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Ordovician organic-walled microphytoplankton (acritarch) distribution: the global scenario

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Abstract

A number of palaeobiogeographical models for Ordovician organic-walled microphytoplankton (acritarchs, prasinophytes, and related groups) have been published during the past 30 years. A modern synthesis of Ordovician acritarch palaeobiogeography, based on previously published acritarch ‘provinces’ and global distribution models, as well as new plots on recently compiled palaeogeographical maps is presented. Review of the literature and new plots indicate that a number of preliminary conclusions can be drawn. Following minor biogeographical differentiation of acritarch assemblages during the Cambrian, ‘provincialism’ started at the Cambrian–Ordovician boundary. In the late Tremadocian a warm-water assemblage, containing the genera *Aryballomorpha*, *Athabascaella* and *Lua*, but no diacrodians, seems to be limited to low-latitude localities such as Laurentia and North China. From the late Tremadocian and throughout most of the Arenig a peri-Gondwana acritarch assemblage with the easily recognisable taxa *Arbusculidium filamentosum*, *Coryphidium*, and *Striatotheca* is present on the southern margin of Gondwana, and its distribution corresponds almost exactly with that of the Calymenacean–Dalmanitacean trilobite fauna. It seems reasonable to consider the acritarchs of Baltica as belonging to a temperate-water ‘province’, which was probably not restricted to the palaeocontinent of Baltica but had a wider distribution at about the same latitude, as some of the elements recorded from Baltica also occur in South China and Argentina. The maximum separation of the continents during the Arenigian, reflected by a pronounced biogeographical differentiation of most Ordovician fossil groups, led to the development of geographically distinct acritarch assemblages. Data from the late Middle Ordovician and the Late Ordovician remain too poor to elucidate global palaeobiogeographical patterns. The biogeographical distribution of Ordovician acritarchs appears similar to that of the resting cysts of modern dinoflagellates, primarily controlled by latitude but also following the continental margins.

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1. Introduction

Following publication of Paris and Robardet’s (1990) paper, which questioned the existence of

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Tornquist's Sea between Avalonia and Baltica, Fortey and Mellish (1992) asked whether some fossils were better than others for inferring palaeogeography. They considered this question in relation to the Early Ordovician of the North Atlantic regions, and concluded that planktonic fossils such as graptolites, chitinozoans and acritarchs were of low palaeogeographical value while benthic organisms such as trilobites, brachiopods and ostracodes were more useful for biogeographical discrimination. Fortey and Mellish's (1992) paper has resulted in an ongoing discussion on the relative merits of palaeobiogeographical indicators in the Ordovician. At the heart of this debate is the question of whether the microphytoplankton were so widely distributed as to be virtually cosmopolitan in the Ordovician world, or whether distinct areas of the Earth were characterised by distinct microfloras, and if so what controlled their distribution.

A number of palaeobiogeographical models for Ordovician organic-walled microplankton (acritarchs, prasinophytes, and other algal groups) have been published during the past 30 years. The aim of this paper is to produce a modern synthesis of their biogeography. The synthesis is based on the Ordovician acritarch data compiled by the acritarch clade team of IGCP project 410 'The Great Ordovician Biodiversification Event' (Servais and Stricanne, 2001).

2. Ordovician palaeogeography, palaeoclimatology, and oceanic currents

Progress made during the last 25 years in understanding Ordovician palaeogeography has resulted from the integration of tectonic, stratigraphic, palaeoclimatological, palaeomagnetic and palaeontological evidence. The palaeogeographical maps of Scotese and McKerrow (1990) have been used to plot the distributions of many fossil groups, including acritarchs (e.g., Playford et al., 1995; Tongiorgi et al., 1995; Vecoli, 1999). On the Ordovician maps of Scotese and McKerrow (1990) and similar reconstructions, the main continents are Laurentia (North America) and Siberia, both found in equatorial positions, Baltica,

located at intermediate latitudes in the southern hemisphere, and the supercontinent Gondwana, by far the largest plate, which included South America, Africa, Antarctica, Australia, India and other marginal terranes. This large continent extended from the South Pole to the Equator but remained separated from Laurentia throughout the Ordovician.

An alternative palaeogeographical model proposed by geologists working in South and Central America (e.g., Dalla-Salda et al., 1992; Dalziel et al., 1994; Dalziel, 1997) postulated a collision between Laurentia and Gondwana during the Middle Ordovician. Both models are permissible on palaeomagnetic evidence because palaeolongitudes cannot be determined by palaeomagnetic data. Palaeontological data, however, disprove the collision hypothesis. The continents remained separated throughout the Ordovician, while a smaller terrane, which included the Precordillera of Argentina, rifted off from Laurentia in the Early Ordovician to drift across the Iapetus Ocean to dock with Gondwanan Argentina at some time prior to the Late Silurian (e.g., Benedetto, 1998). In the more recently published Ordovician palaeogeographical maps (e.g., Scotese et al., 2001; Cocks, 2001; Li and Powell, 2001), Gondwanan Argentina is depicted facing the western margin of Laurentia, across a western Iapetus Ocean that is much narrower than shown on earlier reconstructions.

Models of Ordovician palaeoclimatology and palaeoceanography are rare and remain much more speculative than palaeogeographical reconstructions. Golonka et al. (1994) published palaeotemperature and palaeoclimate maps, constructed using a palaeoclimate-modelling programme developed by Parrish (1982). While there is broad agreement that the end-Ordovician glaciation was due to the formation of an ice cap, following the movement of Gondwana towards the South Pole, there is less agreement on models of oceanic circulation, which vary greatly from one author to another. Bergström (1990, fig. 8), for example, presented an oceanic current circulation model for the Early Ordovician, which included a current in the southern hemisphere that originated in South America, drifted eastwards

along the margin of European Gondwana (passing through the Tornquist's Sea), to reach localities such as Saudi Arabia and South China. This model was used to explain the regional distribution of some conodont taxa. At the same time, graptolite workers presented another circulation pattern model for the Arenig with a current flowing in exactly the opposite direction, originating around Arabia, drifting westwards on the northern margin of European Gondwana (passing through the Tornquist's Sea), to reach Gondwanan Argentina (Finney and Chen, 1990).

A more recent model published by Christiansen and Stouge (1999) also concerns the Arenig. These authors suggested that the temperate low-pressure zones were located at 50° latitude, and the subtropical high-pressure zones at 25° latitude. According to its authors, this model, associated with circulation of discrete water masses, explains the regional distribution, i.e., the provincialism, of graptolites, trilobites, brachiopods and conodonts.

3. Acritarch 'provinces' and previous plots of acritarch distribution

In this chapter the previously published palaeogeographical models applied to Ordovician acritarchs are summarised.

3.1. The earliest models

The first attempt to model Ordovician acritarch biogeography was that of Cramer and Díez (1972, 1974, 1977). Following publication of a global distribution model of Silurian acritarchs (e.g., Cramer, 1968), in which several large-scale acritarch assemblages were interpreted as being controlled by palaeolatitude, Cramer and Díez distinguished two major provinces in the Ordovician, the 'cold African' (named the '*Coryphidium bohemicum* province' in Cramer and Díez, 1977) and the 'warm American Palynological Unit', which they plotted on an available but slightly modified palaeogeographical map. Cramer and Díez's Ordovician and Silurian models are now out of date (Colbath, 1990; Tyson, 1995; Le Hérisse and

Gourvenec, 1995; Servais and Fatka, 1997), mainly because they were based on palaeogeographical maps that have been superseded. In Cramer and Díez's models, acritarch provinces were depicted as being parallel to latitude and following climatic belts.

At about the same time, Vavrdová (1974) compared European Ordovician acritarch assemblages and came to a similar conclusion. She distinguished between 'Arenig–Llanvirnian' assemblages from Bohemia and those of the Baltic area. The Bohemian assemblages were attributed to a 'Mediterranean province', which included Belgium, France, Spain, North Africa, southern Germany, central Bohemia and Bulgaria. Coeval assemblages from the northern part of the former Soviet Union, Sweden, Poland, northern Germany and parts of the British Isles were attributed to the Baltic (or Boreal) province, although assemblages from the British Isles (England and Wales) and northern Germany were subsequently reassigned to the 'Mediterranean' province. Vavrdová's (1974) differentiation of the two provinces was based on general characteristics (prevalence of diacromorph acritarchs (diacrodians) in the Mediterranean province and of acanthomorph acritarchs in the Baltic province).

