

The importance of plankton and nekton distributions in Ordovician palaeogeographical reconstructions

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Key-words. – Acritarchs, Chitinozoans, Graptolites, Trilobites, Radiolarians, Vertebrates, Ordovician, Palaeobiogeography.

Abstract. – Trilobites and brachiopods are the two main fossil groups that allowed construction of the first palaeogeographical maps for the early Palaeozoic. Together with the bivalves and ostracodes, the benthic elements of these fossil groups have proved to be of great palaeobiogeographical importance. For this reason, these groups are usually considered to be ‘better’ fossils for inferring Ordovician palaeogeography. The present study indicates that planktic and nektic fossil groups should not be neglected in such palaeobiogeographical studies. The plotting on a palaeogeographical reconstruction for the Arenig (Lower Ordovician, – 480 Ma) of some planktic (acritarchs, chitinozoans) and nektic (vertebrates, pelagic trilobites) fossil groups indicates that their distribution appears in part surprisingly similar to that of the benthic trilobite faunas that are considered to display the greatest provincialism. For example, the distribution of the ‘peri-Gondwanan’ acritarch province including *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca*, and the distribution of the *Eremochitina brevis* chitinozoan assemblage are almost identical to the palaeogeographical distribution of the Calymenacean-Dalmanitacean trilobite fauna. A review of the different planktic and nektic fossil groups also indicates that it is very important to carefully select ‘good’ palaeogeographical indicators, in most cases from a large number of taxa. It appears that almost all fossil groups include some ‘good’ palaeobiogeographical ‘markers’. Therefore it is important to search for ‘better’ taxa within each fossil group, instead of looking only for the ‘better’ fossil groups as a whole.

L'importance de la distribution du plancton et du necton pour les reconstitutions paléogéographiques de l'Ordovicien

Mots-clés. – Acritarches, Chitinozoaires, Graptolites, Trilobites, Radiolaires, Vertébrés, Ordovicien, Paléobiogéographie.

Résumé. – Les trilobites et les brachiopodes sont les deux groupes fossiles qui ont permis de réaliser les premières reconstitutions paléogéographiques du Paléozoïque inférieur. Avec les bivalves et les ostracodes, les éléments benthiques de ces groupes fossiles se sont avérés être d'une très grande utilité paléobiogéographique. Pour cette raison, ces organismes sont habituellement considérés comme les « meilleurs » groupes pour la paléogéographie de l'Ordovicien. Notre étude montre que les groupes fossiles planctoniques et nectoniques ne devraient pas être négligés pour les analyses paléobiogéographiques. Le positionnement sur une reconstitution paléogéographique de l'Arenigien (Ordovicien inférieur, – 480 Ma) de quelques groupes fossiles planctoniques (acritarches, chitinozoaires) et nectoniques (vertébrés, trilobites pélagiques) indique que la distribution de ces groupes est en partie très similaire à celle des faunes à trilobites benthiques qui sont considérées comme montrant le provincialisme le plus marqué. Par exemple, la distribution de la province « péri-gondwanienne » à acritarches caractérisée par la présence de *Arbusculidium filamentosum*, *Coryphidium* et *Striatotheca*, et la distribution de l'assemblage à chitinozoaires à *Eremochitina brevis* sont presque identiques à la distribution paléogéographique de la faune à trilobites à Calyménacées-Dalmanitacées.

La révision des différents groupes planctoniques et nectoniques indique également qu'il est très important de choisir attentivement les « bons » marqueurs paléogéographiques, et ceci dans la plupart des cas parmi un très grand nombre de taxons. Il apparaît que la majeure partie des groupes fossiles incluent quelques « bons marqueurs » paléogéographiques. Dès lors, il semble plus judicieux de chercher les « meilleurs » taxons à l'intérieur de chaque groupe fossile au lieu de se concentrer uniquement sur le « meilleur » groupe fossile.

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INTRODUCTION

Although the majority of Precambrian palaeogeographical reconstructions remain problematical and debated, Early Palaeozoic palaeogeography is better established, especially for the Ordovician Period, when continental separation was at its maximum and when four major continents were present: Laurentia, Baltica, Siberia and the supercontinent Gondwana.

Numerous results from stratigraphical and sedimentological [e.g., Erdtmann, 2000; Robardet, 2002], structural and tectonic [e.g., Meissner *et al.*, 1994; Dalziel, 1997], palaeoceanographical and palaeoclimatological [e.g., Wilde, 1991; Christiansen and Stouge, 1999], palaeomagnetic [e.g., MacNiocail *et al.*, 1997; Torsvik, 1998; Lewandowski, 2003] and palaeontological [e.g., Webby *et al.*, 2000; Fortey and Cocks, 2003] studies have been compiled in the last decades. The combination and integration of the evidence from the different disciplines allow a fairly clear understanding of Ordovician palaeogeography [e.g., Scotese and McKerron, 1990, 1991; Harper *et al.*, 1996; Scotese *et al.*, 2001; Cocks and Torsvik, 2002].

Palaeontological evidence played an essential role in Ordovician palaeogeographical reconstructions. Spjeldnæs [e.g., 1961, 1967] was one of the first to understand the importance of climatic zones and to recognize faunal migrations in the Ordovician. McKerron and Cocks [1976] subsequently deciphered a progressive faunal migration across the Iapetus Ocean.

