation,
1048 northern Spain (Cramer 1964; Rodriguez Gonzalez 1983), both in Armorica, and from
1049 various formations in the Algerian Sahara (Jardiné & Yapaudjian 1968; Jardiné *et al.*
1050 1972, 1974) and the Tadrardt Formation of western Libya (Le Hérissé 2002), both in
1051 northern Gondwana. These are not the only published records of Lochkovian
1052 acritarch assemblages (see Rubinstein *et al.* 2008*b* for additional references), but
1053 constitute the most diverse and best preserved Lochkovian assemblages described to
1054 date. As environmental conditions play an important role in the distribution of
1055 acritarchs, some of the published acritarch assemblages are of little or no use in
1056 helping to delineate palaeogeographic realms and so are not discussed here.

1057 At high paleolatitudes, Lochkovian acritarch data are from South America (**Fig. 9**)
1058 but, as indicated by Rubinstein *et al.* (2008, p. 170), are still scarce and are restricted
1059 to Argentina (Le Hérissé *et al.* 1997*b*), Bolivia (Vavrdová *et al.* 1996; Vavrdová &
1060 Isaacson 1997; Melo 2000, 2005; Le Hérissé *et al.* 2004), Brazil (Brito 1967; Daemon
1061 *et al.* 1967; Lange 1967; Quadros 1982, 1988, 1999; Dino & Rodrigues 1995) and
1062 Uruguay (Martínez Macchiavelo 1968; Pöthe de Baldis 1978). In addition,
1063 Rubinstein & Steemans (2007) reported on a palynomorph assemblage of late Pragian
1064 to early Emsian age from the Precordillera of Mendoza, Argentina. More recently,
1065 Rubinstein & Muro (2011) discussed the biostratigraphy and diversity trends of
1066 Silurian to Lower Devonian organic-walled phytoplankton and miospores from
1067 Argentina.

1068 The mid palaeolatitude acritarch record seemingly indicates some provincialism
1069 between Laurentia and Armorica on the one hand, and Gondwana on the other, with
1070 about 35% of the species endemic to Laurentia (Le Hérissé *et al.* 1997a). However,
1071 some of this is probably due to lack of a robust published record, and what were
1072 earlier reported to be endemic species have now been recorded elsewhere.

1073 Nonetheless, commonly occurring, distinctive species that are restricted to Laurentia
1074 include, among others, *Ectypolopus elimatus*, *Multiplicisphaeridium ampliatum*,
1075 *Nanocyclopia aspratilis*, *Pterospermella malaca* and *Pterospermella verrucaboia*.

1076 Other common and distinctive Laurentian taxa that have been recorded elsewhere
1077 include *Cymatiosphaera reticulosa* (Podolia), *Dictyotidium biscutulatum* (Podolia),
1078 *Ecthympalla echinata* (Libya) and *Oppilatala vulgaris* (Libya). Commonly
1079 occurring and distinctive taxa that are restricted to Armorica and North Africa include
1080 *Candelasphaeridium insolitum*, *Fulgisphaeridium bristokii* and *Perforella perforata*.

1081 Assemblages from Gondwana include a number of genera and species that are
1082 seemingly endemic to the palaeocontinent, for example *Schizocystia*, which has been
1083 reported from Lower Devonian strata of South America and North Africa. Its
1084 occurrence on the west and north Gondwana margin makes this genus a possible
1085 marker for the Lower Devonian in Gondwanan successions (Rubinstein *et al.* 2008b).

1086 Those taxa that have a widespread geographical distribution, are restricted to the
1087 Lochkovian, and can be used for worldwide stratigraphic correlations (Rubinstein *et*
1088 *al.* 2008b), include the distinctive *Demorhethium lappaceum*, *Riculusphaera fissa* and
1089 *Thysanoprobolus polykion*. Other Devonian acritarch taxa that either first occur in the
1090 upper Silurian or extend into the Pragian and Emsian stages and are commonly
1091 reported include, among others, the *Diexallophasis remota* group, *Evittia* spp.,
1092 *Hapsidopalla sannemannii*, *Pterospermella circumstriata*, *Quadradius fantasticum*
1093 and *Winwaloewsia distracta* (e.g. Playford 1977; Le Hérissé *et al.* 2000). All of these
1094 taxa also have wide geographical distributions.

1095 Notwithstanding the restricted distribution of some genera and species, as noted
1096 above, it now appears, based on the diverse (47 species) and well-preserved
1097 Lochkovian acritarch assemblage reported from the Solimões Basin, northwestern
1098 Brazil, and Lower Devonian acritarch assemblages elsewhere, that there was a more
1099 cosmopolitan nature to the Early Devonian microphytoplankton community than

1100 previously suggested, and “the variations in composition are most probably
1101 progressive from high to low (palaeo)latitudes” (Rubinstein *et al.* 2008*b*, p. 176).

1102

1103 *Mid Devonian*

1104 The amalgamation of Avalonia and Baltica with Laurentia in the mid Silurian led to
1105 the formation of Laurussia, which then continued to move southward and rotate
1106 counterclockwise. By the Early–Mid Devonian transition (397.5 Ma), Laurussia and
1107 its overlying epeiric seas were located at low to mid southern palaeolatitudes (**Fig.**
1108 **10**). In contrast, Gondwana rotated in a northwesterly direction, with the result that
1109 the Rheic Ocean between Laurussia and Gondwana continued to close, bringing the
1110 two continental masses closer together. The mountain building that began during the
1111 late Silurian continued along the eastern margin of Laurussia.

1112 The literature on Middle Devonian acritarch assemblages, particularly from well-
1113 dated and stratigraphically constrained sections, is more extensive than for the Lower
1114 Devonian, but still of uneven geographical and stratigraphical distribution, with most
1115 of the studies from Givetian rather than Eifelian sections. Publications on well-
1116 preserved Middle Devonian acritarch assemblages from sections with good
1117 stratigraphic control in North America include Legault (1973; Givetian, Ontario,
1118 Canada), Playford (1977; upper Pragian–Givetian, Ontario, Canada), Wicander &
1119 Wood (1981; Givetian, Ohio, U.S.A.), Wicander & Wright (1983; Eifelian–Givetian,
1120 Ohio, U.S.A.), Wood & Clendening (1985; Givetian, Kentucky, U.S.A.), Turner
1121 (1991; Givetian–Frasnian, Alberta and Northwest Territories, Canada), Huysken *et al.*
1122 (1992; Givetian–Famennian, Kentucky, U.S.A.) and Wicander & Wood (1997,
1123 Givetian, Iowa, U.S.A.).

1124 Middle Devonian acritarch assemblages from South American are not as well studied
1125 as those from North America and do not always have the best stratigraphic
1126 information. Nonetheless, the following references offer reasonable to good
1127 stratigraphic control: Brito (1967, 1971, 1976; Lower–Upper Devonian, northern
1128 Brazil), Pöthe de Baldis (1974; Eifelian–Givetian, northwestern Paraguay), Barreda
1129 (1986; Givetian–Frasnian, Argentina), Quadros, (1988; Lower–Upper Devonian,
1130 northern Brazil), Wood (1995; Givetian–Frasnian, Bolivia), Ottone (1996; Eifelian–

1131 Frasnian, northwestern Argentina), Vavrdová *et al.* (1996; Lochkovian–Famennian,
1132 Bolivia) and Rubinstein (1999, 2000; Eifelian–Givetian, western Argentina).

1133 The same can be said for Africa, where some of the described acritarch assemblages
1134 have good stratigraphic control, and others not as good but still contain diverse
1135 acritarch assemblages that are very much characteristic of the Middle Devonian.
1136 These include: Jardiné & Yapaudjian (1968; Emsian–Givetian, Algeria), Jardiné
1137 (1972; Lochkovian–Famennian, Algeria), Jardiné *et al.* (1972, 1974; Lochkovian–
1138 Famennian, Algeria), Anan-Yorke (1974; Middle Devonian, Ghana), Moreau-Benoit
1139 (1984; Givetian–Famennian, Libya) and Streel *et al.* (1988; Eifelian–Famennian,
1140 northeast Libya).

1141 Several acritarch assemblages have been described from Armorica by Deunff (1954,
1142 1968, 1981; Middle Devonian), Rauscher (1969; Devonian), Moreau-Benoit (1972,
1143 1974; Silurian–Devonian) and Le Hérissé & Deunff (1988; Givetian–Frasnian), but
1144 will not be discussed below because of their paucity of species or poor preservation.
1145 In a preliminary study, Riegel (1974) described an upper Emsian and Eifelian
1146 acritarch assemblage from the Rhineland, Germany, which contained mostly long-
1147 ranging taxa.

1148 Colbath (1990*b*) described and illustrated a beautifully preserved Givetian–Frasnian
1149 acritarch assemblage from the Canning Basin of Western Australia. More recently,
1150 Zhu *et al.* (2008) described and discussed an Eifelian acritarch assemblage from the
1151 Junggar Basin, China, at the time part of the Kazakhstan Plate and situated in mid
1152 northern palaeolatitudes between Laurussia to the west, North China and South China
1153 to the east, and Gondwana to the south (**Fig. 10**).

1154 Selected taxa that occur in at least three of the previously reported Middle Devonian
1155 diverse acritarch assemblages from North America listed above (excluding Turner,
1156 1991), and are thus geographically widespread and abundant in North America,
1157 include: *Arkonites bilixus*, *Baltisphaeridium distentum*, *Cymatiosphaera winderi*,
1158 *Dictyotidium variatum*, *Diexallophasis simplex*, *Duvernaysphaera angelae*, *D.*
1159 *tenuicingulata*, *Estiastra rhytidoa*, *Exochoderma arca*, *Hapsidopalla chela*, *H.*
1160 *exornata*, *Lophosphaeridium ochthos*, *Muraticavea munificus*, *Navifusa bacilla*,
1161 *Oppilatala sparsa*, *Ozotobrachion furcillatus*, *Palacanthus ledanoisii*, *Polyedryxium*
1162 *decorum*, *P. fragosulum*, *P. pharaonis*, *Pterospermella reticulata*, *Stellinium*

1163 *comptum*, *S. micropolygonale*, *Triangulina alargadum* and *Veryhachium polyaster*.
1164 Other species are abundant in the same Middle Devonian North American
1165 assemblages, but these are cosmopolitan taxa with long stratigraphic ranges such as
1166 *Diexallophasis remota*, *Multiplicisphaeridium ramispinosum*, *Tunisphaeridium*
1167 *tentaculaferum*, *Veryhachium europaeum*, *V. lairdi*, *V. trispinosum* complex and
1168 numerous species of *Micrhystridium*.

1169 The most diverse Middle Devonian acritarch assemblage from South America was
1170 described by Ottone (1996) from the Los Monos Formation of the Tarija Basin,
1171 Argentina. Based on the published record of Middle Devonian South American
1172 acritarch assemblages (see above), there are many similarities to those from North
1173 America. Comparing the Los Monos Formation acritarch assemblage, consisting of
1174 51 species (Ottone (1996), to the seven Middle Devonian North American acritarch
1175 assemblages reported above (excluding Turner, 1991), shows a total of 21 species in
1176 common between the two regions. Such a high degree of similarity suggests that a
1177 somewhat narrow and temperate oceanic link developed between Laurussia and
1178 Gondwana (South America) during the late Mid (Givetian) and early Late Devonian
1179 (Frasnian).

1180 In addition to the similarities, a number of species seem to have been restricted to the
1181 higher southern Gondwana palaeolatitudes (but see below). These include *Bimerga*
1182 *bensoii*, *Duvernaysphaera radiata*, *Maranhites brasiliensis*, *M. mosesii* and
1183 *Pterospermella pernambucensis*, among others that have been reported but are not
1184 particularly abundant. Furthermore, Ottone (1996) reported *Umbellasphaeridium*
1185 *deflandrei* from the Los Monos Formation, and Wood (1984, p. 199) stated that the
1186 distribution of the *Umbellasphaeridium* recurrent species association indicated a
1187 closeness of Africa and South America and that “*Umbellasphaeridium* displays a
1188 ‘southern hemisphere endemism’ in the Middle and Upper Devonian.”