3.2. The 'Mediterranean' or 'peri-Gondwana' province

Most papers on Ordovician acritarchs have been produced from the areas that correspond to Vavrdová's Mediterranean province. Martin (1982) accepted a slightly modified version of Vavrdová's (1974) model, enlarging the Mediterranean province to include the Anglo-Welsh area, eastern Newfoundland and northwestern Argentina. In doing so, she noted the 'peri-Gondwanan' distribution of the province. Li (1987) included his material from the Arenigian Meitan Formation of Guizhou Province, southwest China, in Vavrdová's Mediterranean province, and noted that assemblages described from Hungary, Sardinia, Ireland, southern Britain, Spain, Morocco, Libya and Saudi Arabia also belonged to that province. Li (1987) thus established that Vavrdová's Mediterranean province extended from east-

ern Newfoundland through southern and western Europe, the Mediterranean area and the Middle East to the Upper Yangtze Region of southern China. In a subsequent paper Li (1989) redefined the ‘Mediterranean’ province of Vavrdová (1974), abandoning the prevalence of diacromorph acritarchs as a diagnostic feature. Instead, affinity to the Mediterranean province was determined by the occurrence of the genera *Arbusculidium*, *Coryphidium* and *Striatotheca*.

Following the suggestions of Martin (1982) and Martin and Dean (1988), Albani (1989) observed that the term ‘peri-Gondwanian palaeoprovince’ seemed to be more appropriate than the term ‘Mediterranean’ province, and added *Acanthodiacrodium* and *Dasydiacrodium* to its list of diagnostic elements. The term ‘peri-Gondwana province’ has subsequently been used widely in the literature, extending to Egypt (Gueinn and Rasul, 1986), Brazil (Padilha de Quadros, 1988), Jordan (Keegan et al., 1990), southern Turkey (Dean and Martin, 1992), Pakistan (e.g., Tongiorgi et al., 1994) and Iran (e.g., Ghavidel-Syooki, 1997), in addition to the areas mentioned above. The province is regarded as a cold-water province that extends from Argentina on the border of northern Gondwana to the Yangtze Platform (Vecoli, 1999, fig. 9).

More recent work has proposed refinements to the basic concept of a peri-Gondwanan province, either by splitting the province into subdivisions or by expanding the list of its diagnostic elements. Thus Playford et al. (1995) accepted that the peri-Gondwana province comprised a broad, latitudinally extensive, circumpolar, cold to cool-temperate, palaeogeographic belt extending along the northern margin of Gondwana from Argentina through eastern Newfoundland, North Africa, central and southern Europe, and southern Turkey to South China, but split the province into three units of ‘subprovincial’ rank. The ‘Mediterranean subprovince’ was restricted to the area originally designated by Vavrdová (1974), and the ‘South America subprovince’ and ‘South China subprovince’ were added. Vavrdová (1990) selected 20 species to be characteristic of the ‘high-latitude Arenigian sea’, and later Vavrdová (1997) proposed the name ‘*Coryphidium bohemicum* acritarch bioprovince’ of ‘Arenigian–Llanvirnian’ age for this assemblage.

In her later paper, she provided a list of 16 taxa that she considered diagnostic of this province, and added five species that were considered characteristic for this province in the Llanvirn. Additionally, Vavrdová (1997) noted that ‘a barrier divided the cool, high-latitude peri-Gondwanan region from the warm-water Baltoscandinavia and Laurentia’.

Most recently, Li and Servais (in press) confirmed the existence of the peri-Gondwanan province, which they plotted on the palaeogeographical reconstruction of Li and Powell (2001). Li and Servais showed that the province extended around the southern part of Gondwana, from Argentina to South China, but was absent from the northern part of the supercontinent, i.e. from North China and Australia. In addition, Li and Servais noted that the province should not necessarily be considered typical of cold- or temperate-water environments, as it is present from high latitudes in European Gondwana to low latitudes such as the South China Plate.

3.3. The ‘Baltic province’

Recognition of Vavrdová’s (1974) Baltic province has remained problematical due to the lack of a clear definition. Li (1989) noted that it was difficult to recognise the Baltic province as its characteristic elements, i.e. *Baltisphaeridium*, *Peteinosphaeridium*, and *Goniosphaeridium* (acanthomorph acritarchs), were also found in the Mediterranean province. The Baltic province was therefore only distinguishable by the absence of typical peri-Gondwanan taxa. Brocke et al. (1995) noted that a number of easily recognisable Early to Middle Ordovician taxa, namely *Arbusculidium filamentosum*, *Arkonina*, *Striatotheca*, *Aureotesta* (and *Marrocanium*), *Coryphidium* (and *Vavrdovella*), *Dicrodiacrodium* and *Frankea*, which were considered typical of cold-water assemblages from the peri-Gondwana province between the late Tremadocian and the early Llanvirnian, had never been recorded from Baltica. Servais and Fatka (1997) used the presence/absence of these taxa to distinguish between European microfloras of peri-Gondwanan (including Avalonia and Ar-

morica) and Baltic affinities, thereby delineating the Trans-European Suture Zone. These authors considered the Baltic province to be an area with mixed assemblages that include both cold-water (diacrodians) and warm-water forms (see below), a view also expressed by Volkova (1997). In addition, Servais and Fatka (1997) noted that the distinction between Baltica and warm-water areas remained difficult because the data recovered from the latter areas were too poor.

None of the publications listed above or the papers by Vavrdová (1997), Raevskaya (1999) and Vecoli (1999) identified taxa that were unique to and diagnostic of the Baltic province. Playford et al. (1995), however, listed some species of *Peteinosphaeridium* and related genera (*Cyclospira*, *Liliosphaeridium*) as being ‘confined to the Baltic province’ and others as being ‘very-likely Baltic-restricted’. The subspecies *Peteinosphaeridium trifurcatum cylindroferum*, for example, was considered to be ‘endemic to the Baltic province’. Nevertheless, the concept of a distinguishable Baltic province has so far been followed only by Tongiorgi and his co-workers (Playford et al., 1995; Ribecai and Tongiorgi, 1995, 1999; Tongiorgi et al., 1995, 1998; Yin et al., 1998; Tongiorgi and Di Milia, 1999).

3.4. Warm-water province(s)

Not only did Playford et al. (1995) retain the Baltic province and subdivide the peri-Gondwanan province into three subprovinces, but they also established three new warm-water provinces of North America, North China, and Australia. Playford et al. (1995) identified species of *Peteinosphaeridium* and related genera as the distinctive elements of each palaeogeographical area. The Arenigian species *Peteinosphaeridium? furcatum*, for example, was considered to be indigenous to Western Australia, while the Upper Caradocian species *Peteinosphaeridium indianense* and *Peteinosphaeridium spiraliculum* were regarded as being restricted to North America. Playford and his co-authors summarised their palaeobiogeographical ideas as follows: ‘representatives of the peteinoid genera discussed connote palaeogeographic differentiation in accordance with the rec-

ognised provincial categories’. So far, however, their model, distinguishing North American and Australian provinces, has not been widely adopted, and only Tongiorgi et al. (1995, 1998) have reported a similar distribution pattern.

Volkova (1997) provided an alternative definition of a warm-water province based on the genera *Corollasphaeridium* and *Goniomorpha*, which she considered to be indicative of the warm-water province at the Cambrian–Ordovician boundary. At a slightly higher stratigraphical level, in the late Tremadocian, she considered the presence of the genera *Aryballomorpha*, *Athabascaella* and *Lua* to be characteristic of the warm-water area, noting that late Tremadocian occurrences of these taxa were limited to northeast China (Martin and Yin, 1988), i.e. on the North China Plate, and to two areas on Laurentia, the first being in Alberta, Canada (Martin, 1984, 1992), and the second in Texas (Barker and Miller, 1989). In addition, Volkova (1997) noted that diacrodians were completely absent from these assemblages. *Aryballomorpha* and *Athabascaella*, however, have also been recorded from Baltica, a continent that Volkova (1997) placed in temperate-water environments, where they occur in mixed assemblages that also include cold-water taxa (diacrodians).

3.5. Previous plots of acritarch distribution

Cramer (1968) represented the first attempt to understand the global distribution of Silurian microphytoplankton by plotting their distribution on palaeogeographical maps, but comparable plots for the Ordovician remained rare until the 1990s, although several provincial models had been described. Over the last decade or so, there have been many attempts to depict the distribution of acritarchs on published palaeogeographical maps, to compare and contrast assemblages from different palaeogeographical areas and to test the influence of palaeolatitude (i.e. climatic) and other factors on acritarch distribution.