In their landmark paper on faunal evidence for oceanic separations in the Palaeozoic of Britain, Cocks and Fortey [1982] listed the criteria for the recognition of past continental distributions from fossil evidence and proposed a palaeogeographical position of the continents surrounding the Iapetus Ocean. Moreover, Cocks and Fortey [1982] indicated that it is necessary to compare inner shelf faunas from equivalent habitats to get precise palaeogeographical indications, while planktic or epipelagic forms were considered to be primarily related to palaeolatitude.

Also using the Early Ordovician of the North Atlantic region as an example, Fortey and Mellish [1992] asked the question "Are some fossils better than others for inferring palaeogeography?", concluding that planktic fossils (graptolites, acritarchs) are not very useful, because they do not 'see' a separation between Gondwana and Baltica, which is strongly supported by evidence from other groups, in particular, by trilobites and ostracodes. Fortey and Mellish's [1992] publication has resulted in a debate on the relative palaeogeographical significance of different fossil groups. Servais and Fatka [1997], for example, provided evidence for the recognition of oceanic separation between Avalonia and Baltica on the basis of the palaeobiogeographical distribution pattern of the organic-walled microphytoplankton (acritarchs) during the Early-Mid Ordovician, while at the same time, Cocks *et al.* [1997] considered that these results were not conclusive, because of the absence of benthic indicators. Subsequently, following a workshop at a palaeogeographical congress at Dresden, Germany, in 1998, Cocks and Verniers [2000] discussed the applicability of planktic and nektic fossils to palaeogeographical reconstructions, by concluding that the planktic groups are distributed according to palaeoclimatic bands, and that their palaeogeographical relevance is limited in the

absence of any recorded benthos. On the other hand, new observations on the chitinozoans provided evidence that this group of planktic microfossils also clearly 'sees' the separation between Gondwana and Baltica [e.g., Samuelsson *et al.*, 2001], as do the acritarchs [Servais and Fatka, 1997]. Fortey and Cocks [2003] noted that the taxonomy of acritarchs has been much refined and key species of the latter have been postulated as discriminating between palaeocontinents, suggesting that Fortey and Mellish's [1992] analysis should now be re-run with more modern taxonomy. Moreover, Fortey and Cocks [2003] stressed the importance of the congruence of different palaeogeographical data.

In the present paper, we attempt to revisit the question of whether some fossil groups are better than others for inferring palaeogeography. Are benthic fossils better palaeogeographical indicators, planktic fossil groups less relevant, and nektic fossils almost useless for palaeobiogeography in the Lower Palaeozoic? Following Cocks and Fortey [1982], Fortey and Mellish [1992] and Fortey and Cocks [1992], we use the Early-Mid Ordovician ('Arenig') as an example, in order to compare the different fossil groups by plotting them on the same Early Ordovician palaeogeographical reconstruction.

ORDOVICIAN PALAEOGEOGRAPHY AND PALAEOBIOGEOGRAPHY

Initial Ordovician palaeogeographical reconstructions, including the three major continents Laurentia, Baltica and Gondwana were originally based on the recognition of distinct faunal provinces characterized by endemic faunal assemblages, especially trilobites and brachiopods [Spjeldnæs, 1961; Wilson, 1966; Cocks and Fortey, 1982]. These two fossil groups are among the best known in the Lower Palaeozoic and they have been studied in great detail during more than two centuries. Subsequently, palaeomagnetic data corroborated the first reconstructions that were purely based on palaeontological evidence [e.g., Van der Voo, 1988].

Recent palaeogeographical reconstructions that integrate and combine the results from the different disciplines appear generally consistent, at least at a global scale [e.g., Scotese and McKerron, 1990, 1991; Scotese *et al.*, 2001; Li, 1998; Li and Powell, 2001; Cocks and Torsvik, 2002]. In these recent reconstructions, the main continents are Laurentia (essentially North America) and Siberia, both found at equatorial positions, Baltica, located at intermediate latitudes in the southern hemisphere, and the supercontinent Gondwana, that included South America, Africa, Antarctica, Australia, India and other marginal terranes. This large continent extended from the South Pole to the Equator, and it remained separated from Laurentia throughout the Ordovician. Dalla-Salla *et al.* [1992], Dalziel *et al.* [1994] and Dalziel [1997] proposed an alternative model, based on a collision scenario between Laurentia and Gondwana during the Mid Ordovician, but palaeontological data are at variance with this collision hypothesis. It appears that both Laurentia and Gondwana remained separate throughout the Ordovician, while a smaller terrane, which included the Precordillera of Argentina, rifted from Laurentia in the Early Ordovician to drift across the Iapetus Ocean docking with Gondwanan Argentina at some time prior to the Late

Silurian [e.g., Benedetto, 1998]. The most recent Ordovician palaeogeographical maps [e.g., Scotese *et al.*, 2001; Cocks and Torsvik, 2002; Li and Powell, 2001], therefore reconstruct Gondwanan Argentina facing the margin of Laurentia.