1189 Elsewhere in Gondwanan successions, Anan-Yorke (1974) described an acritarch
1190 assemblage consisting of 37 species from three exploratory oil wells on the shelf and
1191 coastal region of Ghana. Taking into account synonymies, there are at least 11
1192 species in common with published North American and South American acritarch
1193 assemblages. The common, characteristic Middle Devonian species found in all three
1194 regions include *Polyedryxium pharaonis*, *Stellinium micropolygonale* and *Triangulina*
1195 *alargada*, as well as the cosmopolitan species *Diexallophasis remota*,

1196 *Multiplicisphaeridium ramispinosum*, *Tunisphaeridium tentaculaferum*, *Veryhachium*
1197 *europaeum*, *V. lairdi* and *V. trispinosum* complex. *Bimerga bensonii*, *Maranhites*
1198 *brasiliensis*, *Navifusa brasiliensis* and *Umbellasphaeridium saharicum* are also
1199 present in the Ghanaian assemblage, reinforcing the view based on their South
1200 American records that at least some, notably *Bimerga*, are restricted to higher
1201 Southern Hemisphere palaeolatitudes (**Fig. 10**). As noted by Rubinstein (2000), the
1202 presence of *Bimerga bensonii* in Bolivia, Argentina and Ghana confirms the presence
1203 of an oceanic connection between the Gondwanan regions of South America and
1204 Africa during the Mid Devonian.

1205 Middle Devonian acritarch assemblages from western Libya were reported by
1206 Moreau-Benoit (1984). Species that have also been reported from North America,
1207 South America, and, in several cases, Ghana include *Cymatiosphaera winderi*,
1208 *Diexallophasis remota*, *Multiplicisphaeridium ramispinosum*, *Navifusa bacilla*,
1209 *Polyedryxium fragosolum*, *P. pharaonis*, *Tunisphaeridium tentaculaferum*,
1210 *Tyligmasoma alargadum*, *Veryhachium europaeum*, *V. lairdi*, *V. polyaster* and *V.*
1211 *trispinosum* complex. *Maranhites brasiliensis* and *Umbellasphaeridium deflandrei*
1212 are also present, but their occurrence at mid southern palaeolatitudes (c. 30°S, **Fig.**
1213 **10**) suggests that they might have been endemic to Gondwana in the Mid Devonian
1214 rather than just high southern Gondwanan palaeolatitudes. Jardiné & Yapaudjian
1215 (1968), Jardiné (1972) and Jardiné *et al.* (1972, 1974) also recorded some of the same
1216 taxa from Algeria as those mentioned by Moreau-Benoit (1984) from Libya.

1217 Among the Givetian taxa recorded by Colbath (1990*b*) from the Canning Basin of
1218 Western Australia are *Daillydium pentaster*, which first appears in the upper Givetian
1219 in North America, France and North Africa, and *Lophosphaeridium ochthos*, which is
1220 present in the Givetian of North America. *Multiplicisphaeridium ramispinosum*,
1221 *Navifusa bacilla*, *Stellinium micropolygonale* and *Unellium winslowiae*, variously
1222 known from the upper Givetian of North America and North Africa, and the
1223 widespread *Veryhachium trispinosum* complex are also present.

1224 From the Junggar Basin of Xinjiang, northwest China, Zhu *et al.* (2008) reported on a
1225 poorly preserved Middle Devonian (Eifelian) miospore and acritarch assemblage from
1226 the Ulusbasite Formation. The acritarch assemblage consisted of 19 species, most of
1227 which are cosmopolitan. Comparing the Ulusbasite Formation acritarch assemblage
1228 to the seven reported North American acritarch assemblages (excluding Turner,

1229 1991), there are 13 species in common. For South America, there are eight co-
1230 occurring species with the assemblage described by Ottone (1996), and five common
1231 species between China and western Libya (Moreau-Benoit 1984) and the Algerian
1232 Sahara (Jardiné *et al.* 1974) respectively. Although the degree of similarity between
1233 the Ulusubasite Formation and those of comparable age is not high, perhaps due in
1234 part to preservation, there are nonetheless many species in common such as
1235 *Diexallophasis remota*, *Exochoderma arca*, *Hapsidopalla exornata*,
1236 *Multiplicisphaeridium ramispinosum*, *Navifusa bacilla*, *Oppilatala sparsa*, *Stellinium*
1237 *micropolygonale*, *Tyligmasoma alargada* and *Veryhachium trispinosum* complex.
1238 Based on the palaeogeographical distribution of acritarch species recorded from the
1239 Ulusubasite Formation, Zhu *et al.* (2008) confirmed the previously reported marine
1240 link between Laurussia and Gondwana, as well as including the Junggar Basin in that
1241 warm, lower palaeolatitude, temperate marine connection.

1242 In summary, it appears there was a reasonably high degree of cosmopolitanism within
1243 the acritarch assemblages of mid to high palaeolatitudes during the Mid Devonian, as
1244 evidenced by the numerous acritarch species in common between Laurussia (North
1245 America, Avalonia, Baltica), Gondwana (primarily Argentina, Ghana, Libya, Algeria,
1246 western Australia) and western China (Junggar Basin) (**Fig. 10**). In addition to the
1247 similarities between assemblages, however, a number of endemic species seem to be
1248 restricted to the higher southern Gondwana palaeolatitudes or at least to high to mid
1249 palaeolatitudes on the margin of Gondwana. These include *Bimerga bensonii*,
1250 *Duvernaysphaera radiata*, *Maranhites brasiliensis*, *M. mosesii*, *Pterospermella*
1251 *pernambucensis* and *Umbellasphaeridium deflandrei*.

1252

1253 **Late Devonian**

1254 By the Late Devonian, the Rheic Ocean had narrowed significantly such that
1255 Laurussia and Gondwana were in very close proximity (**Fig. 11**). Mountain building,
1256 which began in the late Silurian (the Acadian orogeny), continued along the eastern
1257 margin of Laurussia, and also in the northern portion of Laurussia as a result of the
1258 Ellesmere orogeny (**Fig. 11**). Sedimentological and palaeontological evidence
1259 indicates a rather uniform global climate during this time interval.

1260 Upper Devonian acritarch assemblages have received greater attention than those of
1261 the Lower Devonian or Middle Devonian, although preservation and stratigraphical
1262 control vary. Many of the earliest acritarch studies were from Upper Devonian
1263 sections, but preservation, processing techniques and brief descriptions, as well as
1264 poor illustrations in many cases, render many of the early, pioneering studies difficult
1265 to use. For comprehensiveness, all of those publications that describe and illustrate
1266 Upper Devonian acritarch assemblages are listed, even if many of the taxa erected are
1267 of dubious quality. In discussing the palaeobiogeography of Upper Devonian
1268 acritarch assemblages, discussion, as for the Lower and Middle Devonian acritarch
1269 assemblages, is restricted to those taxa that can be used in a regional or global setting.

1270 In North America, studies of well-dated acritarch occurrences and assemblages
1271 include Staplin (1961; Frasnian, Alberta, Canada), Winslow (1962; Famennian, Ohio,
1272 U.S.A.), Bharadwaj *et al.* (1970; Famennian, Kentucky, U.S.A.), Wicander (1974,
1273 1975; Famennian, Ohio, U.S.A.), Wicander & Loeblich (1977; Frasnian–Famennian,
1274 Indiana, U.S.A.), Reaugh (1978; Famennian, Tennessee, U.S.A.), Molyneux *et al.*
1275 (1984; Famennian, Ohio, U.S.A.), Wicander & Playford (1985; Frasnian, Iowa,
1276 U.S.A.), Turner (1986, 1991; Givetian–Frasnian, Alberta, Canada), Huysken *et al.*
1277 (1992; Givetian–Famennian, Kentucky, U.S.A.) and Playford & McGregor (1993;
1278 Famennian, southern Saskatchewan, Canada).

1279 Publications dealing with Upper Devonian acritarch assemblages from South America
1280 include Brito (1971, 1976, 1978; Middle–Upper Devonian, northern Brazil), Daemon
1281 (1974; Upper Devonian, Brazil), Pöthe de Baldis (1979; Upper Devonian, Paraguay),
1282 Vavrdová *et al.* (1996; Lochkovian–Famennian, Bolivia), Quadros (1999; Frasnian–
1283 Famennian, northern Brazil), Oliveira & Burjack (1997; Frasnian, Brazil), Le Hérissé
1284 (2001; Frasnian–Famennian, northern Brazil) and Wicander *et al.* (2011; Famennian,
1285 Bolivia).

1286 Many of the earliest acritarch studies focused on Europe, and particularly on Upper
1287 Devonian assemblages. Those, and more recent publications, include Stockmans &
1288 Willièvre (1960, 1962*a, b*, 1966, 1967, 1969, 1974; Frasnian–Famennian, Belgium),
1289 Bain & Doubinger (1965; Famennian, France), Deunff (1965, 1981; Upper Devonian,
1290 France), Górka (1974*a, b*; Famennian, Poland), Vanguetaine (1978*b*; Famennian,
1291 Belgium), Deunff (1981; Givetian–Frasnian, France), Martin (1981, 1982*b*, 1985;
1292 Frasnian–Famennian, Belgium), Loboziak *et al.* (1983; Frasnian–Famennian, France),

1293 Vanguetaine *et al.* (1983; Frasnian–Famennian, Belgium), Amirie (1984; Frasnian,
1294 Germany); Le Hérissé & Deunff (1988; Givetian–Frasnian, France), González *et al.*
1295 (2005; Famennian, Spain) and Pereira *et al.* (2008; Famennian, Portugal).

1296 Upper Devonian acritarch assemblages from Africa and the Middle East have been
1297 described by Jardiné (1972; Lochkovian–Famennian, Algeria), Jardiné *et al.* (1972,
1298 1974; Lochkovian–Famennian, Algeria), Moreau-Benoit (1984, Givetian–Famennian,
1299 Libya), Paris *et al.* (1985, Emsian–Famennian, Libya), Streel *et al.* (1988, Eifelian–
1300 Famennian, northeast Libya), Ghavidel-syooki (1994; Frasnian–Famennian, northern
1301 Iran), Hashemi & Playford (1998; Upper Devonian, Iran), Ghavidel-syooki (2001;
1302 Frasnian–Famennian, central Iran), Ghavidel-syooki (2003; Lochkovian–Frasnian,
1303 southern Iran) and Ghavidel-syooki & Owens (2007; Frasnian–Famennian, northern
1304 Iran).

1305 In Australia, Colbath (1990*b*) described a Givetian–Frasnian acritarch assemblage
1306 from the Canning Basin of Western Australia, and Playford (1981) and Playford &
1307 Dring (1981) described a Frasnian acritarch assemblage from the Carnarvon Basin,
1308 also in Western Australia. Li *et al.* (2002*a*) reviewed research on Devonian acritarchs
1309 in China, and details on Upper Devonian acritarchs were published by Gao (1986) and
1310 Lu & Wicander (1988).