Colbath (1990), for example, plotted the Ordovician genus *Frankea* on the Arenig–Llanvirn and Caradoc palaeogeographical maps of Scotese (1986), and concluded that its distribution could be elegantly explained if *Frankea* was restricted to

high latitudes (> approximately 60°S). This model received some criticism from Servais (1993), however, who reviewed the biostratigraphical distribution of the genus and noted that its biogeographical distribution was more complicated than indicated by Colbath. Furthermore, Eiserhardt (1992) plotted *Multiplicisphaeridium raspum* and *Palaeohystrichosphaeridium wimani* on maps derived from Scotese (1986) and Colbath (1990) for the Ordovician–Silurian boundary and the Lower–Middle Silurian, and concluded that the distribution of these taxa was not related to palaeolatitude.

Most plots have been intended to depict the distribution of various provincial microfloras. Thus, Vavrdová (1990) plotted the distribution of some 20 selected taxa from the Mediterranean province on a map of unknown origin in order to compare the assemblage recovered from the Klavava Formation of Bohemia with other areas, such as the Montagne Noire (southern France), southern Britain, Thuringia, Belgium, Newfoundland, Morocco, Sardinia, Hungary and southern China. She subsequently (Vavrdová, 1997) indicated the distribution of her ‘*Coryphidium bohemicum* bioprovince’ on the Arenig palaeogeographic reconstruction of Pickering et al. (1989) and on the Late Ordovician map of Erdtmann (1991), and plotted the occurrences of *Aremoricanium syringosagis*, present in Gondwana, Baltica and Laurentia, on a reconstruction at the Ordovician–Silurian boundary by Pickering et al. (1988) to demonstrate breakdown in provincialism at that time.

Servais et al. (1996) plotted occurrences of *Dicrodiacrodium ancoriforme* on a map first published by Brocke et al. (1995), demonstrating that the species is typical of the peri-Gondwanan province. The same map was used to plot additional taxa that show a similar distribution: *Aureotesta–Marrocanium* (Brocke et al., 1998) and *Arbusculidium filamentosum* var. *filamentosum* (Fatka and Brocke, 1999). Servais and Fatka (1997) subsequently published a map for the Arenig, depicting the European and North African parts of Gondwana together with Avalonia and Baltica, on which the presence/absence of *Dicrodiacrodium*, *Frankea* and *A. filamentosum* was

used to distinguish between peri-Gondwanan and Baltican assemblages at either side of the Tornquist’s Sea.

Servais and Mette (2000) and Vanguetaine and Servais (2002) plotted the occurrence of the *mes-saoudensis–trifidum* assemblage, considered to be typical of the late Tremadocian–early Arenig in the peri-Gondwanan area, and showed that the full assemblage only occurs in high-latitude areas, including the British Isles, Belgium, Germany, Bohemia, Spain and Turkey. Some elements, but not the whole assemblage are also found in Argentina, southern China and north-western Russia. Most recently, Li and Servais (2002) plotted occurrences of the warm-water genera selected by Volkova (1997), namely *Aryballo-morpha*, *Athabascaella* and *Lua*, and the three significant taxa of the peri-Gondwana province selected by Li (1989), i.e. *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca*, on the global palaeogeographical reconstruction for the Arenig (ca. 480 Ma) by Li and Powell (2001). This plot showed a clear distinction between two distributional areas, one around the southern part of Gondwana and the second at low latitudes.

Other authors have used maps by Scotese and McKerrow (1990, 1991), including Playford et al. (1995) and Tongiorgi et al. (1995), for the distribution of Lower to Middle Ordovician peteinoid taxa, and Wicander et al. (1999), who discussed in detail the palaeobiogeography of the Late Ordovician acritarchs at a global scale. The latter authors plotted all investigated localities on a palaeogeographical reconstruction based on maps of Scotese and McKerrow (1991) and Wilde (1991). Volkova (1997) plotted some of the localities bearing elements of the three provinces (peri-Gondwana, Baltica and the warm-water province) on the palaeobiogeographical map of Erdtmann (1986), based in turn on graptolite distribution during the earliest Ordovician (early Tremadocian).

3.6. Interpretations of the impact of ocean currents

There is little doubt that ocean currents played an important role in the global distribution of Ordovician acritarchs, similar to the way in which

modern currents influence the distribution of cysts of marine microphytoplankton in present-day oceans. [Matthiessen \(1995\)](#), for example, reported evidence that the transport of dinoflagellate cysts and other organic-walled microfossils by currents modifies the assemblages found in Recent oceanic surface sediments from the Norwegian–Greenland Sea. [Mudie and Harland \(1996\)](#) noted that the inflow of warm, saline North Atlantic Drift water in the eastern Arctic was considered responsible for a mixture of dinoflagellate assemblages in the modern Arctic Ocean. Models invoking the influence of currents have been applied to Ordovician acritarchs to explain the distribution of selected taxa.

Based on the palaeogeographical maps of [Scotese and McKerrow \(1990\)](#) and on the palaeoclimatological maps of [Wilde \(1991\)](#), several authors have proposed interpretations of the influence of oceanic currents on the distribution of their fossil groups. The first attempt to explain acritarch distributions in such a way was that of [Li \(1991\)](#) who discussed the presence of ‘cold-water’ acritarchs in lower latitudes in South China, where warm-water carbonates are indicative of a warmer environment. He noted that cold-water conodonts ([An, 1987](#)), trilobites ([Zhou and Fortey, 1986](#)) and graptolites ([Berry and Wilde, 1990](#)) were found on the Yangtze Platform during the Arenig–Llanvirnian, and proposed a model of oceanic surface currents based on the palaeogeographic map of [Scotese and McKerrow \(1990\)](#) to explain the presence of the ‘cold-water’ acritarchs in the low-latitude, warmer environments. [Li \(1991, p. 33\)](#) suggested that the taxa *Striatotheca* and *Coryphidium*, considered to be of cold-water affinity by [Cramer and Díez \(1976\)](#) and [Albani \(1989\)](#), may have been introduced into southern China by an ocean current circulation that brought cold water masses from low-latitude Gondwana to southwest China.

Subsequently, [Tongiorgi et al. \(1995\)](#) and [Yin \(1995\)](#) published a similar model, proposing that the northward extension of the Mediterranean province to South China could be attributed to ‘a cool peri-Antarctic (peri-Gondwanan) oceanic current flowing along the subpolar margin of Gondwana...’. In a later paper, [Tongiorgi and Di](#)

[Milia \(1999\)](#) noted that ‘the present reconstructions of oceanic circuits are probably based on overly simplistic assumptions’, and presented a second possible hypothesis to explain ‘changing palaeogeographic affinities’ by ‘sea-level fluctuations related to eustatic cycles’.

[Eiserhardt \(1992\)](#) included a cautious discussion of the possible influence of ocean currents in his investigation of Late Ordovician assemblages. He noted that there were major problems in trying to isolate the effects of ocean currents on the composition of acritarch assemblages. In the first place, he argued that the percentage of individual taxa must be known in detail in all assemblages from the different areas. Furthermore, he noted that it is almost impossible to determine whether a species produced its cysts at only one locality. [Eiserhardt \(1992\)](#) therefore avoided the use of a simplistic model of current circulation to explain the composition of his Late Ordovician assemblages from the southern Baltica area.

4. Palaeobiogeography or palaeoecology?

The spatial distribution of acritarch taxa and morphotypes is a function of their ecological requirements as well as biogeography. Any attempt to describe biogeographical patterns of acritarch distribution must therefore take into account likely palaeoecological controls and distinguish them from palaeobiogeographical influences.

4.1. *The biology of acritarchs*

Although the acritarchs were defined as a utilitarian catch-all category to include organic-walled microfossils of variable and unknown biological affinity ([Evitt, 1963](#)), most Lower Palaeozoic acritarchs are today considered to represent cysts of organic-walled microphytoplankton (e.g., [Martin, 1993](#); [Colbath and Grenfell, 1995](#); [Molyneux et al., 1996](#); [Servais et al., 1997](#); the reader is referred to these papers for reviews of the biological affinities of acritarchs). Most Palaeozoic acritarchs probably constituted the organic-walled marine microphytoplankton of the oceans and may be considered as ‘pre-dinoflagellates’ ([Le](#)

Hérissé, 1989), and can be compared to various algal groups in modern oceans.

Assuming that comparison with modern dinoflagellates and prasinophytes is valid, Palaeozoic phytoplankton distribution was probably controlled by a series of parameters, of which the climate (temperature) signal, the coastal/oceanic (inshore–offshore trend) signal, the salinity signal, and the productivity (coastal upwelling zones) signal are the most important (e.g., Dale, 1996).