In a recent paper, Fortey and Cocks [2003] summarized the palaeontological evidence for global Ordovician-Silurian continental reconstructions. These authors concluded that data from fossils of shelf benthic groups, and in particular trilobites, brachiopods, bivalves and ostracodes, have provided evidence for the position and configuration of continents that has 'stood the test of time', as geophysical and palaeomagnetic evidence have confirmed in numerous cases the initial hypotheses provided by palaeontological data. Fortey and Cocks [2003] illustrated their review paper with some previously published maps, among them the palaeogeographical reconstruction of the Early Ordovician (Arenig, 480 Ma) of Cocks [2001, Fig. 2] and Cocks and Torsvik [2002, Fig. 1]. The latter reconstruction is also used in the present paper for indication of the different planktic and nektic groups in comparison with those based on the distribution of some benthic taxa selected by Cocks and Fortey [1990].

'BETTER' FOSSILS FOR INFERRING PALAEOGEOGRAPHY

Fortey and Cocks [2003] indicated that palaeobiogeographical evidence provided from different fossil groups has often been the subject of contention, because the specialists in different fossil groups do not appreciate the peculiarities of the 'signal' of their preferred organisms. In many cases, the specialists believe that 'their' organisms are the most significant. Fortey and Cocks [2003] listed a series of comparative studies of the 'effectiveness' of one Lower Palaeozoic taxonomic group as opposed to another. The examples cited by Fortey and Cocks [2003] emphasize the advantages of the two fossil groups investigated by the two authors, i.e., the trilobites and the brachiopods. Other examples would probably provide a different picture on the relative importance of the different fossil groups.

The Avalonia-Baltica oceanic separation

A highly disputed question during the two last decades has been the importance of the oceanic separation between Gondwana and Baltica. As neither brachiopod nor trilobite Baltic endemics have been found in the Early Ordovician of Avalonia, the Tornquist's Ocean was relatively wide in the model of Cocks and Fortey [1982]. Subsequently, Paris and Robardet [1990] minimized the Avalonia-Baltica separation, because they observed similarities in graptolite and chitinozoan faunas from both sides of the ocean. Today, it is widely accepted that Avalonia and Baltica were clearly separated during the Early Ordovician, and the palaeogeographical reconstruction of Paris and Robardet [1990, Fig. 2], placing the southern part of the British Isles as a southwestern continuation of Baltica, cannot be sustained.

Fortey and Mellish [1992] used this discussion to develop arguments in favour of a greater palaeobiogeographical importance of the benthic groups. The planktic organisms were declared of low importance, as they may

not 'recognize' a barrier of significance to benthic organisms.

The main problem with the provocative statement of Fortey and Mellish [1992], that resulted in a series of publications in the following years, probably lies in the poor knowledge and understanding (that we partly still have today) of the distribution of some of the planktic fossil groups. Graptolites, acritarchs, chitinozoans and radiolarians are completely different biological groups with different life modes and distribution patterns. These groups cannot simply be put together as 'planktic organisms with low palaeobiogeographical significance'. While numerous data exist concerning the graptolites at a world-wide scale for all stratigraphical intervals in the Ordovician, investigations on Ordovician palynomorphs (acritarchs and chitinozoans) are not yet as comprehensive. Our knowledge of Ordovician radiolarians is even poorer, as studies on this group, one of the principal plankton groups in modern oceans, remain very sporadic for the Lower Palaeozoic.

Concerning the graptolites, it appears that this major plankton group does not clearly 'see' the Avalonia-Baltica separation in the Early-Mid Ordovician. Most graptolite taxa show a cosmopolitan distribution. On both sides of the Tornquist Sea, didymograptids were dominant with high diversity and abundance both on Avalonia and on the southern margin of Baltica [e.g., Maletz, 1998]. Although a differentiated palaeogeographical distribution scheme can be observed at a global scale (see below), the graptolites do not allow a separation to be distinguished between Avalonia and Baltica.

Regarding the palynomorphs, clear global distribution models indicating endemic taxa, did not exist in the early 1990s, neither for the acritarchs nor the chitinozoans. Fortey and Mellish [1992] therefore probably integrated these two planktic groups rather uncritically in their statistical analyses. It has subsequently been proved that at least the acritarchs clearly see the Avalonia/Baltica separation during the Early-Mid Ordovician. None of the typical peri-Gondwanan acritarch taxa (among them *Arbusculidium filamentosum*, *Aureotesta*, *Coryphidium*, *Dicrodiacrodium*, *Frankea*, *Striatotheca*) is present in Baltica, and the distinction between the Baltic and Gondwanan acritarch assemblages is therefore straightforward [Servais and Fatka, 1997; Servais *et al.*, 2003].

Recent investigations of the chitinozoans indicate a similar distribution of this palynomorph group during the same time interval. Although numerous genera are in common during the Arenig, some Ordovician chitinozoan taxa, that are widespread over Gondwana, have never been found on Baltica, among them *Eremochitina brevis*, *Sagenachitina oblonga* or *Siphonochitina formosa* [Samuelsson *et al.*, 2001]. These endemic elements of Gondwana thus clearly allow a distinction from Baltic assemblages.

New cluster analysis and parsimony methods of biogeographical analysis, as used by Fortey and Mellish [1992] and Lees *et al.* [2002], but integrating the new data summarized above, would provide completely different results. It appears evident that it would be necessary that the databases, that are used for establishing biogeographical similarities, are critically evaluated by specialists of each fossil group.