1311 Several general papers deal with the palaeobiogeographical distribution of acritarchs
1312 during the Late Devonian. Colbath (1990*a*) examined the biogeographical
1313 distribution of Frasnian assemblages based on 10 well-documented microfloras, all
1314 from open-shelf, cratonic deposits. Similarity in composition between the
1315 assemblages was computed using the Simpson Index, and then clustered using
1316 weighted average linkage pair-group analysis. Based on this analysis, Colbath
1317 concluded that the clustering reflected biogeographical, rather than local ecological
1318 differences between the assemblages. Earlier, Wood (1984) had discussed the
1319 stratigraphical, palaeoecological and palaeobiogeographical distribution of
1320 *Umbellasphaeridium deflandrei* and *Umbellasphaeridium saharicum* from North
1321 America and South America, as well as from Africa. Vanguetaine (1986*b*)
1322 synthesized 80 publications relating to Upper Devonian and Carboniferous acritarchs
1323 and their stratigraphical and palaeogeographical distribution. Vavrdová & Isaacson
1324 (1997, 1999, 2000) considered the previously established *Umbellasphaeridium*
1325 *saharicum* Bioprovince (Wood 1984) as a possible indicator of a close connection

1326 between the eastern North American region and South America's Central Andes,
1327 based on high palaeolatitude-generated cold-water currents. Finally, Clayton *et al.*
1328 (2002) discussed regional differences in Upper Devonian palynomorph assemblages
1329 from southwest Portugal, Algeria, Libya and North America.

1330 The references listed above show that the majority of acritarchs had a global
1331 distribution during the Late Devonian, but with some evidence for an endemic
1332 province at high southern palaeolatitudes, and with periodic incursions of the high
1333 palaeolatitude assemblage into the low palaeolatitude regions of Laurussia and
1334 northern Perigondwanan areas (Vavrdová & Isaacson, 1999).

1335 Based on analysis of data contained in the numerous publications listed above, plus
1336 the syntheses by Wood (1984), Vanguetaine (1986b), Streele *et al.* (1988) and
1337 Vavrdová & Isaacson (1997, 1999, 2000), Upper Devonian acritarchs can be
1338 categorized as cosmopolitan, those that occurred primarily in the low palaeolatitude
1339 region of Euramerica (Laurentia, Baltica, Avalonia), Australia and Iran, and those that
1340 were typically confined to the higher palaeolatitude Perigondwana region.

1341 The majority of reported Frasnian and Famennian acritarchs can be considered
1342 cosmopolitan, ranging from the low to mid palaeolatitudes and into higher
1343 palaeolatitudes (60°S or higher). Furthermore, many of these species were restricted
1344 to the Late Devonian, or first appeared in the Mid Devonian in one region and
1345 extended their latitudinal and palaeogeographical range during the Late Devonian. Le
1346 Hérissé *et al.* (2000) list 60 acritarch species that are restricted to the Upper Devonian
1347 or extend slightly into the lowermost Carboniferous.

1348 Cosmopolitan acritarchs are found at a number of localities in both the broadly
1349 defined Euramerican and Gondwanan regions, including Australia and China, and
1350 thus cover a wide range of palaeolatitudes. They include *Chomotriletes vedugensis*,
1351 *Cymatiosphaera perimembrana*, *Daillydium pentaster*, *Dictyotidium litum*,
1352 *Diexallophasis remota*, *Gorgonisphaeridium ohioense*, *G. plerispinosum*,
1353 *Multiplicisphaeridium ramispinosum*, *Palacanthus ledanoisii*, *Polyedryxium*
1354 *pharaonis*, *Solisphaeridium spinoglobosum*, *Stellinium comptum*, *S. micropolygonale*,
1355 *Tornacia sarjeantii*, *Unellium lunatum*, *U. piriforme*, *U. winslowiae*, *Veryhachium*
1356 *lairdii*, *V. pannuceum*, *V. polyaster* and *V. trispinosum* complex. Other species
1357 reported from these areas are possibly endemic, but they may occur only in one or a

1358 small number of localities and are not particularly common and so are not included
1359 here.

1360 Some acritarch species, however, are abundant and seem to be limited to the low
1361 palaeolatitudes of the Euramerican region, Australia, Iran and China. These include,
1362 among others, *Craterisphaeridium sprucegrovense*, *Deltotosoma intonsum*,
1363 *Gorgonisphaeridium condensum*, *G. discissum*, *G. winslowiae*, *Lophosphaeridium*
1364 *deminutum* and *Papulogabata annulata*. There is a high degree of similarity between
1365 the Euramerican region and Australia and China, with 17 out of 48 species from the
1366 Frasnian of Western Australia (Playford 1981; Playford & Dring 1981) and 27 out of
1367 29 species from China (Lu & Wicander 1988) also reported from Upper Devonian
1368 Euramerican acritarch assemblages.

1369 Taxa recorded from Perigondwanan localities include *Crassiangulina tesselita*,
1370 *Horologinella horologia*, *H. quadrispina*, *Maranhites brasiliensis*, *M. mosesii*,
1371 *Pyloferites pentagonalis*, *Umbellasphaeridium deflandrei* and *U. saharicum*. Of
1372 these, *Crassiangulina tesselita*, *Horologinella horologia*, *H. quadrispina* and
1373 *Pyloferites pentagonalis* were apparently restricted to high palaeolatitude
1374 Perigondwana regions and were not dispersed into lower palaeolatitudes during the
1375 Late Devonian. *Maranhites brasiliensis*, *M. mosesii*, *Umbellasphaeridium deflandrei*
1376 and *U. saharicum*, however, appear to have been characteristic of, but not limited to
1377 high palaeolatitude Perigondwana regions during the Mid Devonian, but migrated into
1378 lower palaeolatitudes during the Late Devonian as shown by their occurrences in
1379 North America, Portugal and Spain (Wood 1984; González *et al.* 2005; Pereira *et al.*
1380 2008.). Other species of *Maranhites* and *Umbellasphaeridium* have been reported
1381 from these regions, but we only list the two common species of each genus.

1382 It should be noted that González (2009) proposed a reassessment of *Maranhites*,
1383 suggesting that many of the previously named species were not distinct taxa, but
1384 represented different ontogenetic stages of *Maranhites mosesii*. To address the
1385 implications of this reassessment is beyond the scope of this paper, and we are
1386 following past convention by listing previously named species of this genus.

1387 In summary, the acritarch flora during the Late Devonian can be characterized as
1388 having had a large cosmopolitan element, as indicated by the wide palaeogeographical
1389 distribution of numerous species that are either stratigraphically long-ranging or

1390 restricted to the Late Devonian. In addition, there is strong evidence for warm-water,
1391 low to mid palaeolatitude oceanic interchange between the Euramerican region,
1392 Australia, Iran and China. Endemic acritarch assemblages also existed during the
1393 Late Devonian as seen by the high palaeolatitude occurrences of several genera within
1394 the Perigondwana region. However, some characteristic high palaeolatitude
1395 Perigondwana species were dispersed into mid to low palaeolatitude Euramerican
1396 areas, possibly by cold-water gyres.

1397

1398 *Synopsis of Devonian phytoplankton biogeography*

1399 Much has changed since the early attempts at reconstructing Devonian acritarch
1400 palaeobiogeographical distributions. Palaeogeographical maps for the Early, Mid and
1401 Late Devonian (**Figs 9–11**) show a Gondwana continent and associated seas located
1402 predominately at mid to high southern palaeolatitudes, a continued closing of the
1403 Rheic Ocean between Gondwana and Laurussia with Gondwana continuing to move
1404 northward and resulting in a very narrow seaway by the end of the Devonian, and the
1405 movement and collision of several microcontinents and blocks. We can therefore
1406 discuss the distribution of acritarchs during the Devonian in terms of those that are
1407 cosmopolitan, those from generally low to mid palaeolatitudes, and those from a high
1408 palaeolatitude province. The apparent provincialism, however, might reflect local
1409 conditions or lack of geographic coverage and adequately described palynofloras.

1410 During the Early Devonian, a mid palaeolatitude province was present in Laurentia
1411 and Armorica and extended across North Africa. Although each region appears to
1412 have had some endemic species, a number of other species are found throughout this
1413 latitudinal belt, and as more localities are studied, the apparent provincialism
1414 diminishes. The seemingly endemic nature of some assemblages is probably due, in
1415 part, to lack of described material from well-dated sections. Among taxa that were
1416 seemingly restricted to particular regions during the Early Devonian, *Schizocystia* spp.
1417 have only been reported from north and west Gondwana. Other species that have a
1418 stratigraphical range restricted to the Lower Devonian and a cosmopolitan distribution
1419 include *Demorhethium lappaceum*, *Riculusphaera fissa* and *Thysanoprobolus*
1420 *polykion*.

1421 As the Rheic Ocean continued to close, bringing Gondwana and Laurussia closer
1422 together during the Mid Devonian, a reasonably high degree of cosmopolitanism
1423 developed among acritarch assemblages, as shown by the numerous acritarch species
1424 in common between Laurussia (North America), Gondwana (primarily Argentina,
1425 Ghana, Libya, Algeria, Western Australia) and western China (Junggar Basin). A
1426 number of species, however, seem to have been endemic to the higher southern
1427 Gondwana palaeolatitudes.

1428 During the Late Devonian, a large number of both stratigraphically long ranging
1429 species and many species that were restricted to the Late Devonian can be
1430 characterized as cosmopolitan. There is strong evidence for oceanic connections
1431 within the low palaeolatitude areas of the Euramerican region, Australia, Iran and
1432 China. There are also a number of endemic acritarchs that occur within the high
1433 palaeolatitude Perigondwana region. In addition, it appears that oceanic circulation
1434 patterns provided the means for dispersal of some characteristic high palaeolatitude
1435 Perigondwana species into low paleolatitude Euramerican areas.

1436

1437 **Discussion**

1438 The review of phytoplankton biogeography presented above shows that a lot of
1439 relevant data from the Cambrian to the Devonian has been published since Colbath's
1440 (1990*a*) assessment, some of it in passing in publications dealing with other aspects of
1441 Palaeozoic palynology, and some in papers with a biogeographical focus. Yet, we
1442 still do not fully understand the pattern of Palaeozoic phytoplankton biogeography or
1443 many of the controls influencing its distribution. In part, this is due to incomplete
1444 spatial datasets for many time periods. Almost nothing is known of Early–Mid
1445 Ordovician phytoplankton from the Appalachian margin of Laurentia, for example, at
1446 a time when the Perigondwana Province was present along the margin of Gondwana
1447 and adjacent Perigondwanan terranes. Similarly, very little has been published on late
1448 Cambrian marine phytoplankton from Laurentia and other areas, such as Australia. In
1449 part, our understanding of the patterns and factors influencing them is also hindered
1450 by biases introduced by sampling (e.g. of different facies) or by different taxonomic
1451 treatment of material, and by the difficulties of unravelling the complex interactions

1452 of various controls on phytoplankton distribution. Nevertheless, some common
1453 themes have begun to emerge.

1454

1455 ***Latitude versus other controls***

1456 Latitude is no longer seen as the primary factor influencing phytoplankton as it was,
1457 for example, in Cramer's model (1971; Cramer & Díez 1972, 1974a, b) of Silurian
1458 phytoplankton distributions. Assemblages once regarded as being restricted to
1459 latitude-parallel climatic belts, such as Cramer's *Deunffia*, *Domasia* and
1460 *Neoveryhachium carminae* biofacies, can now be shown, using more up-to-date
1461 palaeogeographical reconstructions, to occur along continental margins at both low
1462 and high palaeolatitudes, where their distribution is controlled by other factors.
1463 Besides latitude, factors that are now thought to have influenced the spatial
1464 distribution of Palaeozoic phytoplankton include depositional environments,
1465 differences between water masses of oceanic and cratonic settings, and oceanic
1466 circulation patterns. Oceanic circulation, for example, has been invoked by a number
1467 of authors to explain, at least in part, the distribution patterns that they discerned.
1468 Hence, Playford *et al.* (1995) and Tongiorgi *et al.* (1995, 1998) proposed that oceanic
1469 circulation was at least a partial control on spatial distribution patterns of genera and
1470 species in the Early–Mid Ordovician, and Le Hérissé & Gourvennec (1995) suggested
1471 the same to explain patterns in the mid Silurian (late Llandovery–Wenlock).