On a global scale, modern dinoflagellate species tend to occur in broad latitudinal bands, forming low-, middle- and high-latitude assemblages (Taylor, 1987). Similarly, Ordovician acritarchs should provide some information about the palaeolatitude of ancient continents, and also about the position of continental ridges. In addition, acritarchs may indicate the influence of longitudinal barriers to oceanic circulation. Despite the reservations of Eiserhardt (1992), ocean currents may also have exerted an influence on acritarch distribution.

4.2. *The palaeoecology of acritarchs: the temperature signal*

In Mesozoic, Cenozoic and Recent dinoflagellate assemblages, only a few taxa appear to be significant for biostratigraphy, (palaeo)biogeography or (palaeo)ecology. Dale (1996) proposed a model of dinoflagellate cyst ecology and discussed the geological implications. Among the different environmental signals observed in recent cyst assemblages, one of the most important is surface water temperature.

Dale (1996) noted that surface water temperatures in the oceans are determined by interactions of physical factors and that they have a direct impact on the constitution of dinocyst assemblages. He indicated that a temperature difference of only a few degrees over a period of time might reasonably be presumed to cause biological differentiation into biogeographical zones. One of the most pronounced temperature-related boundaries in the distribution of recent dinoflagellate cysts has been identified as a main cooler/warmer water boundary in the North Atlantic. On the western side of the Atlantic Ocean, this boundary occurs

on the coast between Cape Cod and Nova Scotia (at about 42–43°N) and between the English Channel and southwestern Norway on the eastern side (at about 50–65°N), depending on which species is used (e.g., Dale, 1983; Taylor, 1987). Dale (1996, fig. 1) showed the distribution of selected recent and living dinoflagellate cyst types compared with standard biogeographical zones (polar, subpolar, temperate, equatorial) for the Atlantic Ocean. According to this scheme, some recent taxa range from the polar region in the northern hemisphere to subpolar regions in the southern hemisphere. The living species that produce these resting cysts may thus be considered to be insensitive to climate. The distribution of other taxa, however, is limited to smaller geographical areas. While some cysts only occur in polar and subpolar areas in the northern Atlantic, others, for example, are only found in temperate to equatorial biogeographical zones. These taxa may therefore be useful for biogeographical studies.

Based on this model of recent dinoflagellate distribution, Li and Servais (2002) attempted to select some acritarch taxa that may be indicative of possibly temperature-related zones during the Early to Middle Ordovician. According to Li and Servais (2002), some taxa seem to be restricted by palaeolatitude, and therefore their distribution might be controlled by palaeotemperature. It appears that it is possible to distinguish cold-water (high-latitude) and warm-water (low-latitude) forms, as well as ubiquitous taxa that are found at all latitudes. Li and Servais (2002) proposed the following differentiation:

Cold-water forms: the Early to Middle Ordovician (Arenigian) taxa *Arbusculidium filamentosum*, *Coryphidium-Vavrdovella* and *Arkonia-Striatotheca* appear to be most common around the South Pole up to palaeolatitudes of 60°S, and more rarely up to 30°S. These taxa were possibly distributed only in polar and subpolar zones, and to a lesser extent in temperate zones, assuming that the Ordovician biogeographical zonal scheme was more or less comparable to that of today (see Wilde, 1991; Christiansen and Stouge, 1999). The galeate taxa (sensu Servais and Eiserhardt, 1995) and the diacromorph acritarchs are also more abundant in higher southern hemisphere lat-

itudes, but may occur more frequently than the previously listed taxa at localities around 45–20°S, i.e., these taxa are probably more likely to be recorded from the temperate zone of the southern hemisphere than the first group.

Warm-water forms: the genus *Lua* has so far only been recorded from low latitudes, and might therefore indicate an ‘equatorial zone’ in the Ordovician. In addition, the genera *Aryballomorpha* and *Athabascaella* have been recorded from low and intermediate latitudes, but never from high latitudes. Both these genera may indicate an equatorial to temperate zone in the Ordovician. Some taxa that were first considered to be of ‘warm-water’ affinity, because they were first recorded in lower latitudes, may range further to the south. *Rhopaliophora* was first described from Laurentia (Tappan and Loeblich, 1971) and Australia (Playford and Martin, 1984), and so its occurrence was believed to be limited to low latitudes. Subsequently it has been found in other localities from higher latitudes, for example from northern England (Cooper and Molyneux, 1990), Argentina (Rubinstein and Toro, 2001), and Iran (Ghavidel-Syooki, 2001). This taxon therefore has a wide distribution.

Ubiquitous taxa: many acritarch taxa are recorded from most palaeocontinents, i.e. in most latitudes. Although some may be biostratigraphically significant or indicate special palaeoecological conditions, these taxa appear to have little application to palaeobiogeographical studies. Among these taxa, Li and Servais (2002) listed the highly variable genera *Micrhystridium*, *Baltisphaeridium*, *Peteinosphaeridium* and *Polygonium* (= *Goniosphaeridium*).

Li and Servais (2002) noted that their model was a first attempt at selecting climate-related morphotypes in the Early Ordovician, and that future investigations would show if some of these taxa had restricted geographic distributions and thus really occupied different climatic zones.

4.3. The palaeoecology of acritarchs: the coastall oceanic signal

In his analysis of the ecology of recent dinoflagellates, Dale (1996) noted that one of the stron-

gest ecological boundaries for phytoplankton in the marine realm is the limit between nutrient-rich coastal/neritic waters and the relatively nutrient-poor oceanic waters. This boundary may be reflected by an inshore–offshore trend in dinoflagellate communities, which has been observed by many dinoflagellate workers (e.g., Head and Wrenn, 1992). Mudie (1992), for example, provided evidence for inshore–offshore trends in transects across the temperate, the subarctic and the arctic regions of the eastern Canadian margin (respectively south of Nova Scotia, from northeastern Newfoundland to the Labrador Sea, and from the Labrador Sea to the Saglek Bank). Together with seasonal parameters, latitudinal differences and surface currents, the inshore–offshore data set enabled the preparation of a map that depicted the modern geographical distribution of selected dinoflagellate cysts in the northwestern Atlantic Ocean (Mudie, 1992, fig. 10A–F).

Fossil communities were probably distributed in a similar way. Brinkhuis (1994), for example, provided a distribution pattern of the dinoflagellate cysts and other palynomorphs, including prasinophytes, spores, pollen and foraminiferal linings, for the continental shelf-slope transect of the Upper Eocene–Lower Oligocene of the Trento Shelf, Italy. While the prasinophytes are only common in nearshore environments, the dinoflagellates include taxa that are more common in the inner neritic, outer neritic or oceanic environments.

Similar models for Lower Palaeozoic transects remain rare and it is still difficult to attribute particular acritarch taxa to specific environments. The most cited work is that of Dorning (1981), who documented acritarch distribution in the Ludlovian (Silurian) shelf sea of South Wales and the Welsh Borderland. Dorning (1981) analysed the percentages of selected acritarch taxa in his transects and indicated the relative abundance of 17 Silurian genera. He concluded that acritarchs showed a low diversity nearshore and in deeper-water environments, and a much higher diversity over much of the shelf area. Wright and Meyers (1981) indicated a similar trend in the Middle Ordovician of Oklahoma, where acritarch diversity increases from nearshore to open marine

sites. Many authors came to similar conclusions and today it is widely accepted that assemblages from offshore shelf environments contain the most abundant and diverse acritarchs. Nearshore and deep-water acritarch assemblages are of lower diversity, dominated by sphaeromorphs with rare acanthomorphs and polygonomorphs.

The inshore–offshore model of acritarch distribution is likely to be simplistic, in the sense that acritarch distribution along an inshore–offshore gradient is likely to be affected by other parameters, including complex hydrodynamic factors that involve the distribution of water masses of varying physico-chemical type and sea-level fluctuations (e.g., [Jacobson, 1979](#); [Colbath, 1980](#)). Nevertheless, [Dorning's \(1981\)](#) model has been widely adopted to interpret acritarch distribution throughout the Palaeozoic. Various authors have used the inshore–offshore model of acritarch distribution for Ordovician acritarch assemblages to interpret conditions of sedimentation. [Hill and Molyneux \(1988\)](#), for example, interpreted Late Ordovician acritarch assemblages of Libya as indicating a relatively shallow, open marine shelf environment. [Wicander et al. \(1999\)](#) interpreted their Late Ordovician assemblage from northeastern Missouri, USA, as being deposited in a low-energy, offshore, normal marine environment, consistent with the available sedimentological data and the information from other fossil groups. [Vecoli \(2000\)](#) also considered the palaeo-environmental implications of acritarchs from the Cambrian–Ordovician of the northern Sahara Platform, and concluded that some stratigraphically important acritarch species, e.g., *Acanthodiacrodium angustum*, appeared to be facies-sensitive.