It is important to note that among the numerous taxa of the planktic organisms, many appear to have at least a pandemic, if not a cosmopolitan distribution. Only a limited number of taxa seems to be of palaeogeographical significance. It is thus extremely important to fully understand the distribution mechanisms of the investigated organisms. This is particularly valid for the acritarchs. For example, as indicated by Li and Servais [2002, Fig. 2], many acritarch taxa (among them the genera *Micrhystridium*, *Baltisphaeridium*, *Peteinosphaeridium* and *Polygonium*) have a cosmopolitan distribution, and they are present all over Gondwana, Baltica, Siberia and Laurentia. If such taxa are put in a set to be used for statistical biogeographical analyses, no meaningful result can be expected.

It is beyond the scope of this paper to compile complete datasets of all fossil groups to compare their palaeogeographical significance with statistical methods. In the present paper, we simply plot the distribution of some planktic and nektonic organisms on one of the most recent palaeogeographical reconstructions. In addition, the distribution of other organisms is briefly discussed below.

THE PALAEOGEOGRAPHICAL DISTRIBUTION OF THE PLANKTON AND NEKTON IN ORDOVICIAN SEAS

In order to understand the palaeobiogeographical distribution of the different planktic fossil groups, we propose to compare their distribution with that indicated by the groups considered by Fortey and Cocks [2003] to be the 'good' palaeobiogeographical indicators.

We use the Arenig (late Early and early Mid Ordovician) as an example, continuing the discussion developed by Fortey and Mellish [1992]. Among the different palaeogeographical reconstructions for this time interval, we chose the map published by Cocks [2001, Figs. 1-2] and also Fortey and Cocks [2003, Fig. 8], that was based on the continental distributions from the C.R. Scotese PaleoGIS for

Arcview Package. These maps were used by Cocks [2001] and Fortey and Cocks [2003] to include the plots of some palaeogeographically significant trilobite faunas, that were adopted from Cocks and Fortey [1990]. It is particularly interesting to compare the plots of the different planktic groups with the distribution of these trilobite assemblages illustrated in figure 1.

The organic-walled microphytoplankton (acritarchs) [TS]

It is important to emphasize that the acritarchs are an artificial group of organic-walled microfossils of unknown biological affinity [Evitt, 1963; Servais *et al.*, 1997]. Although the exact biological affinity of the individual taxa is not established, it is widely accepted that the majority of the Palaeozoic acritarchs are most probably the equivalent of the organic-walled cysts of present day living dinoflagellates.

The distribution of modern dinoflagellate cysts is clearly influenced by a series of parameters, of which the salinity (inshore-offshore) and the temperature (latitudinal) gradient are among the most important [Dale, 1996]. As organic-walled dinoflagellate cysts can reasonably be assumed to be the modern equivalent of Palaeozoic acritarchs, it would be logical to expect that different acritarch assemblages were distributed in different water depths (inshore-offshore trends) and in different latitudinal belts during the Palaeozoic. In addition, biogeographical maps presenting the distribution of acritarch-dinoflagellate cysts in modern oceans clearly display a provincial distribution of selected assemblages. These provinces not only follow latitudinal belts, but also the continental margins [e.g., Mudie and Harland, 1996], and it would be reasonable to expect different acritarch 'provinces' to be seen on Early Palaeozoic palaeogeographical reconstructions.

Such 'provinces' have indeed been recognized. Initial palaeobiogeographical models for Early Palaeozoic acritarchs were presented by Cramer [1968] and Vavrdová

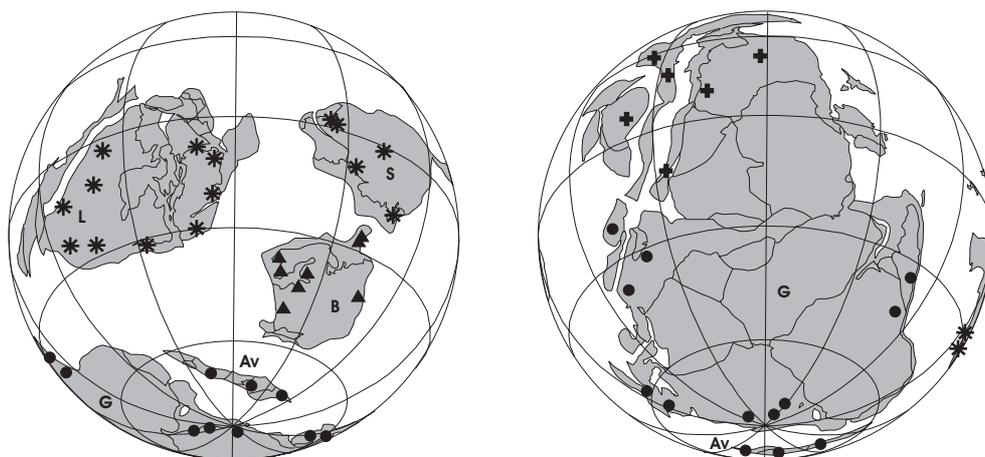


FIG. 1. – Slightly tilted early Ordovician (- 480 Ma: Arenig) palaeogeographical reconstruction, modified from Cocks [2001], based on C.R. Scotese PaleoGIS for Arcview package, illustrating the distribution of the main shallow-water benthic faunas data adapted from Cocks and Fortey [1990]; bathyrid fauna (stars), ptychopygine-megalaspid fauna (triangles), calymenacean-dalmanitacean fauna (black dots), and dikelocephalinid fauna (crosses). L: Laurentia; S: Siberia; B: Baltica; Av: Avalonia; G: Gondwana.