1472 Nevertheless, the idea that phytoplankton distribution might, at least in part, reflect
1473 latitude has persisted, and Li & Servais (2002), for example, considered that some
1474 acritarch taxa might be restricted to certain palaeolatitudinal belts. They suggested that
1475 *Arbusculidium filamentosum* and the *Coryphidium-Vavrdovella* and *Arkonias-*
1476 *Striatotheca* generic complexes were most common at high southern palaeolatitudes
1477 during the Early to Mid Ordovician (essentially Arenig), from polar regions up to
1478 60°S and more rarely up to 30°S. They also argued that although galeate and
1479 diacromorph acritarchs were to be found at high southern palaeolatitudes, they were
1480 more likely to be recorded from mid to low palaeolatitudes around 45–20°S.

1481 Furthermore, they noted that the acritarch genera *Aryballomorpha*, *Athabascaella* and
1482 *Lua*, which characterized Volkova's (1997) warm-water assemblage, also occurred at
1483 low to mid palaeolatitudes.

1484 Li & Servais (2002) were clear that their model was a first tentative attempt to
1485 identify climate-related latitudinal distributions among phytoplankton for the Early–
1486 Mid Ordovician and was subject to modification by subsequent reinterpretations of
1487 palaeogeography or further data on distributions. This has proved to be the case.
1488 *Arbusculidium filamentosum* and species of the *Coryphidium-Vavrdovella* and
1489 *Striatotheca-Arkonion* complexes are significant, if not always numerous constituents
1490 of Arenig assemblages from the Yangtze Platform (Li 1987, 1990; Brocke *et al.* 1999,
1491 2000; Tongiorgi *et al.* 1995, 1998, 2003a; Li *et al.* 2002b; Yan *et al.* 2011), located at
1492 low palaeolatitudes in the reconstructions of Torsvik & Cocks (2013). On the other
1493 hand, *Athabascaella* has been recorded from lowest Ordovician (Tremadocian)
1494 successions deposited at high southern palaeolatitudes, from Belgium (uppermost
1495 Tremadocian, Avalonia, Breuer & Vanguetaine 2004) and Tunisia (lower
1496 Tremadocian, Gondwana, Vecoli 2004).

1497 One genus not included in Li & Servais' (2002) analysis is *Frankea*, which Colbath
1498 (1990a) showed as being restricted to palaeolatitudes of about 60°S or higher.
1499 *Frankea* still appears to have had a spatial distribution that was restricted to relatively
1500 high palaeolatitudes during the Early–Mid Ordovician (**Fig. 5**). It is unreported from
1501 Baltica or low palaeolatitude Perigondwanan assemblages such as those from South
1502 China. The lowest palaeolatitude at which the genus occurred during the Arenig
1503 (Floian–early Darriwilian) was between about 45°S and 60°S in Avalonia (eastern
1504 Newfoundland: Dean & Martin 1978; the Isle of Man: Molyneux 1999; Chadwick *et al.*
1505 2001; the English Lake District: Cooper *et al.* 1995, 2004; Molyneux 2009;
1506 Belgium: Martin 1977; Martin & Rickards 1979; Vanguetaine 1986a) and on the
1507 western margin of Gondwana (Saudi Arabia: Le Hérisse *et al.* 2007).

1508

1509 ***Distal versus proximal (oceanic versus cratonic) distribution patterns***

1510 One of the themes to have emerged from recent assessments of Palaeozoic
1511 phytoplankton biogeography is the spatial differentiation between assemblages from
1512 distal, oceanic settings and those from more proximal cratonic settings. Changes in
1513 the diversity of phytoplankton assemblages along onshore–offshore gradients are well
1514 documented. Assemblages from proximal and deep basinal settings are generally
1515 characterized by low diversity and the predominance of relatively simple forms such

1516 as leiospheres (sphaeromorph acritarchs). In contrast, the most diverse assemblages
1517 with a range of often complex morphospecies are generally associated with fully
1518 marine, shelf successions. The evidence to emerge from analysis of Palaeozoic
1519 phytoplankton biogeography is that the taxonomic character of assemblages changes
1520 along with diversity. Examples include the spatial differentiation of the
1521 *Neoveryhachium carminae* and *Deunffia-Domasia* biofacies along the eastern margin
1522 of Laurentia (Le Hérissé & Gourvenec 1995), and distinction between ocean-facing
1523 assemblages with Perigondwanan characteristics and more proximal assemblages with
1524 Baltic characteristics in the Lower–Middle Ordovician of South China (Playford *et al.*
1525 1995; Tongiorgi *et al.* 1998, 2003a).

1526 A further example is provided by the distinction between Lower–Middle Ordovician
1527 phytoplankton assemblages from the intracratonic Canning and Georgina basins of
1528 north-western and central Australia (Playford & Martin 1984; Playford & Wicander
1529 1988; Quintavalle & Playford 2006a, b) and those from the low palaeolatitude
1530 Perigondwanan region of South China (**Fig. 5**). For the most part, assemblages from
1531 the Canning and Georgina basins lack the key Perigondwanan Lower–Middle
1532 Ordovician marker genera. The exception is *Striatotheca*, but even this genus is only
1533 present in the middle to upper Darriwilian *Aremoricanium solaris* and *Dactylofusa*
1534 *striatogranulata* biozones of the Canning Basin (Quintavalle & Playford 2006b, text-
1535 figs 1, 6). In contrast, *Striatotheca* is present from the lower Floian upwards in South
1536 China (Yan *et al.* 2011).

1537 As well as the key Perigondwanan markers, *Arbusculidium*, *Coryphidium* and
1538 *Striatotheca*, assemblages from South China include species of other genera that have
1539 well-documented Perigondwanan and/or Baltic distributions. Among them are
1540 species of diacromorph acritarch genera (*Acanthodiacrodium*, *Actinotodissus*,
1541 *Dicrodiacrodium*), galeate acritarchs (*Caldariola*, *Cymatiogalea*, *Stelliferidium*), and
1542 species of *Adorfia*, *Arkonina*, *Aureotesta*, *Barakella*, *Cycloposphaeridium*, *Ferromia*,
1543 *Liliosphaeridium*, *Picostella*, *Stellechinatum*, *Tongzia*, *Tranvikium*, *Vavrdovella* and
1544 *Vogtlandia*. Altogether, 35 genera present in South Chinese assemblages, including
1545 those listed above, have not been recorded from the Canning or Georgina basins
1546 (Table 2).

1547 In contrast, assemblages from the Coolibah Formation of the Georgina Basin, of Early
1548 Ordovician age (Zhen *et al.* 2003, fig. 6), contain *Dictyodiscus*, *Pytinomorpha*,

1549 *Tunisphaeridium* and *Uncinisphaera* (Playford & Wicander 1988). None of these
1550 genera have been recorded from South China (Table 2), although *Uncinisphaera* has
1551 been recorded from South Wales (Molyneux 1987) at about the same level and higher,
1552 and from late Floian to Darriwilian successions in Bohemia (Vavrdová 1990*a, b*),
1553 North Africa (Vecoli 1999), Saudi Arabia (Le Hérisse *et al.* 2007) and Oman
1554 (Molyneux *et al.* 2006; Rickards *et al.* 2010).

1555 The succession studied by Quintavalle & Playford (2006*a, b*) in the Canning Basin
1556 comprises the Willara, Goldwyer and basal Nita formations, and covers a longer
1557 stratigraphical interval than that investigated in the Georgina Basin, extending from
1558 the middle Floian to the upper Darriwilian. Genera recorded from the Canning Basin
1559 that have not been recorded from South China are *Dilatisphaera*, *Pylantios*,
1560 *Pytinomorpha*, *Sertulidium*, *Tribulidium*, *Tunisphaeridium* and *Uncinisphaera* (Table
1561 2). Of these, *Pylantios*, *Pytinomorpha*, *Sertulidium* and *Tribulidium* appear to have
1562 been endemic to the intracratonic Australian basins. Quintavalle & Playford (2006*b*)
1563 noted that assemblages from the Canning Basin differed from coeval suites of the
1564 Perigondwana Province in lacking diacromorph and trispinose veryhachid acritarchs,
1565 in having moderate to high frequencies of quadrate veryhachid and herkomorph
1566 acritarchs, and in yielding an abundance of forms with pylomes.

1567 Cluster analyses of genera and species in Dapingian–lower Darriwilian assemblages
1568 from the Canning Basin and adjacent regions of the western Perigondwanan margin
1569 highlight the distinctive nature of the Canning Basin microflora (**Fig. 12**). The
1570 composition of the acritarch assemblage from the *Comasphaeridium setaricum*
1571 Biozone of the Canning Basin, of late Dapingian–early Darriwilian age (Quintavalle
1572 & Playford 2006*b*), is compared with approximately coeval assemblages from the Saq
1573 Formation of Saudi Arabia (Le Hérisse *et al.* 2007), from the Taurus Range (Taurides
1574 Terrane) and Border Folds (Arabian Plate) of Turkey (Paris *et al.* 2007), from the
1575 Zard-Kuh Formation, Palynological Zones O3 and O4, of the Zagros Basin (Arabian
1576 Plate: Ghavidel-syooki 1997) and the Lashkarak Formation, zones III (upper) and IV,
1577 of the Central Alborz Range, Iran (Alborz Terrane: Ghavidel-syooki 2006), from
1578 Pakistan (Karakorum Terrane: Tongiorgi *et al.* 1994; Quintavalle *et al.* 2000) and
1579 from South China (Brocke *et al.* 1999, 2000; Tongiorgi *et al.* 2003*a*; Yan *et al.* 2011).
1580 In each case, the Canning Basin is clearly separated from and does not cluster with the
1581 Perigondwanan regions.

1582 A further point to note in connection with acritarch records from the Canning Basin is
1583 that, whereas species such as *Pirea ornata*, *Dasydorus cirritus* and *Striatotheca*
1584 *rarirrugulata* are present in South Chinese assemblages from the Floian or Dapingian
1585 onwards (Brocke *et al.* 2000; Tongiorgi *et al.* 1995, 2003a; Yan *et al.* 2011), the
1586 FADs of these or similar forms in the Canning Basin are in the Darriwilian. The FAD
1587 of *Pirea* cf. *P. ornata* is in the *Sacculidium aduncum* Biozone, which Quintavalle &
1588 Playford (2006b, text-fig. 6) correlate with the *Didymograptus artus* Graptolite
1589 Biozone of early Darriwilian (early Llanvirn) age, and the FADs of *Dasydorus*
1590 *cirritus* and *Striatotheca rarirrugulata* are in the *Aremoricanium solaris* Biozone, of
1591 mid Darriwilian (mid Llanvirn) age and correlated with the upper *D. artus* to lower
1592 *Didymograptus murchisoni* biozones.

1593 Although some biogeographical differentiation is apparent between South China and
1594 the intracratonic Australian basins, such differentiation between ocean margin and
1595 cratonic settings is not so evident elsewhere. The Silurian intracratonic basins of the
1596 South American part of Gondwana are a case in point. Assemblages from the
1597 Paranaíba and Paraná basins, for example, reviewed by Rubinstein (1997), comprise
1598 species that had widespread distributions during the late Llandovery–early Wenlock,
1599 including along the margins of Gondwana and in some cases in Laurentia. These
1600 basins might have had better connections to more oceanic settings than other
1601 intracratonic basins, and might have been connected directly to the basins of north and
1602 west Africa, as suggested by Rubinstein (1997), or to the ocean-facing Central
1603 Andean Basin (e.g. Díaz-Martínez *et al.* 2011, fig. 1).

1604

1605 ***Continental margin distributions***

1606 A further theme to emerge from recent work is that phytoplankton assemblages with
1607 particular characteristics can be traced along continental margins, often crossing
1608 palaeolatitudes. One of the best examples is the Early to Mid Ordovician
1609 Perigondwana Province (**Fig. 5**), but other examples include the *Neoveryhachium*
1610 *carminae* and *Deunffia-Domasia* biofacies (**Fig. 7**).