In some cases, it may be difficult to distinguish the palaeoecological signals of Ordovician acritarchs from palaeogeographical information. It seems that some species are sensitive to specific ecological conditions and to sedimentological facies, while others are sensitive to temperature, i.e. to latitudes. While the first group of species may have important palaeoecological implications, the second group may be significant for palaeobiogeography. As palaeoecological data were generally missing from the earliest acritarch investiga-

tions, many ‘palaeobiogeographical’ distributions found in the literature may thus simply reflect different sediment facies or different palaeoecological conditions. Further study, including reinvestigation of previously published material, is required to understand fully the spatial distribution of selected morphotypes at all scales. In addition, it is important to know the total assemblage and not only a selection of taxa.

4.4. *The palaeoecology of acritarchs: the salinity signal*

Not only does the distribution of modern cyst-forming dinoflagellates cover a wide temperature range, from arctic to tropical waters, but it also covers the full range of present-day salinities, from freshwater to hypersaline aquatic environments. The potential for using dinoflagellates as salinity indicators is poorly developed, although it appears that dinoflagellates follow a similar distribution to that of recent molluscs, i.e. with three main salinity regimes ([Wall et al., 1977](#)).

Recent experiments on dinoflagellates in culture show that the morphology and the size of the cysts may vary considerably for a single biological species under different salinity conditions. The greatest variation affects the number, distribution, length and structure of the processes. [Wall and Dale \(1973\)](#) interpreted the varying morphology of the resting cysts of *Lingulodinium machaerophorum* as being a result of low salinity in estuarine environments of the Black Sea. [Turon \(1984\)](#) came to a similar conclusion, correlating reduced process length with lower salinity. [Ellegaard \(2000\)](#) also demonstrated that a number of dinoflagellate species displayed shorter processes under conditions of reduced salinity. In addition, [Hallett and Lewis \(2001\)](#) provided evidence of a relationship between cell biochemistry, process length and salinity.

These results may have important repercussions for acritarchs. So far, the effects of changing salinity on Lower Palaeozoic acritarchs have not been documented systematically, although [Servais et al. \(2001\)](#) suggested that an increased length of processes on specimens of the galeate acritarch plexus (sensu [Servais and Eiserhardt, 1995](#)) in

the Cambrian–Ordovician boundary beds of the Algerian Sahara might be related to water depth and possibly to salinity.

The morphology of the peteinoid acritarchs (sensu Playford et al., 1995) is possibly also influenced by salinity. The classification of the peteinoids is based essentially on morphological criteria related to the processes, which for dinoflagellate cysts are known to vary with environmental changes such as changes in salinity or temperature (see Kokinos and Anderson, 1995; Ellegaard, 2000; Hallett and Lewis, 2001). Bagnoli and Ribecai (2001) described a continuous morphological change in the processes of *Liliosphaeridium* from two nearby sections in Sweden, which may indicate that a palaeoecological parameter (such as salinity or temperature) may have changed in the sequence analysed. From this, it is evident that detailed investigations of the variability of *Peteinosphaeridium* and related genera are needed to separate the influence of palaeoecology on morphology from that of palaeobiogeography.

4.5. The palaeoecology of acritarchs: the productivity signal

Several microfossil groups, including foraminifera, coccolithophorids and radiolarians, are known to indicate palaeoproductivity signals as well as ancient upwelling zones (e.g., Golonka et al., 1994). Few studies indicate so far that recent dinoflagellates may also reflect modern upwelling zones. Wall et al. (1977), for example, distinguished an upwelling signal from Peru and southwestern Africa on the basis of dinoflagellate cyst distribution. The identification of ancient upwelling zones based on acritarch distribution remains extremely poor to date. The data set is too meagre and much work remains to be done before tentative correlations can be made between Ordovician acritarch assemblages and putative upwelling zones such as those indicated by Golonka et al. (1994) on their palaeogeographical and palaeoclimatic maps. So far, only Raevskaya et al. (in press) have discussed the possible influence of upwelling zones on the distribution of acritarch assemblages. These authors noted that the differ-

ences between the Baltic and South Chinese assemblages might be related to different physiographic situations, with different nutrient conditions depending either on fluvial or upwelling input.

5. Ordovician acritarch distribution: the global scenario

Thorough compilations of Ordovician acritarch literature (Servais, 1998) and species (Servais and Stricanne, 2001) provide the basis for a reassessment of Ordovician acritarch biogeography. Some secure palaeobiogeographical interpretations are possible, while others should be considered as tentative because the available data set remains too sparse. The Ordovician acritarch data available for each palaeocontinent are summarised below.

5.1. Laurentia

Laurentia is well defined (e.g., by Scotese and McKerrow, 1990; Cocks, 2001) as a continental mass that was situated across the Equator throughout the Ordovician. Acritarch occurrences have been reported mainly from the Late Ordovician (Wicander in Servais et al., in press), whereas descriptions of Early Ordovician (Tremadocian and Arenig) Laurentian acritarchs are few. Martin (in Dean and Martin, 1982; Martin, 1984, 1992) described and illustrated Tremadocian and Arenig acritarch assemblages from Wilcox Pass, Alberta, Canada, and Barker and Miller (1989) mentioned similar assemblages from a borehole in the Tremadocian of Texas. Assemblages from both areas include taxa that so far have only been recorded from low latitudes, i.e., *Aryballomorpha*, *Athabascaella* and *Lua*.

Similarly, the Middle Ordovician acritarchs of Laurentia are not known in great detail. Loeblich and Tappan (1978 and references therein) described assemblages from the Middle Ordovician (approximately Llanvirn–Llandeilo) of Oklahoma, and Martin (1983) reported coeval material from the St. Lawrence Lowland in Ottawa, Montreal, and Québec City areas of Ontario and Québec, Canada. Nevertheless, the data are too sparse

to assess the palaeobiogeographical relationships of this material.

Late Ordovician acritarchs are by far the best studied from Laurentia. Investigations include localities from Indiana, Kansas, Kentucky, Ohio, Oklahoma, Anticosti Island, the St. Lawrence Lowland and Gaspé. The palaeobiogeographical significance of these assemblages was discussed in some detail by [Wicander et al. \(1999\)](#).

5.2. *Siberia and Kazakhstan*

Siberia was one of the major continental masses located at low latitudes during the Ordovician. It was separated from Baltica, but was possibly connected to Kazakhstan (e.g., [Scotese and McKerrrow, 1990](#); [Torsvik et al., 1995](#)). Very little has been published on Ordovician microphytoplankton from these areas (e.g., [Timofeev, 1963](#); [Sheshegova, 1971](#); [Sheshegova in Moskalenko, 1984](#)). In the latter paper, Sheshegova illustrated numerous Ordovician acritarchs from three sections in northwest Siberia, located in the Igaro–Norilsk Region and the Moierokan River basin. The oldest assemblages recorded were of latest Arenigian age, from the Kimaiskiy Substage, Kulumbe section, so there is no information on Tremadocian and Early to Middle Arenigian acritarchs to compare with data from other regions. Nevertheless, no peri-Gondwanan marker species were observed among the diverse acritarch assemblages recorded from higher parts of the Ordovician succession. Furthermore, the Upper Ordovician assemblages from the Moierokan section show a high degree of similarity to coeval assemblages from Laurentia.

5.3. *Baltica*

The palaeogeography and palaeobiogeography of Baltica have been investigated in some detail (e.g., [Cocks and Fortey, 1998](#)), and a large number of acritarchs papers covering all series from the Lower to the Upper Ordovician have been published, covering sections in Norway, Sweden, Finland, Poland, the Baltic States and northwest Russia ([Servais, 1998](#)).

Although Baltica is noted for its endemic bra-

chiopod and trilobite faunas ([Cocks, 2001](#)), the identification of endemic acritarch taxa remains problematical. Several attempts have been made to identify taxa that might be diagnostic of a Baltic province, and selected species of *Peteinosphaeridium* and related genera have been suggested for that role ([Tongiorgi and Di Milia, 1999](#)). However, as yet there is insufficient evidence to show that the intraspecific variability of the peteinoid acritarchs reflects palaeogeographical separation rather than local environmental effects (see also [Section 4](#)).