FIG. 1. – Reconstitution paléogéographique de l'Ordovicien Inférieur (- 480 Ma : Arénig), avec le globe légèrement incliné, modifiée d'après Cocks [2001], basée sur le C.R. Scotese PaleoGIS for Arcview package, avec la représentation de la distribution des faunes benthiques majeures peu profondes ; données de Cocks et Fortey [1990] : faune à Bathyridés (étoiles), faune à Ptychopygines-Mégalaspides (triangles), faune à Calyménacées-Dalmanitacées (points ronds), et faune à Dikéloképhalinides (croix). L : Laurentia ; S : Siberia ; B : Baltica ; Av : Avalonia ; G : Gondwana.

[1974], who both observed two clearly distinct 'cold' and 'warm' provinces, respectively in the Silurian and in the Ordovician. In addition, the first distribution scenario by oceanic currents for the Early to Mid Ordovician was proposed by Li [1989, 1991], who explained the occurrence of 'cold-water' acritarch taxa on the South China plate by the movement of oceanic currents.

The inshore-offshore distribution of individual acritarch taxa has also been investigated since the 1960's, and it is clear that nearshore environments have low diversity assemblages with simple morphologies, whereas the highest diversity is reached on onshore shelf environments with complex acritarch morphologies [e.g., Li *et al.*, 2004].

By putting all the information together, we now have a clearer picture than a few years ago and it is possible to identify those Ordovician acritarch taxa that are significant for biostratigraphical purposes (short-lived and geographically widespread), those useful for palaeoecological investigations (limited to specific palaeoenvironments), and those that appear important for palaeobiogeographical problems. These three groups of taxa are limited in number, and they must be identified within a large number of morphotypes present in the palynological assemblages. Most other taxa probably have no particular geological significance. In all fossil groups, but in acritarchs in particular, it is thus very important to select the 'good' taxa for palaeogeographical investigations among the large number of taxa present.

Although many areas remain poorly investigated and hence the picture of Ordovician acritarch distribution is far from complete [Servais *et al.*, 2004], preliminary palaeobiogeographical conclusions can be drawn [Servais *et al.*, 2003]. In the Early Ordovician a 'warm-water assemblage' has been defined by Volkova [1997], containing the genera *Aryballomorpha*, *Athabascaella* and *Lua*. Assemblages containing these genera are so far only recognized in localities from Laurentia, North China, and Baltica. Plotted on the

palaeogeographical reconstruction used by Cocks [2001], it appears that this 'warm-water assemblage' only occurs at low and intermediate latitudes (fig. 2). So far, detailed acritarch investigations from Siberia and Australia are lacking, but it would not be surprising if *Aryballomorpha*, *Athabascaella* and *Lua* also occur in coeval sediments from these two areas.

Of particular interest is the 'peri-Gondwanan acritarch assemblage' that includes the easily recognisable taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* [Li, 1989]. This assemblage is present in all localities on Avalonia and has been recorded all over the southern part of the supercontinent of Gondwana, from its eastern part in South America, through North Africa, central and southern Europe, Turkey, Arabia, Iran, Pakistan to South China [Servais *et al.*, 2003]. As indicated by Li and Servais [2002], the generally adopted interpretation that this 'peri-Gondwanan assemblage' was principally controlled by palaeolatitude and typical of 'cold-water' environments must be revised, because the distribution of this 'province' extends all around the southern margin of the supercontinent Gondwana from the South Pole to the equator. Plotted on the reconstruction used by Cocks [2001], the distribution of this assemblage (fig. 2) almost perfectly corresponds to the distribution of the Calymenacean-Dalmanitacean trilobite fauna of Cocks and Fortey [1990] (fig. 1). Further comparisons of the distribution of Early-Mid Ordovician acritarchs with the trilobite faunas of Cocks and Fortey [1990] are to date difficult to achieve. The current knowledge of acritarchs from Laurentia and Siberia is very poor and it is therefore not known if endemic taxa are present, that could be compared to the distribution of the bathyurid trilobite fauna. Similarly, clear endemic taxa within the Baltic acritarch assemblages, that have usually been considered to belong to a 'temperate' province, between the 'warm' and 'cold-water' assemblages, are so far also difficult to detect.