1611 As discussed above, taxa that are characteristic of the Perigondwana Province occur
1612 along the margin of Gondwana from high to low palaeolatitudes. Cramer & Díez
1613 (1974b) referred to this as the “*Coryphidium bohemicum* province”, but it is clear

1614 from their description of it as being Lower Ordovician and occurring in North Africa,
1615 Arabia, Bohemia and France, as well as the reference to Vavrdová's (1965, 1966,
1616 1972, 1974) papers and the inclusion of *C. bohemicum* in its name, that they were
1617 referring to the same biogeographical unit. Intriguingly, Cramer & Díez (1974b, p.
1618 142) also referred to the *C. bohemicum* province as apparently being present in
1619 Victoria, Australia, on the north-eastern margin of the Gondwanan craton, although
1620 they provided no further information and cited no references. If so, the province
1621 might be truly Perigondwanan, extending around the northern promontory of
1622 Gondwana from South China in the west to Argentina in the east (**Fig. 5**). Data from
1623 Lower–Middle Ordovician successions in south-west Australia, Tasmania and/or New
1624 Zealand ought to provide information to test this suggestion.

1625 The distribution of the Perigondwana Province, however, is not simply restricted to
1626 the continental margin. Key taxa used to define the province, namely species of
1627 *Arbusculidium*, *Coryphidium* and *Striatotheca*, also occur in terranes derived from
1628 Gondwana, notably Avalonia. This raises other questions. In the reconstructions by
1629 Torsvik & Cocks (2013, fig. 12), Avalonia had separated from Gondwana long before
1630 the late Dapingian (469 Ma) and had moved northwards so that by then it straddled
1631 the same mid southern palaeolatitudes as Baltica (**Fig. 5**). Yet none of the key
1632 Perigondwana Province markers are known from Baltica, not even from the pale grey
1633 and black silty shales of the Tøyen Formation, of latest Tremadoc–mid Arenig age,
1634 which were deposited on the continental slope that formed the western edge of the
1635 Baltic platform (Bruton *et al.* 2010). Tongiorgi *et al.* (2003b), for example, noted that
1636 acritarch assemblages from the Galgeberg Member, which comprises the upper part of
1637 the Tøyen Formation in the Oslo region and is of Billingen to early Volkhov age (late
1638 Floian to early Dapingian, or mid Arenig), lacked species of *Arbusculidium*,
1639 *Aureotesta*, *Coryphidium* and *Striatotheca*. On the other hand, all species identified in
1640 the Galgeberg Member were known from coeval levels on the Yangtze Platform of
1641 South China, where, of course, the key Perigondwanan markers are also present. If
1642 Tongiorgi *et al.*'s (2003a) interpretation of Perigondwana-type assemblages as distal
1643 oceanic assemblages applies, Perigondwana-type assemblages might be expected to
1644 occur in the deep-water successions of Baltica, but as yet there is no evidence that
1645 they do. So why are Perigondwanan assemblages characteristic of Early–Mid
1646 Ordovician Avalonia but not known from Baltica, although these palaeocontinents are

1647 interpreted as being at about the same palaeolatitude and deep-water facies have been
1648 sampled in Baltica? Did oceanic circulation mean that the distribution of
1649 Perigondwanan assemblages by-passed Baltica, or did other factors come into play?
1650 Did historical contingency and the original derivation of Avalonian assemblages from
1651 Gondwana have something to do with this, and if so what mechanisms maintained the
1652 Perigondwanan affinities of Avalonian microfloras?

1653

1654 ***Changes in biogeographical ranges through time***

1655 One thing that becomes apparent when Palaeozoic phytoplankton distributions are
1656 examined in detail is that biogeographical ranges change through time, or at least can
1657 appear to do so. The Ordovician acritarch *Loeblichia*, for example, has been recorded
1658 from Baltica in the lower–middle Floian (Raevskaya 1999), from Baltica, South China
1659 and Australia (Georgina Basin) in the upper Floian–lower Dapingian (Brocke *et al.*
1660 2000; Playford & Wicander 1988; Raevskaya *et al.* 2004; Tongiorgi *et al.* 1995,
1661 2003*a, b*; Yan *et al.* 2011), and from South China and Australia (Canning Basin) in
1662 the Dapingian–lower Darriwilian (Brocke *et al.* 2000; Quintavalle & Playford 2006*a,*
1663 *b*; Tongiorgi *et al.* 2003*a*; Yan *et al.* 2011). Hence, its biogeographical range seems
1664 to shift eastwards from the early Floian to the early Darriwilian, i.e. through the
1665 Arenig. A further example is provided by *Neoveryhachium carminae*, which was
1666 apparently endemic to Gondwana in the Late Ordovician (see ***Late Ordovician***
1667 above), but had a more widespread distribution in the mid Silurian (**Fig. 7**).

1668 These apparent shifts in biogeographical range might, of course, be artefacts,
1669 introduced, for example, by sample bias, but the possibility that ranges might expand
1670 and contract is not generally acknowledged in papers addressing Palaeozoic
1671 phytoplankton biogeography. From a practical standpoint, there are implications for
1672 defining provinces or other biogeographical units. If, for example, biogeographical
1673 units are based on time slices that are too broad, or even mixed as in the case of Li &
1674 Servais' (2002) study, where data from Volkova's (1997) late Tremadocian warm-
1675 water assemblage was combined with data from the Arenig Perigondwana Province to
1676 determine latitudinally restricted ranges, biogeographical signals might be lost.

1677

1678 ***Cosmopolitanism, endemism and community breakdown***

1679 Unsurprisingly perhaps, Palaeozoic phytoplankton assemblages usually exhibit a
1680 degree of both cosmopolitanism and endemism, with cosmopolitan species occurring
1681 alongside endemic forms, but the degree to which assemblages might be described as
1682 cosmopolitan or endemic varies. The review of Late Ordovician biogeography
1683 presented above suggests that assemblages with a high degree of cosmopolitanism in
1684 the Katian (late Caradoc to pre-Hirnantian Ashgill) were succeeded by assemblages
1685 showing a high degree of endemism in the Hirnantian (**Fig. 6**). However, very few
1686 attempts, if any, have been made to quantify the degree of endemism or to determine
1687 how it might change through time. Quantitative data on these aspects are vital for an
1688 understanding of how changes in Palaeozoic phytoplankton biogeography might
1689 respond to changes in environmental parameters.

1690 In a study of the response of marine diatom communities to climate change during the
1691 past 250 kyr, Cermeño *et al.* (2010, fig. 4) showed cycles in which community
1692 similarity, calculated using the Jaccard and Bray-Curtis indices, decreased and then
1693 recovered coincident with changes in atmospheric CO₂ concentration and
1694 atmosphere/ocean physical forcing. In two out of the three localities that they studied,
1695 community breakdown, indicated by a decrease in similarity indices, showed a clear
1696 coincidence with reductions in atmospheric CO₂ concentration, and community
1697 recovery with its increase. The questions this raises are whether other phytoplankton
1698 groups show similar community dynamics in response to climatic perturbations, and if
1699 so whether this also applies throughout geological time and at different timescales. Is
1700 the apparent increase in phytoplankton endemism in the Hirnantian part of a similar
1701 community response to the climatic perturbations of the time? Does community
1702 departure from similarity, i.e. increased biogeographical differentiation, correlate with
1703 other environmental perturbations such as changes in sea level, and if so is there a link
1704 between the magnitude of the disturbance and extinction, as opposed to increased
1705 endemism? Addressing these questions will require a more quantitative approach to
1706 Palaeozoic phytoplankton biogeography than has been the case up till now.

1707 One of the conclusions reached by Colbath (1990a) was that progress in the analysis
1708 of the Palaeozoic phytoplankton biogeography would require the application of
1709 numerical methods, but few studies have undertaken quantitative analysis of
1710 distribution patterns. The most notable exceptions are Colbath's (1990a) own
1711 analysis of Frasnian distributions, which used weighted average pair-group clustering

1712 based on the Simpson index of similarity, Le Hérissé & Gourvenec's (1995) analysis
1713 of late Llandovery–Wenlock distributions and Le Hérissé *et al.*'s (1997a) analysis of
1714 late Silurian and Devonian distributions, which both used cluster analysis based on the
1715 Jaccard index.

1716 In a paper dealing with the methods used to delineate present-day biogeographical
1717 regions, Kreft & Jetz (2010) noted that, historically, such regions had been based on
1718 qualitative assessments of criteria such as levels of endemism, but that this had set
1719 constraints on their utility and replicability and had introduced inconsistencies and
1720 confusion. They observed (p. 2031) that “...different schools and traditions in
1721 biogeography – as well as varying extent, grain and quality of data – have left the
1722 biogeographical regions of the world ambiguously defined...”. They also noted that
1723 multivariate methods overcame some of these difficulties, a particular strength being
1724 their ability to produce replicable results, and explored the relative usefulness of
1725 ordination and clustering methods, recommending the use of non-metric
1726 multidimensional scaling (NMDS) as an ordination method and UPGMA (unweighted
1727 pair-group method using arithmetic averages) clustering. Some of the criticisms
1728 levelled by Kreft & Jetz (2010) at traditional methods of delineating present-day
1729 biogeographical regions could also be levelled at approaches to Palaeozoic
1730 phytoplankton biogeography, with the inference that the routine application of
1731 numerical methods might at least provide a transparent, reproducible means of
1732 addressing biogeographical questions.

1733

1734 **Conclusions**

1735 Since Colbath's (1990a) assessment of Palaeozoic phytoplankton was published,
1736 more data have become available on spatial distributions and we have reached a better
1737 understanding of both phytoplankton distribution patterns and the factors that might
1738 influence them. We perhaps appreciate better the fact that distribution patterns are the
1739 result of many interacting factors, including palaeolatitude and therefore presumably
1740 palaeotemperature, oceanic circulation patterns, the disposition of continents,
1741 differentiation between oceanic and more cratonic (or distal and proximal)
1742 assemblages, and sedimentary environments and facies, the last, for example, in the
1743 case of the mid Silurian *Neoveryhachium carminae* and *Deunffia-Domasia* biofacies.

1744 There are also indications that biogeographical ranges of taxa might shift over time,
1745 so defining biogeographical units requires an appreciation of this. Even so, many
1746 uncertainties remain. Some of these factors, for example oceanic circulation, are
1747 themselves interpretations and introduce the danger of circularity into the argument if
1748 they cannot be tested independently. How, for example, do we explain the absence of
1749 key Perigondwanan taxa from Early–Mid Ordovician deep-water settings around
1750 Baltica, in contrast to their contemporaneous presence in Avalonia at similar
1751 palaeolatitudes and from lower palaeolatitudes around Gondwana? Do we invoke an
1752 oceanic circulation that somehow by-passed Baltica to explain this pattern, and if so is
1753 there independent evidence to substantiate this?

1754 Moving our understanding of Palaeozoic phytoplankton biogeography forward will
1755 require: (i) targeted investigation of regions and time periods for which no or little
1756 data exist, for example the Cambrian of Laurentia or Lower–Middle Ordovician deep-
1757 water successions in Australia; (ii) quantitative analysis of data to investigate, for
1758 example, how similarity varies through time and how this might correlate with other
1759 datasets such as carbon isotope stratigraphy or sea level; (iii) rigorous application of
1760 well-defined time slices to investigations so that we are comparing coeval
1761 assemblages, at least within the limits of resolution. Applying these principles might
1762 enable us to discern more biogeographical patterns, and perhaps more importantly,
1763 might also enable us to investigate linkages between environmental parameters and
1764 phytoplankton dynamics, including endemism and the development of provincialism,
1765 decreases in community similarity and its recovery, and the turnover, origination and
1766 extinction of genera and species.