Rather than containing a unique set of taxa, Baltic assemblages on the whole seem to comprise intermediates between high- and low-latitude assemblages. So, although lowermost Ordovician (lower Tremadocian) assemblages contain predominantly cold-water taxa (diacrodians), upper Tremadocian and lowermost Arenig assemblages comprise a mixture of taxa from high- and low-latitude realms ([Volkova, 1997](#)), while middle and upper Arenigian assemblages include a high number of widespread species that are not considered to be typical elements of any province. Widespread acanthomorph acritarchs (*Baltisphaeridium*, *Goniosphaeridium*, *Peteinosphaeridium*, etc.) appear to be the dominant taxa in the latter assemblages, while the less common genera *Ampulula* (and *Stelomorpha*), *Pachysphaeridium*, *Rhopaliophora*, *Sacculidium* ([Ribecai et al., 2002](#)) and *Tongzia* are also frequently recorded. However, none of these taxa is limited to Baltica, and most of these acritarchs have also been recorded from coeval sediments from South China and the Precordillera of Argentina, where they are mainly associated with distinctive peri-Gondwanan taxa.

For these reasons, it seems reasonable to consider the acritarchs of Baltica as belonging to a temperate-water ‘province’, which was probably not restricted to the palaeocontinent of Baltica but had a wider distribution at about the same latitude. Perhaps because of oceanic water mass circulation, the ‘province’ might have extended to the margins of South China and Argentina, at least during the Arenig. Lack of information on Late Ordovician acritarchs from both Argentina and South China inhibits comparison with the Late Ordovician material from Baltica.

5.4. China: three plates

Ordovician China can be divided into three major plates, the Sino-Korean (North China) Plate, the Tarim Plate, and the Yangtze Platform, with several additional minor terranes (e.g., [Scotese and McKerrow, 1990](#); [Li, 1998](#)). During the Early Palaeozoic, these plates were separated from each other and were located in different latitudes. During most of the Ordovician, the North China Block was dominated by warm-water carbonates and was located near the Equator and/or in low latitudes in the northern hemisphere. The Yangtze Platform and Tarim Plate were located further south, with the Yangtze Platform occupying a position close to the Equator or in low latitudes in the southern hemisphere and Tarim being located further south. Palaeontological data indicate that the Yangtze Platform was probably located near Australia during most of the Palaeozoic ([Scotese and McKerrow, 1990](#)).

Few papers dealing with Ordovician acritarchs from North China have been published to date ([Li et al., 2001](#)). Most papers (e.g., [Martin and Yin, 1988](#)) focus on the acritarchs from the Cambrian–Ordovician boundary in Jinlin Province, northeast China. [Volkova \(1997\)](#) used the occurrence of *Aryballomorpha*, *Athabascaella* and *Lua* to assign the Early Ordovician of the North China Plate to her ‘warm-water province’, along with Laurentia.

Ordovician acritarchs from the Tarim Plate are also poorly known, and data from the Early Ordovician are lacking. Middle to Late Ordovician acritarchs have been described from the Tarim Basin of Xinjiang, North China, in a series of papers (for references see [Li et al., 2002b](#)). The assemblages show some similarities with assemblages from the type Caradoc of England and with coeval material from the mid-continent of North America ([Li, 1995](#)). However, it would be premature to draw definitive palaeobiogeographical conclusions at present.

Early to Middle Ordovician acritarchs from localities on the Yangtze Platform, South China, have been described in a number of papers (for references see [Li et al., 2002b](#)). [Li \(1987\)](#) included the Yangtze Platform in the ‘Mediterranean prov-

ince’ of [Vavrdová \(1974\)](#), before proposing a water mass circulation model that brought ‘cold-water’ acritarchs into the area ([Li, 1991](#)). [Li and Servais \(2002\)](#) argued that southern China should be included in the ‘peri-Gondwana province’, adding that this palaeogeographical area should not be considered as being necessarily restricted to a ‘cold-water’ setting (see also below).

Patterns of acritarch abundance and diversity within the Yangtze Platform probably result from environmental and facies changes, as documented in several papers. [Li et al. \(2002a\)](#), for example, indicated that acritarch diversity and abundance was probably related to an inshore–offshore gradient that could be observed from the western (nearshore) to the eastern (open marine) part of the Platform. [Brocke et al. \(2000\)](#) considered that it is too early to confirm the model of [Tongiorgi et al. \(1998\)](#), who indicated that ‘palaeobiogeographical affinities’ of the acritarch assemblages throughout the early to later Arenigian parts of the Dawan Formation could be attributed to a modification in the pattern of ocean currents or to sea-level fluctuations. [Raevskaya et al. \(in press\)](#) noted that different conditions of nutrient input might have affected the composition of the South Chinese assemblages.

5.5. Australia: northern Gondwana

The supercontinent of Gondwana, also referred to as Gondwanaland, occupied a major part of the southern hemisphere during the Ordovician. According to the most recent reconstructions (e.g., [Cocks, 2001](#); [Li and Powell, 2001](#)), Australia occupied a northerly position in Gondwana, at low latitudes, very probably close to the Equator. Southeast Australia faced Antarctica, an area from which Ordovician acritarchs are so far unknown. To the south, Gondwana included the present-day Indian subcontinent, from which acritarch data also remain absent.

Ordovician acritarch data from Australia are too sparse to assess their palaeobiogeographical affinities, with only a few assemblages described from sections of the ‘Arenig–Llanvirn’ ([Playford and Martin, 1984](#); [Playford and Wicander, 1988](#)). These authors did describe the total assemblages

from two areas, but in contrast to areas such as the Yangtze Platform, the complete picture of Australian Ordovician acritarch assemblages, with full descriptions of assemblages from a wider range of palaeoenvironments and all stratigraphical intervals, is not yet known. Playford et al. (1995) indicated that the species *Peteinosphaeridium? furcatum* was only known from Western Australia. Future studies are needed to clarify if the ‘endemic’ taxa of the ‘Australia province’ (Playford et al., 1995; Tongiorgi et al., 1995) are really limited to the Australian part of the Gondwana continent. Investigations of Arenig acritarchs of Laurentia and Siberia, that remain absent so far, could indicate the presence of ‘Australian’ acritarchs in coeval sequences from other areas at low latitudes.

5.6. South America: western Gondwana

Rubinstein and Toro (2001) reviewed papers published on South American acritarchs. Most concern the Early to Middle Ordovician of the Eastern Cordillera, northwestern Argentina, for which Playford et al. (1995) created the ‘South America’ subprovince. Other areas of South America have also been investigated, including Brazil (Padilha de Quadros, 1988), Colombia (Théry et al., 1986), and Bolivia (Gagnier et al., 1996).

Following an initial investigation by Bultynck and Martin (1982) on the Ordovician acritarchs of the Eastern Cordillera, Ottone et al. (1992, 1995) confirmed the presence of distinctive elements of the peri-Gondwanan province. Rubinstein and Toro (2001) noted that the acritarch assemblages of the Argentinian Precordillera appear to indicate a temperate palaeolatitudinal location, near the boundary of the cold-water peri-Gondwana realm, while graptolite affinities are with faunas from intermediate latitudes. To some extent, the assemblages can be compared with the southern Chinese material. They are clearly peri-Gondwanan because the taxa *Arbusculidium filamentosum*, *Coryphidium*, and *Striatotheca* are present. However, elements from lower latitudes, indicating possibly warmer water, such as *Rhopalio-phora*, may also be found in these areas. Future

investigations should aim to reach a better understanding between assemblages from Gondwanan Argentina and the Precordillera microterranes, which is thought to have rifted away from Laurentia in the Early Ordovician (see Benedetto, 1998).

5.7. Avalonia, ‘Armorica’, ‘Perunica’ and southern peri-Gondwana

Most Ordovician acritarch studies have been based on material from western and southern Europe, North Africa and the Middle East. More than 50 papers concern the British Isles (which apart from Scotland and northern Ireland comprised part of Avalonia), more than 40 articles deal with the French Ordovician, followed by more than 30 articles on Bohemia (the microcontinent ‘Perunica’), and more than 20 articles of Belgium and Germany respectively. The investigations of French oil companies since the late 1950s in North Africa mean that this latter area is also fairly well investigated with numerous papers from Morocco, Algeria, Tunisia, and Lybia. Additional data have been published from Egypt, Jordan, Saudi Arabia, Iran and Pakistan (Servais, 1998).

All these areas yield typical peri-Gondwanan assemblages throughout most of the Arenig and have been included in the ‘Mediterranean province’ since the early 1970s. Nevertheless, local differences in the composition of the assemblages are common. Such differences probably relate to different local environmental conditions, and it appears difficult to separate the Arenig assemblages of the different microterranes in order to distinguish between assemblages from Avalonia, ‘Perunica’ or ‘Armorica’.