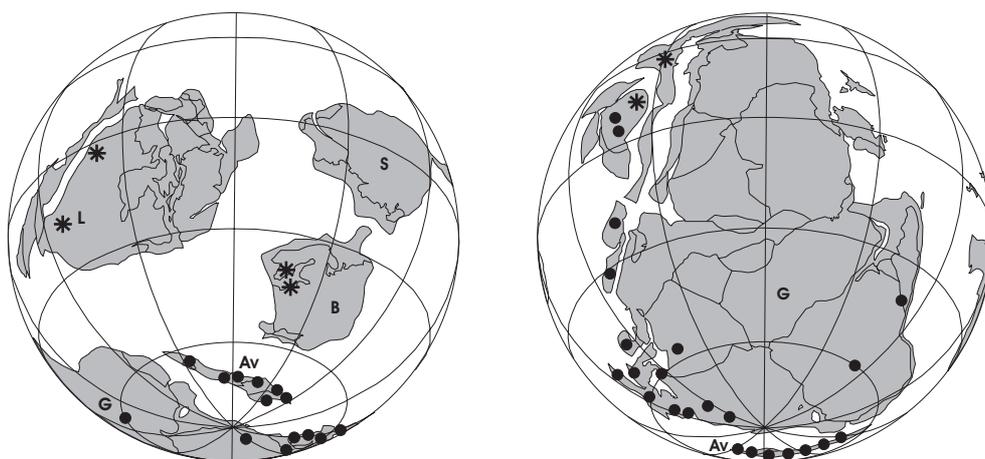


FIG. 2. – Early Ordovician reconstruction (for legend see figure 1) illustrating the distribution of the two main acritarch assemblages data adapted from Li and Servais [2002] and Servais *et al.* [2003]: 'warm-water' assemblage of Volkova [1997] including the taxa *Aryballomorpha*, *Athabascaella* and *Lua* (stars); 'peri-Gondwanan' acritarch province defined by Li [1989] including the taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* (black dots).

FIG. 2. - Reconstitution paléogéographique de l'Ordovicien inférieur (pour la légende voir fig. 1), avec la représentation de la distribution des deux assemblages majeurs d'acritarches données de Li et Servais [2002] et de Servais *et al.* [2003] : assemblage d'eaux chaudes de Volkova [1997], avec les taxons *Aryballomorpha*, *Athabascaella* et *Lua* (étoiles); assemblage péri-Gondwananien défini par Li [1989] avec les taxons *Arbusculidium filamentosum*, *Coryphidium* et *Striatotheca* (points ronds).

Chitinozoa [FP]

The chitinozoans are a group of bottle- to urn-shaped organic-walled microfossils with a typical planktic distribution. They are not thought to belong to the microphytoplankton (i.e. chitinozoans are not included within the acritarchs), but are currently considered to probably be the egg cases of an enigmatic, so far unidentified and perhaps unknown soft-bodied organism [Paris and Nolvak, 1998].

This group of organic-walled microfossils, similarly to the acritarchs, has only been studied in detail since the early 1960's, when the palynomorphs became extremely important for stratigraphical investigations initiated by the oil industry. As with the organic-walled microphytoplankton, current knowledge of Ordovician chitinozoans is thus not complete and some areas remain poorly studied [Servais and Paris, 2000], so that a comprehensive picture of the palaeogeographical distribution cannot be drawn yet [Paris *et al.*, 2004]. In comparison with some of the 'classical' Ordovician fossil groups, the organic-walled microfossils are thus fairly 'young' fossil groups, that have only been investigated for half a century, while trilobites, brachiopods and graptolites have been studied in detail for over two centuries.

Achab [1988] first summarized the palaeobiogeographical information provided by the chitinozoans by identifying different assemblages at low and at high latitudes for the Early, Mid and Late Ordovician. Subsequently, based on analysis of the similarity coefficients of different assemblages, Achab [1991] noted that the assemblages of Baltica occupy an intermediate position between the low latitude ones recorded from Laurentia and the high latitude assemblages identified in southwest Europe and North Africa. Additional information confirming this scheme was also provided by Achab *et al.* [1992], Paris [1991, 1993] and Winchester *et al.* [2000].

Achab [1988] was first to plot several chitinozoan species on a palaeogeographical reconstruction [Scotese *et al.*, 1979], indicating that for the Arenig, *Eremochitina baculata* is only present on the margins of southern Gondwana, while *Conochitina langei* is only recorded from Laurentia and from similar palaeolatitudes on Australia.

Figure 3 indicates the occurrences of selected chitinozoan taxa plotted on the map of Cocks [2001]. It is interesting to note that the distribution of the genus *Eremochitina*, and in particular of the assemblage including *Eremochitina brevis*, is very similar to the distribution of the 'peri-Gondwanan acritarch assemblage' (fig. 2), and thus to the calymenacean-dalmanitacean trilobite fauna (fig. 1). The taxa of the *Eremochitina brevis* assemblage (including a.o. *Lagenochitina obelgis* and *Velatachitina* spp.) have never been recorded from the coeval deposits of Laurentia, where other endemic taxa occur, such as *Conochitina langei*, *C. poumoti* and *C. combazi*. So far, the *Eremochitina brevis* assemblage has also not been recorded from Baltica. However, the dataset is not complete, and future studies are needed to develop a more comprehensive picture of the distribution of the palaeogeographically significant chitinozoan taxa.

Besides their biostratigraphical significance, it thus appears that the chitinozoans also display a palaeogeographical importance. As with the acritarchs, the palaeobiogeographically 'good' morphotypes among the chitinozoans

must be distinguished from the larger number of pandemic or cosmopolitan taxa.

Graptolites [CX]

The best known and most extensively studied Lower Palaeozoic planktic group is the graptolites. This group has been investigated in detail over the two last centuries, similar to the trilobites and brachiopods. Graptolites have long been the stratigraphical guide fossils in the Ordovician and Silurian, and, together with the conodonts, are still today one of the most useful fossil groups for Lower Palaeozoic stratigraphy, and in particular for use in international correlation, such as in the definition of the Global Boundary Stratotypes Sections and Points (GSSP). The graptolites are usually interpreted as having a cosmopolitan distribution, which is indeed the case for most taxa. The didymograptid and isograptid graptolites, for example, have a very widespread distribution, suggesting that latitude may not have exerted a primary control on their distribution [e.g., Cooper *et al.*, 1991].