1767 Finally, there is much current interest in the biogeography of extant microbial
1768 organisms, and, in particular, whether the processes that determine the
1769 biogeographical distributions of organisms with a body size of about 2 mm or less
1770 differ fundamentally from those that influence the biogeography of larger organisms
1771 (Fontaneto 2011). At the heart of this debate is the question of whether the
1772 biogeography of microorganisms conforms to the ubiquity hypothesis (also known as
1773 E_iE, from the paradigm that ‘everything is everywhere, but the environment selects’)
1774 or whether some other hypothesis such as the ‘moderate endemism model’ applies
1775 (Fontaneto & Brodie 2011). Such questions might well inform our approach towards
1776 phytoplankton biogeography in the Palaeozoic. At the same time, this raises a further

1777 question of whether we can use the fossil record of phytoplankton to investigate their
1778 biogeography under conditions that differ from those of the present day and at
1779 timescales beyond those of direct human observation, and thereby reach some
1780 understanding of fundamental biogeographical and macroecological processes and
1781 principles affecting these organisms.

1782

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- 2880

2881 **Figure and Table captions**

2882

2883 **Figure 1.** Distribution of *Skiagia*-bearing assemblages plotted on a
2884 palaeogeographical reconstruction at about the base of Stage 5 (510 Ma). Localities
2885 plotted from Moczyłowska & Zang (2006, figs 1, 2), with the addition of New
2886 Brunswick (Palacios *et al.* 2011) and the Amadeus Basin, central Australia (Zang &
2887 Walter 1992). Map from BUGPLATES, Galls Projection.

2888

2889 **Figure 2.** Seriation of acritarch genera from the Tempe Formation of the Amadeus
2890 Basin (**AB**), central Australia, dated as early mid Cambrian (Zang & Walter 1992),
2891 and from *Skiagia*-bearing assemblages of equivalent age from Baltica (**S**: Sweden,
2892 Eklund 1990, Assemblage D - top Lingulid Sandstone, Glauconite Sandstone,
2893 *oelandicus* Mudstone; **EEP**: East European Platform, Moczyłowska 1998,
2894 *oelandicus* Superzone, *insularis* and *praecurrens* zones).

2895

2896 **Figure 3.** Late Cambrian acritarch localities plotted on a palaeogeographical
2897 reconstruction for the mid Furongian (Stage 9, 495 Ma). **1.** Missouri, Arkansas
2898 (Wood & Stephenson 1989). **2.** Severnaya Zemlya (Raevskaya & Golubkova 2006).
2899 **3.** Northern Norway (Welsch 1986). **4.** Kolguev Island (Moczyłowska & Stockfors
2900 2004). **5.** East European Platform (Volkova 1990). **6.** Nova Scotia (Palacios *et al.*
2901 2009). **7.** Eastern Newfoundland (Martin & Dean 1981, 1988; Parsons & Anderson
2902 2000). **8.** England and Wales (Downie 1984; Young *et al.* 1994). **9.** Belgium
2903 (Ribecai & Vanguetaine 1993). **10.** Algeria (Vecoli 1996; Vecoli & Playford 1997).
2904 **11.** Spain (Albani *et al.* 2006). **12.** Tunisia (Albani *et al.* 1991). **13.** High Zagros
2905 Mountains, Iran (Ghavidel-syooki & Vecoli 2008). **14.** Eastern Cordillera, Northwest
2906 Argentina (Rubinstein *et al.* 2003). Map from BUGPLATES, Galls Projection.

2907

2908 **Figure 4.** Two-way Q- and R-mode cluster analysis (UPGMA algorithm, Jaccard
2909 Index) of Upper Cambrian (Furongian) acritarch genera. Localities and data sources
2910 as for Figure 4.

2911

2912 **Figure 5.** Early–Mid Ordovician acritarch localities and the distribution of the
 2913 Perigondwana and Baltic phytoplankton provinces plotted on a palaeogeographical
 2914 reconstruction for the late Dapingian (late Arenig, 469 Ma). Assemblages from South
 2915 China (22) and northwest Argentina (24) contain taxa with Perigondwanan affinities
 2916 as well as those with Baltic affinities. Coeval assemblages from the Canning Basin
 2917 (23) are distinct from the Perigondwanan and Baltic microfloras (see Discussion and
 2918 Fig. 12). **Avalonia.** **1.** Eastern Newfoundland (Dean & Martin 1978); **2.** Southern
 2919 Ireland (Maziane-Serraj *et al.* 1999, 2000); **3.** Isle of Man (Molyneux 1999; Chadwick
 2920 *et al.* 2001); **4.** English Lake District (Cooper *et al.* 1995, 2004; Molyneux 2009); **5.**
 2921 South Wales (Molyneux 1987); **6.** Belgium (Martin 1977, 1982a; Martin & Rickards
 2922 1979; Vanguetaine 1986a). **Baltica.** **7.** Norway (Ribecai *et al.* 1999, 2002;
 2923 Tongiorgi *et al.* 2003b); **8.** Sweden (Bagnoli & Ribecai 2001; Ribecai & Tongiorgi
 2924 1995; Ribecai *et al.* 2002; Tropepi & Ribecai 2000); **9.** Estonia (Uutela & Tynni
 2925 1991); **10.** Baltic Russia (Ribecai *et al.* 2002); **11.** Arctic Russia (Raevskaya *et al.*
 2926 2006). **Gondwana/Perigondwana.** **12.** North Africa (Cramer & Díez 1976, 1977;
 2927 Cramer *et al.* 1974a, b; Deunff 1977; Elaouad Debbaj 1984; Vecoli 1999); **13.** Saxo-
 2928 Thuringia (Burmam 1968, 1970; Heuse *et al.* 1994); **14.** Sardinia (Albani 1989;
 2929 Tongiorgi *et al.* 1984); **15.** Bohemia (Vavrdová 1977, 1986, 1993); **16.** Turkey –
 2930 Taurides Terrane (Paris *et al.* 2007); **17.** Turkey – Border Folds, Arabian Plate (Paris
 2931 *et al.* 2007); **18.** Iran – Alborz Terrane (Ghavidel-syooki 2006); **19.** Iran – Zagros
 2932 (Ghavidel-syooki 1997); **20.** Saudi Arabia (Le Herisse *et al.* 2007); **21.** Pakistan –
 2933 Karakorum Terrane (Tongiorgi *et al.* 1994; Quintavalle *et al.* 2000); **22.** South China
 2934 (Brocke *et al.* 1999, 2000; Tongiorgi *et al.* 2003a; Yan *et al.* 2011); **23.** Canning
 2935 Basin (Playford & Martin 1984; Quintavalle & Playford 2006a, b); **24.** Northwest
 2936 Argentina (Achab *et al.* 2006; Rubinstein 2003; Rubinstein *et al.* 2011). Map from
 2937 BUGPLATES, Galls Projection.

2938

2939 **Figure 6.** Pairwise comparisons of taxonomic similarity for latest Katian and
 2940 Hirnantian acritarch assemblages from Anticosti Island, Estonia and Gondwana, based
 2941 on ranges shown in Delabroye *et al.* 2011a, figs 5, 6, 7 and 8, and showing decreasing
 2942 similarity through the Hirnantian glaciation.

2943

2944 **Figure 7.** Distribution of *Neoveryhachium carminae*, *Domasia* and *Deunffia* in the
2945 mid Silurian (late Llandovery – early Wenlock) plotted on a late Llandovery (430 Ma)
2946 palaeogeographical reconstruction. Distributions of *Dactylofusa maranhensis*, the
2947 *Estiastra–Hoegklintia–Pulvinosphaeridium* association and *Dilatisphaera williereae*
2948 based on Le Hérissé & Gourvennec (1995, fig. 2). Data sources. **Laurussia. 1, 2.** SE
2949 USA, NE USA, Canada: Cramer 1971, Cramer & Díez 1972. **3.** England and Wales:
2950 Davies *et al.* 1997, in press; Dorning 1981; Hill 1974; Hill & Dorning 1984;
2951 Mabillard & Aldridge 1985. **4.** Scotland: Molyneux *et al.* 2008; White *et al.* 1991. **5.**
2952 Norway: Smelror 1987. **6.** Sweden: Le Hérissé 1989b. **7.** Denmark: Smelror 1989.
2953 **8.** Belgium: Martin 1969, 1974, 1989. **Gondwana/Perigondwana. 9, 10.** Bolivia,
2954 Peru: Díaz-Martínez *et al.* 2011. **11.** Algeria: Jardiné & Yapaudjian 1968; Jardiné *et*
2955 *al.* 1974. **12.** Libya: Deunff & Massa 1975; Hill & Molyneux 1988. **13.** Jordan:
2956 Keegan *et al.* 1990. **14.** Turkey (Taurides): Dean & Monod 1990; Dean *et al.* 1993.
2957 **15.** Bohemia: Dufka & Pacltova 1988. **16.** Iraq: Al-Ameri 2010. **17.** Saudi Arabia:
2958 Le Hérissé *et al.* 1995; Le Hérissé 2000. **18.** Iran (Zagros): Ghavidel-syooki 1997.
2959 **19.** Argentina (Precordillera): Melendi & Volkheimer 1982, 1983; Pöthe de Baldis
2960 1987; Rubinstein 1997, 2001; Rubinstein & Brussa 1999. **20.** Argentina (Central
2961 Andean Basin): Bultynck & Martin 1982; Rubinstein 2005; Rubinstein *et al.* 2008a;
2962 Rubinstein & Muro 2011. **21.** Argentina (Chaco-paranense Basin): Pöthe de Baldis
2963 1974. **22.** Paraguay (Paraná Basin): Wood & Miller 1991; Gray *et al.* 1992. **23.**
2964 Brazil (Parnaíba Basin): Brito 1967; Quadros 1982; Rubinstein 1997.

2965

2966 **Figure 8.** Late Silurian acritarch biogeography plotted on a palaeogeographical
2967 reconstruction for the late Ludlow (419 Ma). After Le Hérissé *et al.* (1997a, fig. 1),
2968 with additional records of *Visbysphaera bonita* and *V. jardinei* from the Central
2969 Andean Basin, Bolivia (Cramer *et al.* 1974c), and the Pomeranian Caledonides,
2970 Poland (Jachowicz 2000; Le Hérissé 2002).

2971

2972 **Figure 9.** Early Devonian palaeogeography, modified from Le Hérissé *et al.* (2009)
2973 and Rubinstein *et al.* (2008b), and based on the reconstruction of Cocks & Torsvik
2974 (2002, fig. 8). The solid circles indicate the major Lochkovian localities from which
2975 well-preserved and diverse acritarch assemblages have been published and are

2976 discussed in the text. These include Laurentia: Oklahoma, U.S.A.; Armorica: Crozon
2977 peninsula of France, and northern Spain; Gondwana: Algerian Sahara and western
2978 Libya, Africa; Argentina, Bolivia, Brazil, and Uruguay, South America.

2979

2980 **Figure 10.** Mid Devonian (Givetian) palaeogeography, modified from Scotese &
2981 McKerrow (1990, fig. 15). The solid circles indicate the major Middle Devonian
2982 (Eifelian, Givetian) localities from which well-preserved and diverse acritarch
2983 assemblages have been published and are discussed in the text. These include
2984 Laurentia: Iowa, Kentucky, Ohio, U.S.A., and Ontario, Canada; Junggar Terrane:
2985 Junggar Basin, western China; Armorica: France and Germany; Gondwana: Canning
2986 Basin, Western Australia; Algeria, Libya, and Ghana, Africa; Argentina, Bolivia,
2987 Brazil, and Paraguay, South America.