6. New plots

6.1. The ‘Tremadocian–Arenig’ boundary

Acritarchs from the Tremadocian–Arenig boundary of peri-Gondwana comprise the distinctive *messaoudensis–trifidum* assemblage, which has a wide distribution (Vanguetaine and Servais,

2002) and enables biostratigraphical correlation between localities in England, Wales, southern Ireland, Belgium, Germany, Spain, Bohemia and Turkey (Martin, 1996; Servais and Mette, 2000). Some of the elements of this distinctive assemblage are also found in southern Baltica (Raevskaya, 1999), China (Brocke, 1997) and Argentina (Rubinstein et al., 1999). Plotting the *messaoudensis-trifidum* assemblage on a recent palaeogeographical reconstruction for the late Tremadocian–early Arenig (Fig. 1) indicates that the assemblage is geographically restricted to the border of peri-Gondwana in high latitudes. Most localities bearing the assemblage are located around the South Pole (> 60°S), but the distribution also extends slightly northwestwards on the peri-Gondwanan margin to latitudes between 60 and 30°S.

Coeval low-latitude assemblages contain *Aryballomorpha*, *Athabascaella* and *Lua* (Volkova, 1997). Li and Servais (2002) plotted the distribution of these genera on the reconstruction by Li and Powell (2001), and showed that they were

restricted to areas of Laurentia (Texas, USA, and Alberta, Canada), North and South China (not visible on the reconstruction of Fig. 1) and Baltica. According to the reconstruction presented in Fig. 1, all of these localities were located at low latitudes, but also extended to higher latitudes up to around 60°S.

6.2. The ‘Arenigian’

Localities bearing the distinctive elements of the Arenig peri-Gondwanan assemblage, namely *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca*, are plotted (Fig. 2) on a palaeogeographical reconstruction based on the recently published map of Cocks (2001). The peri-Gondwanan acritarch assemblage on this map shows almost exactly the same distribution as that of the Calymenacean–Dalmanitacean trilobite fauna of Cocks (2001). Both the trilobite fauna and the peri-Gondwanan acritarchs are distributed around the southern margin of the Gondwana continent. The geographical range of the peri-

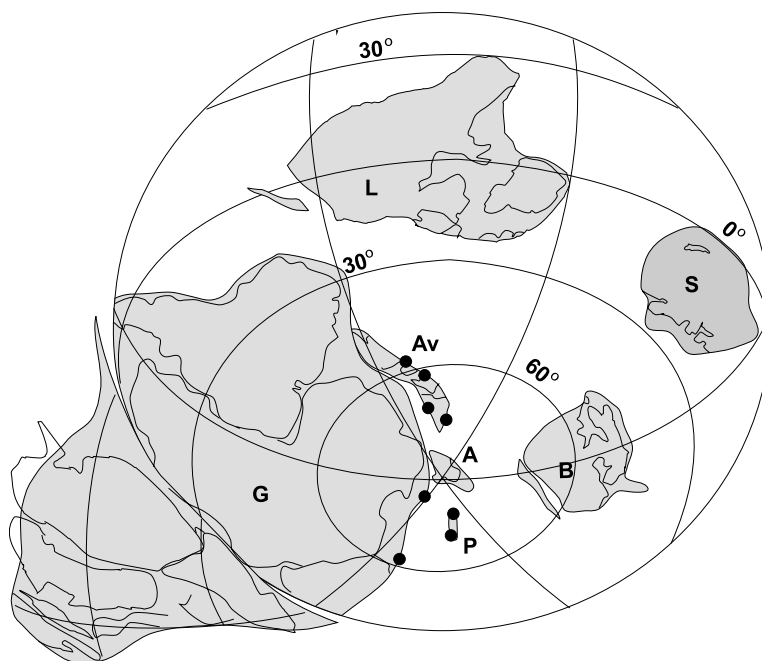


Fig. 1. Tilted Early Ordovician (Tremadocian–Arenig) palaeogeographical reconstruction of Popov (in Bassett et al., in press) illustrating the distribution of the *messaoudensis-trifidum* acritarch assemblage (black dots). Microfloral data available from Van-guestaine and Servais (in press). L, Laurentia; S, Siberia; B, Baltica; G, Gondwana; Av, Avalonia; A, Armorica; P, Perunica.

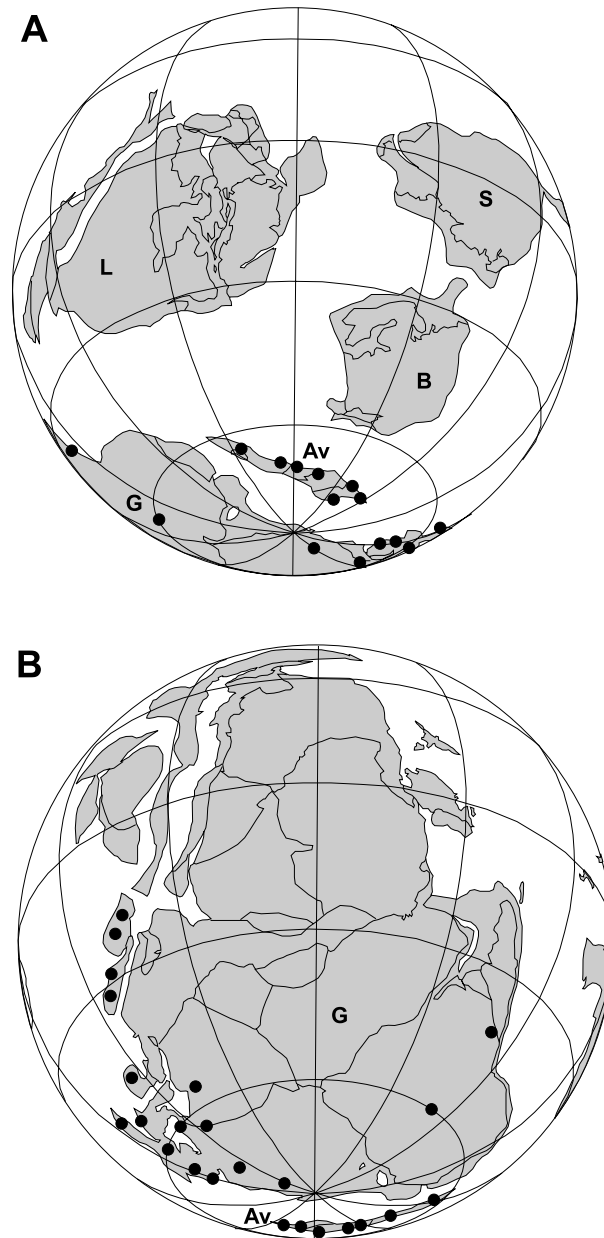


Fig. 2. Slightly tilted Early to Middle Ordovician (Arenig) palaeogeographical reconstruction of Cocks (2001) illustrating the distribution of the peri-Gondwana acritarch assemblage defined on the occurrence of the taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* (black dots). Microfloral data available from Servais (1997), Fatka and Brocke (1999) and Li and Servais (2002). L, Laurentia; S, Siberia; B, Baltica; G, Gondwana; Av, Avalonia.

Gondwanan acritarch assemblage starts in eastern Gondwana (Argentina, Brazil), extends to Avalonia and areas located around the South Pole, including North Africa and southern Europe (i.e.

on the border of Gondwana and the related terranes of Iberia, Armorica, Perunica), and then to Turkey, Saudi Arabia, Jordan, Iran and Pakistan. It reaches intermediate latitudes in southern Chi-

na. Thus, the distinctive peri-Gondwanan elements, *A. filamentosum*, *Coryphidium* and *Striatotheca*, cross lines of latitude to range from high southern latitudes to lower latitudes.

The Arenig reconstruction in Fig. 2 also shows the palaeogeographical distribution of the continents of Baltica, at intermediate latitudes, and Laurentia and Siberia continents in equatorial positions. As noted above, the distinctive elements of peri-Gondwana have never been recorded from these areas.