Nevertheless, some genera seem to have a clearly limited palaeogeographical distribution. Harris and Keble [1932] were first to recognize two different graptolite faunas at a global scale. In the 1970's, these two major graptolite faunas, then named the Pacific and Atlantic faunas, were widely used by many authors [e.g., Bulman, 1971; Boucek, 1972; Skevington, 1974; Berry, 1979]. Following publication of the first palaeogeographical reconstructions, Ordovician graptolite provincialism was discussed in more detail. McKerrow and Scotese's Memoir included no less than three papers dedicated to graptolite biogeography: Berry and Wilde [1990], Finney and Chen [1990], and Rickards *et al.* [1990].

Skevington [1974] and subsequent authors [Cooper *et al.*, 1991; Chen, 1994; Cooper, 1998, 1999] recognized and discussed the three basic parameters that mostly influenced graptolite distribution: latitudinal distribution, oceanic currents and depth zonation. The last parameter rather reflects local or regional palaeoecology, that can be observed within the same palaeocontinent or major terrane. At a global scale, graptolites thus appear mostly distributed following palaeolatitudes and oceanic currents.

In the last few years, graptolite palaeogeography has been principally based on the presence or absence of a few characteristic, palaeogeographically significant taxa, because most taxa appear to be cosmopolitan at a global scale. Skevington [1974] indicated that the Pacific fauna could be attributed to warm-water and the Atlantic fauna to cold-water environments. Additionally, he noted that the diversity of the graptolite assemblages increased towards warmer-water environments (Pacific fauna). However, a clear concept and the precise composition of the Pacific and Atlantic graptolite faunas have never been provided and it is therefore possible to see 'Atlantic' graptolites in low diversity and abundance described in the 'Pacific fauna' [Zalasiewicz *et al.*, 1995; Maletz and Servais, 1998].

Plots of graptolite taxa on the palaeogeographical reconstruction of the Arenig, used here [Cocks, 2001], are not presented, because they do not provide a clear picture of provincialism on this map at this time interval. Nevertheless, it is important to indicate that for the Darriwilian (late Mid Ordovician), it is possible to distinguish *Cardiograptus*,

Oncograptus, and the sinograptid genera as typical Pacific taxa, and the genus *Didymograptus* as a typical Atlantic graptolite. The Pacific taxa are distributed in low to middle latitudes coinciding with a tropic-subtropic belt and the southern and northern extension of an arid belt. *Didymograptus*, however, is distributed in a restricted European region (including southern Gondwana and Baltica) that can be attributed to a high latitude belt. The 'Atlantic' genus *Didymograptus* may also be found in the Pacific region, but it is then always present with low species diversities and in low abundances.

It can thus be summarized that the first, highly diversified graptolite fauna in low to middle latitudes is predominated by Pacific taxa, while the second fauna was predominated by Atlantic taxa during the Darriwilian.

Radiolaria (MC)

The radiolarians are microplanktonic predators with a siliceous skeleton. Today, they live in all oceans and they can be found in all parts of the water column (from deep to shallow water). Few precise data allow a quantification of their abundance in the water masses, but their relative abundance allows them to be used as productivity indicators [De Wever *et al.*, 2003].

The compositions of modern radiolarian assemblages (relative specific diversity) show a biogeographical distribution following a broadly latitudinal distribution, that can also be influenced by water mass circulation and the presence of upwelling zones [e.g., Molina Cruz, 1977; Johnston and Nigrini, 1980; De Wever *et al.*, 2003]. The modern distribution scheme can thus partly be compared with that of the organic-walled microphytoplankton which indicates that studies on radiolarian assemblages may also have a high potential for (palaeo-)biogeographical analyses.

The study of Ordovician radiolarians is very young, and taxonomical and biostratigraphical data are still scarce. The evolution and distribution of Palaeozoic radiolarians is summarized in De Wever *et al.* [2003], while Danielan [1999]

and Noble and Danielan [2004] reviewed the Ordovician literature.

So far, Ordovician data are too sparse to differentiate low- and high-latitude radiolarian assemblages, as most studies have concentrated on providing the first taxonomic descriptions of Ordovician radiolarians. Webby and Blom [1986] noted a strikingly close faunal similarity of possible biogeographical significance between Late Ordovician outer shelf assemblages from Nevada and Estonia. This would indicate that similarities exist for assemblages of low to middle latitudes. More recently, Danielan and Floyd [2001] analyzed the radiolarian diversity of the Ordovician of Scotland, while Danielan and Popov [2003] commented on the biodiversity of Ordovician radiolarians from Kazakhstan, but palaeogeographical relations were not discussed.

However, it is too early to draw any biogeographical conclusions and not yet possible to plot distinct assemblages on any palaeogeographical reconstructions. The palaeogeographical potential of Ordovician radiolarians can be exploited in the future if the preservation of the siliceous skeletons is taken into account. This is related to many factors, such as water chemistry, depth, facies, and diagenesis. In addition, the dissolution of skeletons may be selective at a specific level, so that comparisons of Palaeozoic assemblages necessitate a good understanding of the evolution of the sediment fabric hosting radiolarians.