2988

2989 **Figure 11.** Late Devonian (Famennian) palaeogeography, modified from Scotese &
2990 McKerrow (1990, fig. 16). The solid circles indicate the major Late Devonian
2991 (Frasnian, Famennian) localities from which well-preserved and diverse acritarch
2992 assemblages have been published and are discussed in the text. These include
2993 Laurentia: Indiana, Iowa, Kentucky, Ohio, Tennessee, U.S.A., Alberta, Saskatchewan,
2994 Canada; North China: Xinjiang, China; Armorica: Belgium, France, Germany,
2995 Poland, and Spain; Gondwana: Canning Basin, Western Australia; Algeria, Iran, and
2996 Libya, Africa and the Middle East; Bolivia, Brazil, and Paraguay, South America.

2997

2998 **Figure 12.** Cluster analysis (UPGMA algorithm, Jaccard Index) comparing the
2999 acritarch assemblage from the late Dapingian – early Darriwilian *Comasphaeridium*
3000 *setaricum* Biozone of the intracratonic Canning Basin of Australia, with coeval
3001 assemblages from the western margin of Gondwana and adjacent Perigondwanan
3002 terranes. A. Genera; B. Species. See text for data sources and discussion.

3003

3004 **Table 1.** Jaccard similarity coefficients for Upper Cambrian data used in cluster
3005 analysis (Fig. 4). Lowest values (least similarity) are indicated by grey-filled cells. In

3006 all cases, either Missouri/Arkansas (Laurentia), Kolguev Island (Baltica) or NW
3007 Argentina is least similar to other regions.
3008
3009 **Table 2.** Occurrence of genera in Lower–Middle Ordovician phytoplankton
3010 assemblages from South China (Perigondwana) and the intracratonic Gondwanan
3011 Canning and Georgina basins of north-western and central Australia. Stratigraphic
3012 intervals and data sources are as follows. **South China:** lower Floian–lower
3013 Darriwilian, *Tetragraptus approximatus*–*Undulograptus austrodentatus* graptolite
3014 biozones; Brocke *et al.* 1999, 2000; Huang *et al.* 1994; Li 1987, 1990; Li *et al.* 2002*b*;
3015 Lu 1987; Tongiorgi *et al.* 1995, 1998, 2003*a*; Yan *et al.* 2011; Yin 1994. **Canning**
3016 **Basin:** Willara, Goldwyer and Nita formations, middle Floian–upper Darriwilian,
3017 *Athabascaella rossii* to *Dactylofusa striatogranulata* acritarch biozones; Playford &
3018 Martin 1984; Quintavalle & Playford 2006*a, b*. **Georgina Basin:** Coolibah
3019 Formation, middle–upper Floian (upper Bendigonian–lower Chewtonian, Zhen *et al.*
3020 2003, fig. 6); Playford & Wicander 1988.
3021

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.

Molyneux, Delabroye, Wicander & Servais: Table 2

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

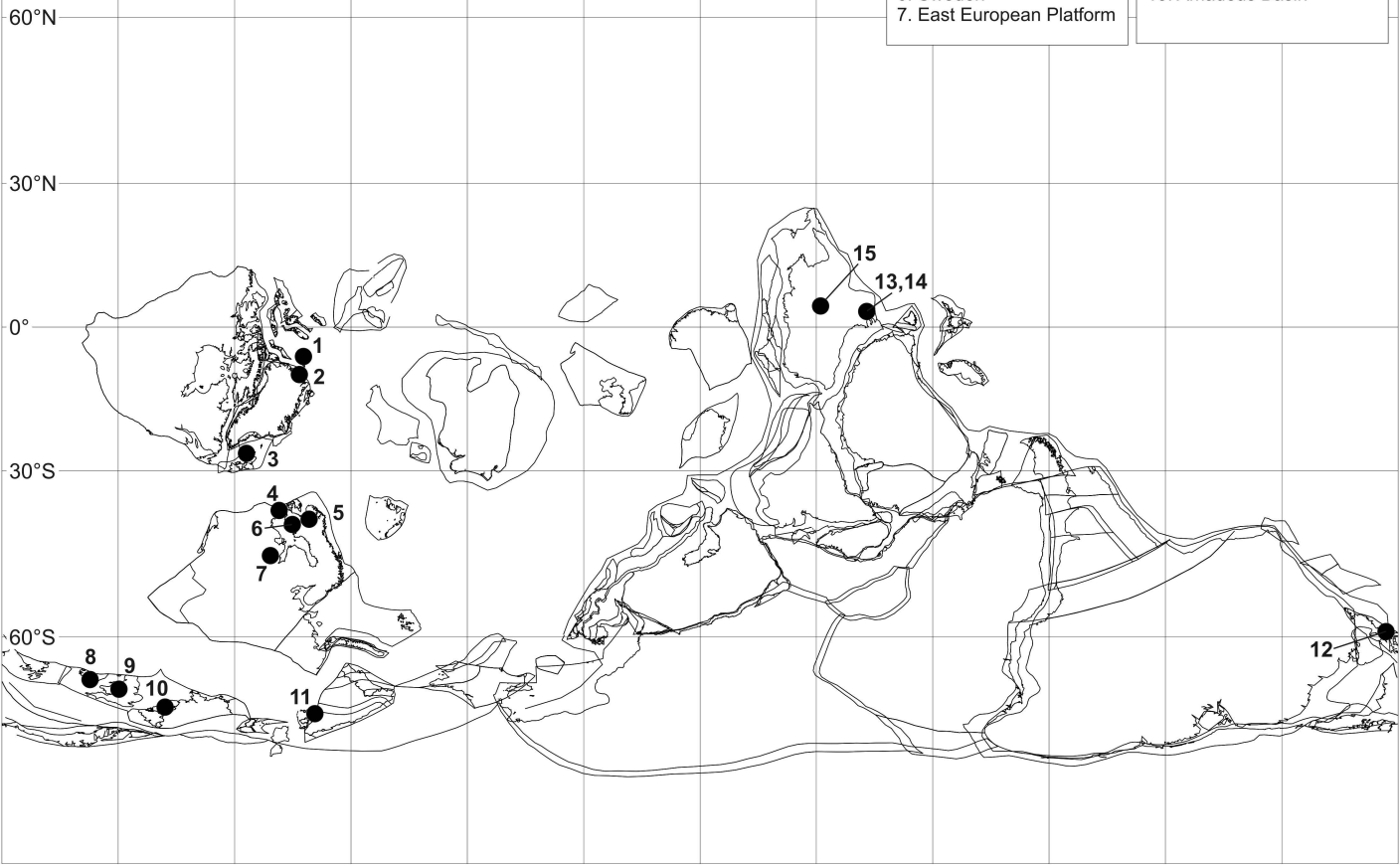
Molyneux, Delabroye, Wicander & Servais: Table 2

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

Table 2.

510 Ma (early Middle Cambrian, base Stage 5)

- | | |
|---|--|
| Laurentia
1. Svalbard
2. North Greenland
3. NW Scotland | Gondwana/Perigondwana
8. Ireland
9. England and Wales
10. Belgium
11. Spain
12. New Brunswick
13. Arrowie Basin
14. Stansbury Basin
15. Amadeus Basin |
|---|--|