6.3. The ‘Arenigian–Llanvirnian’ boundary

The reconstruction in Fig. 3 illustrates the position of the Ordovician palaeocontinents at the Arenig–Llanvirn boundary. The Avalonian microcontinent was located in the Tornquist’s Sea between Gondwana and Baltica, while the terranes of Armorica and Perunica were considered to be still on the periphery of Gondwana. The acritarch genus *Frankea* first appeared in the late Arenig and had its widest distribution during the Llanvirn (Servais, 1993). When plotted (Fig. 3), the occurrence of this genus is limited to localities

on the peri-Gondwanan border and to terranes that are considered to have rifted away from Gondwana, i.e., Avalonia, ‘Armorica’ and ‘Perunica’. Its distribution is restricted to localities at high and intermediate latitudes ($> 30^{\circ}\text{S}$), but the genus has never been reported from Baltica, although this plate was located at similar latitudes (between 30 and 60°S) and many sections from this continent have been investigated in great detail. So far the genus has not been recorded from southern China. The distribution of *Frankea* depicted here (Fig. 3) extends that shown by Colbath (1990), in which known occurrences of *Frankea* were restricted to areas at approximately 60°S palaeolatitude or higher.

7. Discussion

7.1. The evolution of acritarch palaeobiogeography through the Palaeozoic

Although this paper is focused on Ordovician acritarch palaeobiogeography, it is useful to compare the distributional models presented for dif-

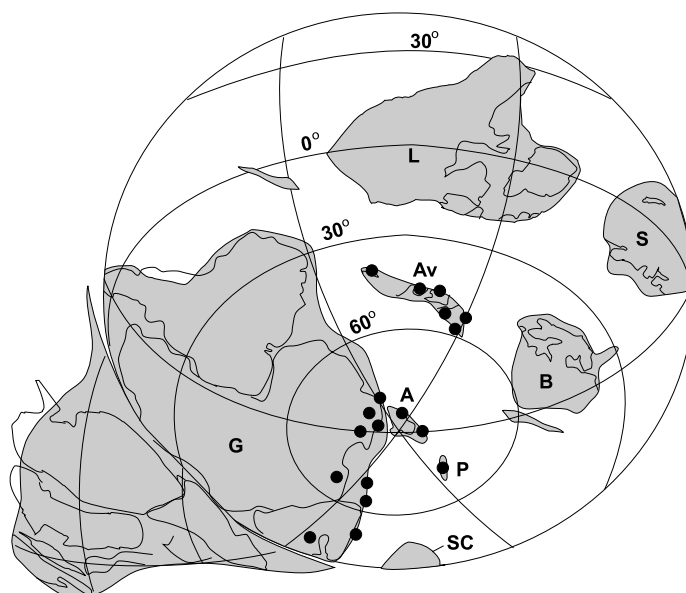


Fig. 3. Tilted Middle Ordovician (Llanvirn) palaeogeographical reconstruction of Popov (unpublished) illustrating the distribution of the acritarch genus *Frankea* (black dots). Microfloral data available from Servais (1993) and Servais (unpublished). L, Laurentia; S, Siberia; B, Baltica; G, Gondwana; Av, Avalonia; A, Armorica; P, Perunica; SC, South China.

ferent times in the Ordovician with those in other Palaeozoic systems.

Palaeobiogeographical models for Cambrian acritarchs are almost absent. Nevertheless, [Modczydlowska \(1998\)](#) indicated that taxonomically comparable acritarch assemblages of Cambrian age are found in shelf basins of the Gondwanan margin ranging from low latitudes in the northern hemisphere (Australia, South China) to southern European and North African areas, located at intermediate to high latitudes. The same assemblages were also recorded from the southern margin of Siberia and the northern margin of Baltica, facing each other, as well as around the Laurentian continental margin. [Vanguetaine \(1991\)](#) plotted localities from which Early and Middle Cambrian have been described on a map that was based on the reconstruction of [Erdtmann \(1982\)](#). [Vanguetaine \(1991\)](#) noted that all these localities provided assemblages that show similarities with the material he described from Belgium. Hence there is no pronounced ‘provincialism’ reported for Cambrian assemblages. [Volkova \(1995, 1997\)](#) considered that ‘provincialism’ only arose at the Cambrian–Ordovician boundary.

As discussed here, the Arenig–Llanvirn was a time when differences between acritarch assemblages from different geographical areas were most pronounced. The same distinction has also been observed for many other fossil groups. This pronounced provincialism was probably due to a maximum separation of the continents at that time, as shown in the most recent palaeogeographical reconstructions ([Cocks, 2001](#); [Li and Powell, 2001](#); [Scotese et al., 2001](#)). As noted above, the data set remains too poor to comment definitively on palaeobiographical differences in the Late Ordovician (see [Wicander et al., 1999](#)).

Later in the Palaeozoic, distinct, geographically restricted assemblages have been reported from both the Silurian and the Devonian. [Le Hérisse and Gourvenec \(1995\)](#) reviewed the data published on the Silurian, and argued that the acritarch *Dactylofusa maranhensis* was limited to intermediate and high latitudes on the Gondwanan border during the late Llandovery to Wenlock, whereas the *Estiastra–Hoegklintia–Pulvinosphaeridium* association was restricted to low latitudes,

ranging from about 30°S to about 20°N. Differentiation of palaeobiogeographical areas in the mid-Silurian was thus similar to that in the Arenigian. On the other hand, [Le Hérisse and Gourvenec \(1995\)](#) noted that the distribution of *Deunffia* and *Domasia*, both considered to be ‘pelagic’ species, was apparently controlled by parameters that were not directly related to palaeolatitude.

[Le Hérisse et al. \(1997\)](#) plotted Devonian assemblages on recent palaeogeographical reconstructions, and concluded that a geographical restriction of several acritarch genera and species could be observed for the Early Devonian. In particular, they reported pronounced differences between North Gondwanan and eastern North American microfloras. Later in the Devonian, the acritarch microfloras became more similar, indicating that the provinciality probably decreased ([Le Hérisse et al., 1997, 2000](#)).

7.2. Comparison with the Ordovician distribution of the chitinozoans

Like acritarchs, the chitinozoans are considered to be a group of planktonic organic-walled microfossils. [Achab \(1988\)](#) summarised palaeobiogeographical information, and indicated that Ordovician chitinozoans from Québec, Canada, belonged to an assemblage that was restricted to low palaeolatitudes. She also plotted the distribution of selected chitinozoan species on palaeogeographical reconstructions for the Early, Middle and Late Ordovician, and showed that some taxa were limited to a given palaeolatitude while others were more widely distributed across latitudes. In a subsequent paper, [Achab \(1991\)](#) noted that a biogeographical differentiation could be made between high-latitude chitinozoan assemblages, present in North Africa, southwest Europe, Great Britain and Bohemia, and low-latitude assemblages recovered from eastern Canada, Australia, Spitsbergen and the United States. According to [Achab \(1991\)](#) the Baltic region provided faunas that appear to have occupied an intermediate position. [Paris \(1991\)](#) presented a similar model and also discussed the possible influence of water mass currents. The geographical distribution pattern of

Ordovician chitinozoans, also discussed by Oulebsir and Paris (1995), thus parallels the distribution of Ordovician acritarchs.

Achab et al. (1992) and Paris et al. (1995) noted that a similar distribution pattern was also observed for the Silurian. While some chitinozoan taxa were cosmopolitan, and thus of limited palaeogeographical importance, other taxa were limited to the Gondwanan border, and others to the Baltica continent, on either side of the Rheic Ocean which separated these two continents.

8. Conclusions

Investigation of Ordovician acritarch biogeography is still at an early stage, compared to study of the biogeography of other Ordovician fossil groups. In particular, the present review shows gaps in knowledge for the Ordovician of Laurentia and Australia, and indicates that there is almost no information on Ordovician acritarchs from Siberia and Kazakhstan. Study of acritarch assemblages from these areas is needed in order to document and understand the palaeobiogeographical distribution patterns of Ordovician acritarchs.

Nevertheless, a number of preliminary conclusions can be drawn. There was apparently little biogeographical differentiation of acritarch assemblages during the Cambrian, but the situation changed at about the Cambrian–Ordovician boundary. The maximum separation of the continents during the Arenig, reflected by a pronounced ‘provincialism’ of most Ordovician fossil groups, was probably also responsible for the development of geographically distinct acritarch assemblages. A peri-Gondwana acritarch assemblage with the easily recognisable acritarch taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* is present on the southern margin of Gondwana, and its distribution corresponds almost exactly with that of the Calymenacean–Dalmanitacean trilobite fauna (Cocks, 2001). A warm-water assemblage with the acritarch genera *Aryballomorpha*, *Athabascaella* and *Lua*, but without diacrodians seems to be limited to localities at low to intermediate latitudes, including Laurentia,

North China and Baltica. The data set remains too poor to make statements about the palaeobiogeography of the marine organic-walled microphytoplankton in the late Middle Ordovician and the Late Ordovician.

The biogeographical distribution of Ordovician acritarchs appears similar to that of the resting cysts of modern dinoflagellates, controlled by latitude but also following the continental margins.

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