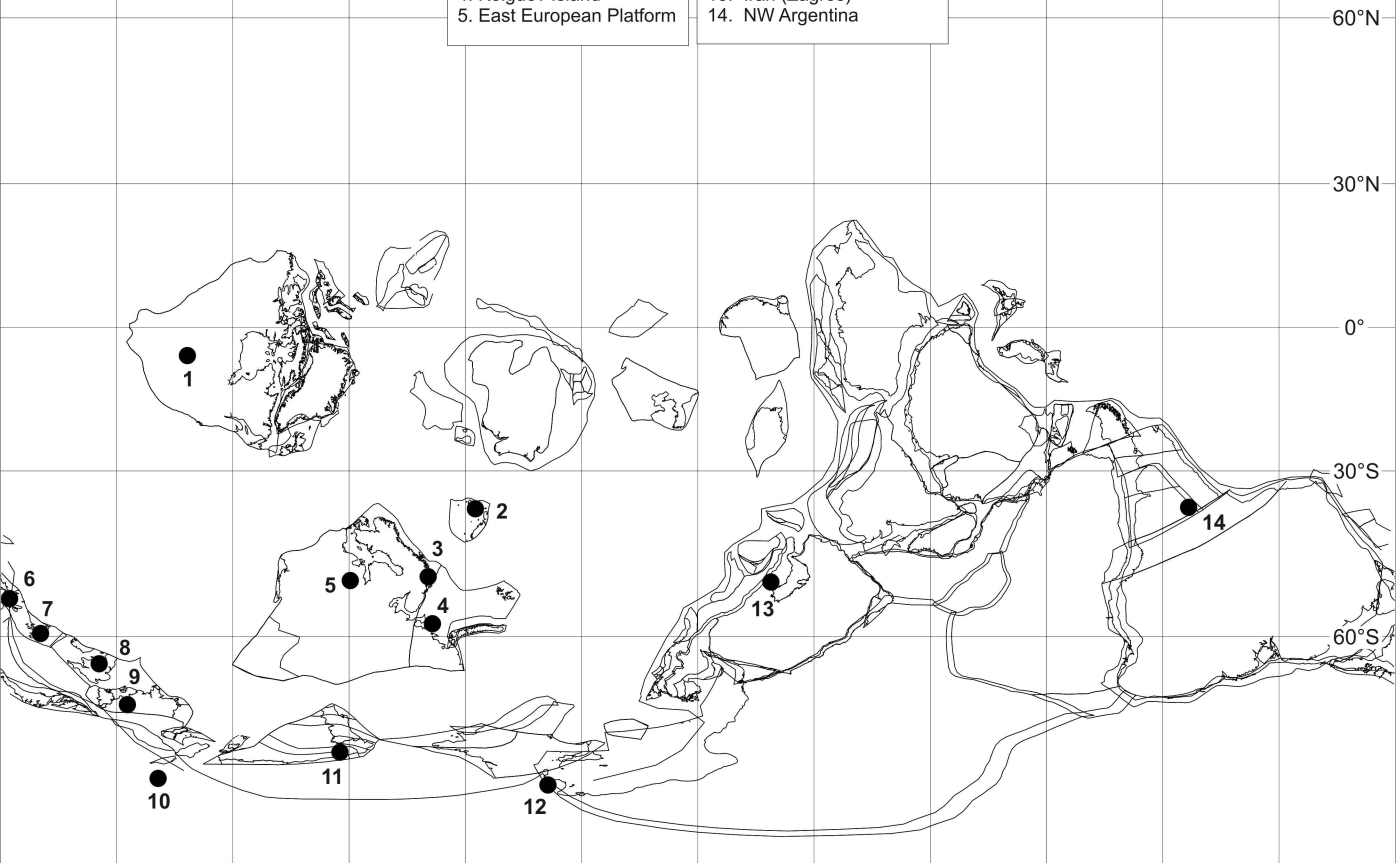


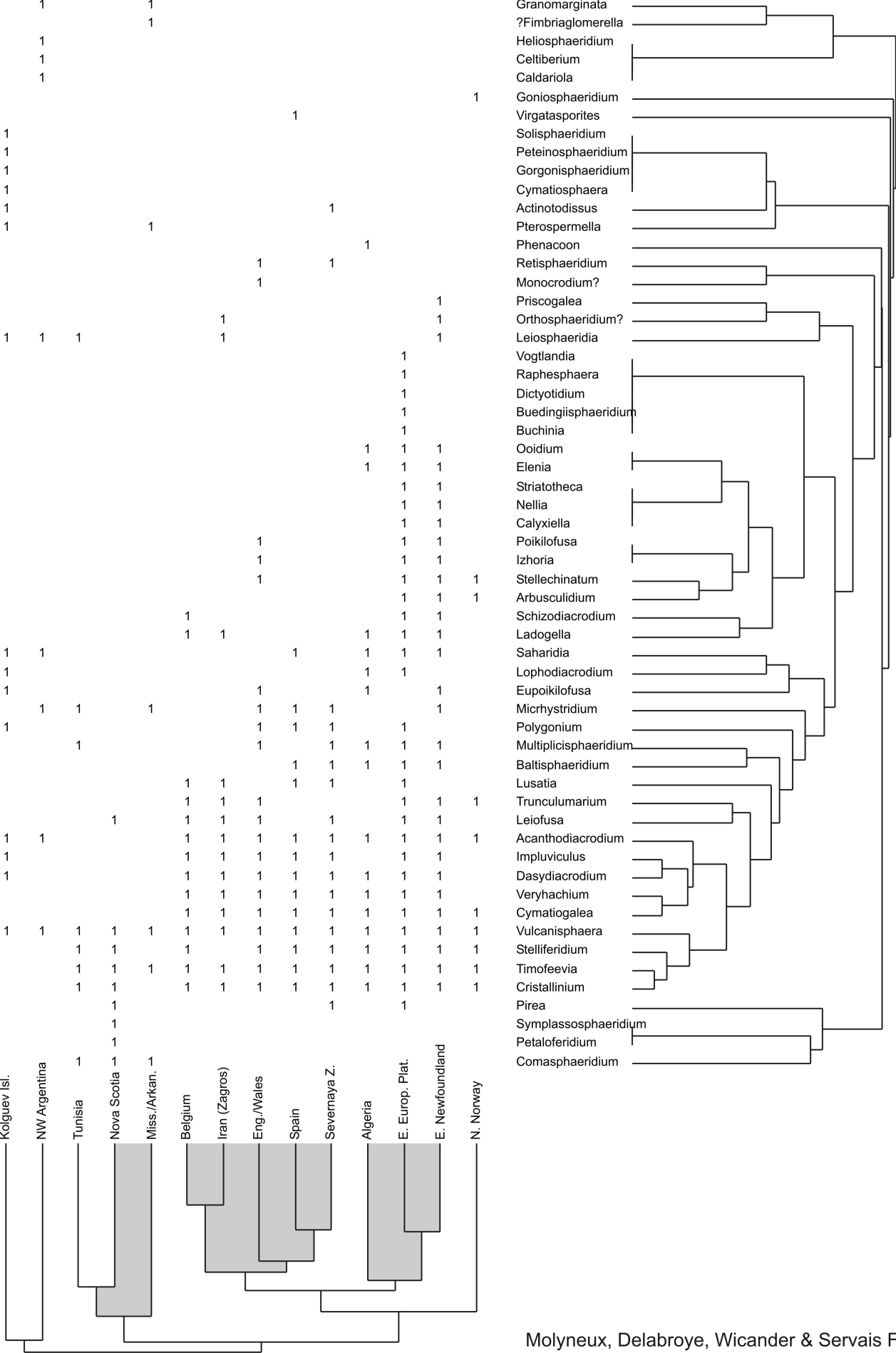
	S	EPP	AB
<i>Tasmanites</i>	■		
<i>Leiovalia</i>	■		
<i>Multiplicisphaeridium</i>	■	■	
<i>Lophosphaeridium</i>	■	■	
<i>Cristallinium</i>	■	■	
<i>Heliosphaeridium</i>	■	■	
<i>Comasphaeridium</i>	■	■	
<i>Retisphaeridium</i>	■	■	
<i>Goniosphaeridium</i>	■	■	
<i>Pterospermella</i>	■	■	
<i>Cymatiosphaera</i>	■	■	
<i>Ovulum</i>	□	■	
<i>Revinotesta</i>	■	■	
<i>Leiosphaeridia</i>	■	■	■
<i>Adara</i>	□	■	□
<i>Dictyotidium</i>	■	□	■
<i>Micrhystridium</i>	■	■	■
<i>Duplisphaera</i>	□	■	□
<i>Alliumella</i>	□	■	□
<i>Asteridium</i>	■	■	■
<i>Aranidium</i>	□	■	□
<i>Skiagia</i>	■	■	■
<i>Eliasum</i>	□	■	□
<i>Solisphaeridium</i>	□	■	□
<i>Timofeevia</i>	□	■	□
<i>Polygonium</i>	□	■	□
<i>Estiastra</i>	□	■	□
<i>Globosphaeridium</i>	□	□	■
<i>Simia</i>	□	■	■
<i>Stictosphaeridium</i>	□	■	■
<i>Sinianella</i>	□	■	■
<i>Sphaerocongregus</i>	□	■	■
<i>Oscillatoriopsis</i>	□	■	■
<i>Chomotriletes</i>	□	■	■
<i>Clavitrichoides</i>	□	■	■
<i>Paleasphaeridium</i>	□	■	■
<i>Eomycetopsis</i>	□	■	■
<i>Glomovertella</i>	□	■	■
<i>Leiofusa</i>	□	■	■
<i>Myxococcoides</i>	□	■	■
<i>Synsphaeridium</i>	□	■	■
<i>Satka</i>	□	■	■
<i>Pirea</i>	□	■	■

495 Ma (Furongian, Stage 9)

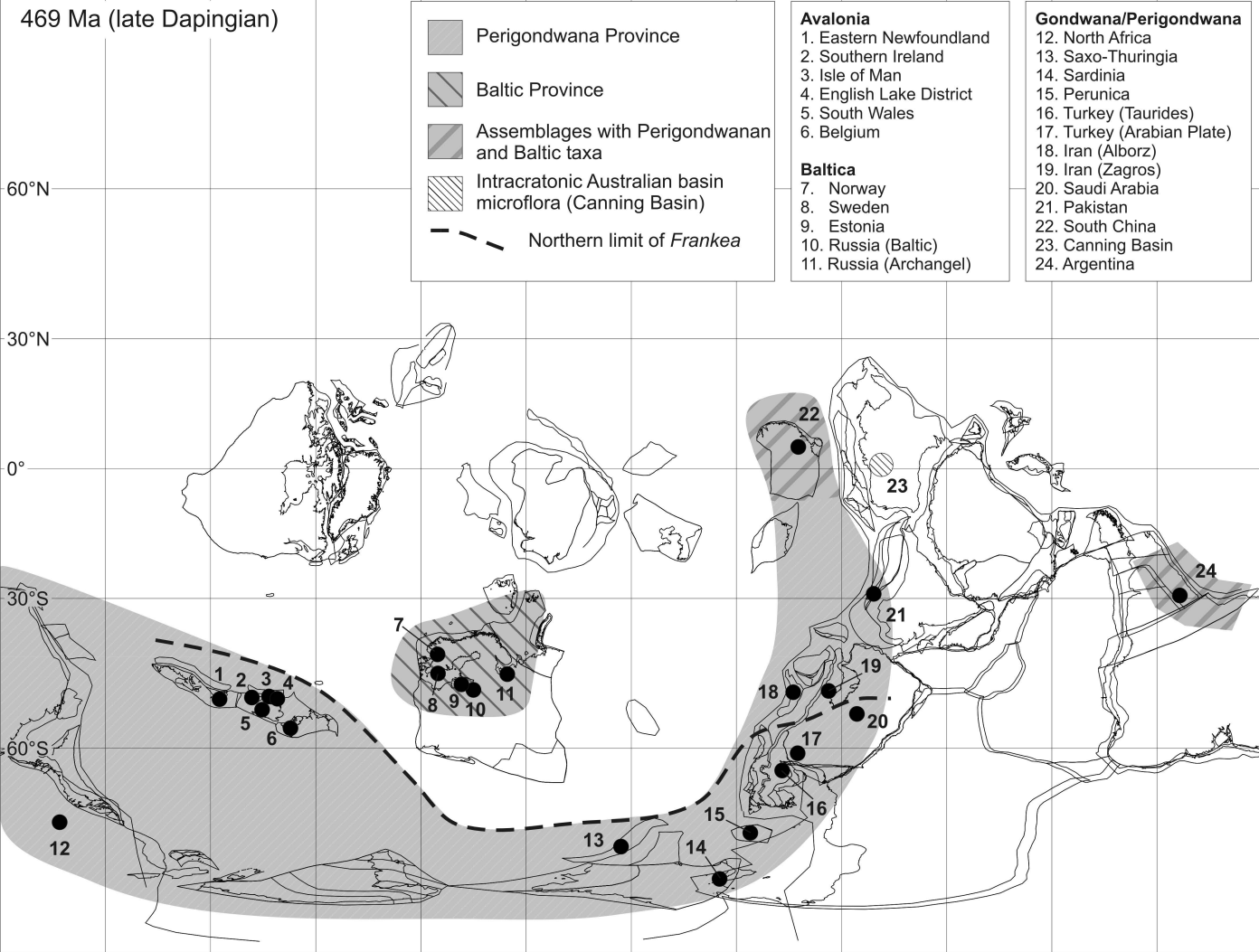
- Laurentia**
1. Missouri, Arkansas
- Kara**
2. Severnaya Zemlya
- Baltica**
3. Northern Norway
4. Kolguev Island
5. East European Platform

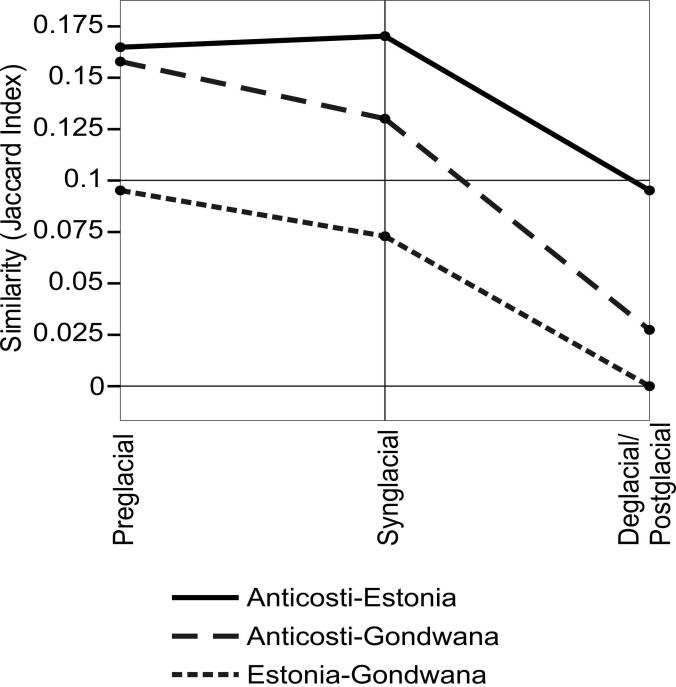
- Gondwana/Perigondwana**
6. Nova Scotia
7. Eastern Newfoundland
8. England and Wales
9. Belgium
10. Algeria
11. Spain
12. Tunisia
13. Iran (Zagros)
14. NW Argentina



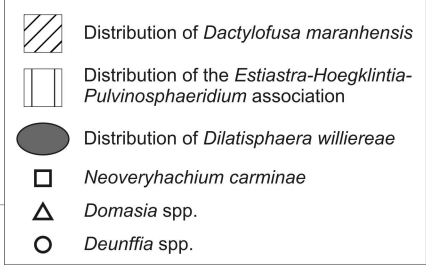


469 Ma (late Dapingian)





430 Ma (late Llandovery)



- Laurussia**
1. SE USA
 2. NE USA, Canada
 3. England and Wales
 4. Scotland
 5. Norway
 6. Sweden
 7. Denmark
 8. Belgium

- Gondwana/Perigondwana**
9. Bolivia
 10. Peru
 11. Algeria
 12. Libya
 13. Jordan
 14. Turkey (Taurides)
 15. Bohemia
 16. Iraq
 17. Saudi Arabia
 18. Iran (Zagros)
 19. Argentina (Precordillera)
 20. Argentina (Central Andean Basin)
 21. Argentina (Chaco-paranense Basin)
 22. Paraguay (Paraná Basin)
 23. Brazil (Parnaíba Basin)