Vertebrates: the palaeogeographical distribution of nektonic taxa [AB]

After the brief discussions of the different planktic groups, it is relevant to have a look at the various fossil groups that constituted the nekton in the Ordovician seas. The same palaeogeographical reconstruction is used here for the plots of some nektonic groups, in order to compare the distribution schemes of the nekton with that of the benthic trilobite assemblages illustrated in figure 1 and the planktic groups in figures 2 and 3.

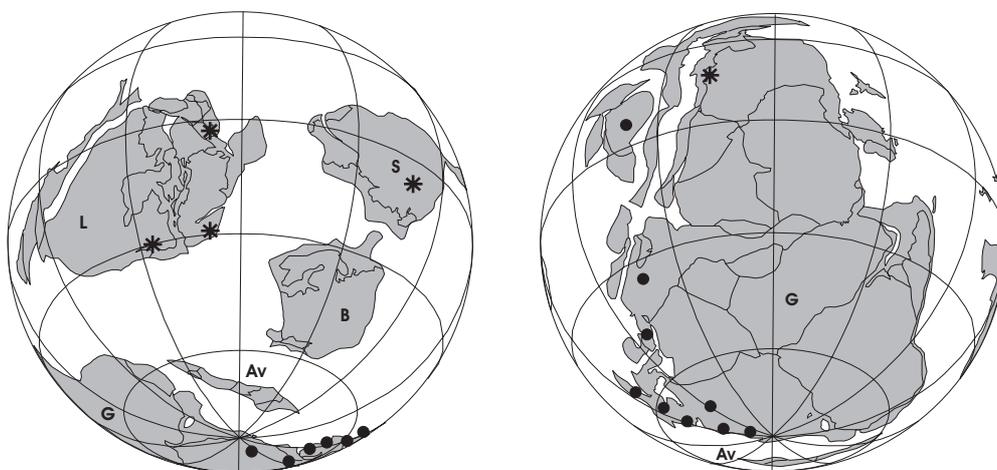


FIG. 3. – Early Ordovician reconstruction (for legend see figure 1) illustrating the distribution of characteristic chitinozoan assemblages ; data from Achab [1988], Achab *et al.* [1992] and F. Paris, unpublished: *Conochitina langei* assemblage (stars); *Eremochitina brevis* assemblage (black dots).

FIG. 3. – Reconstitution paléogéographique de l'Ordovicien inférieur (pour la légende voir fig. 1), avec la représentation de la distribution des assemblages caractéristiques de chitinozoaires ; données de Achab [1988], Achab *et al.* [1992] et F. Paris, inédit: assemblage à *Conochitina langei* (étoiles) ; assemblage à *Eremochitina brevis* (points ronds).

The evolution and biodiversification of Ordovician vertebrates (agnathans and gnathostomes, excluding conodonts) has recently been reviewed by Turner *et al.* [2004], while their palaeogeographical distribution was revised by Blicek and Turner [2003]. The latter authors indicate that a strong endemic pattern can be observed for Ordovician vertebrates, with a 'Gondwana Endemic Assemblage' in the Early Ordovician to the early Late Ordovician, and a 'Laurentia-Baltica-Siberia Assemblage' in the Late Ordovician. Interestingly, despite a short stratigraphical overlap, it appears that no common genera exist between both assemblages. Although some palaeontologists consider the fishes to be of low palaeogeographical interest, because they are 'free-swimming' (nekctic), Blicek and Turner [2003] indicated that the Ordovician genera described to date correspond to taxa with very limited distribution, apparently confined by marine barriers (i.e., wide oceanic areas, longitudinal oceanic currents), either on continental shelves in true marine environments, or restricted to non-marine-brackish environments. Most Ordovician taxa would thus correspond to the 'continental' grouping of Rosen [1974].

Discoveries of Ordovician fishes remain rare, and it is therefore impossible to provide a clearer picture on the palaeobiogeography of Ordovician vertebrates. Nevertheless, we propose here a plot of the arandaspid agnathan localities of Arenig-Llanvirn age on the palaeogeographical reconstruction that was used for the other fossil groups (fig. 4). The plot of this monophyletic group of vertebrates defines an assemblage limited to Gondwana, that is here named the 'Gondwana Endemic Assemblage'.

Nautiloid cephalopods

The palaeogeographical distribution of the nautiloid cephalopods is also far from being clear. This group only started to diversify in the Ordovician [Frey *et al.*, 2004]. Data appear too poor to draw any palaeobiogeographical scenario.

Pelagic trilobites [MFT]

Although most trilobites were benthic or nektobenthic, some groups are thought to have been more or less active swimmers. Though some Cambrian trilobites could have been pelagic (Elviniidae, *Centropleura*) [Fortey, 1985: 221], this habit was better represented in the Ordovician. Taxa such as *Opipeuter*, *Carolinites* (Telephinidae), *Girvanopyge* (Remopleuridacea) and the Cyclopygidae satisfy three independent criteria, based on functional morphology, analogy, and geological occurrence, in favour of a pelagic mode of life [Fortey, 1985]. Telephinids may have lived in the upper part of the water column and are therefore regarded as epipelagic, whereas the family Cyclopygidae was adapted to a mesopelagic life-style, occupying the depth zone of about 150-700 m [Fortey, 1985; Fortey and Owens, 1987; McCormick and Fortey, 1998].

In addition, some other trilobites may have swam in the water column. Fortey [1985] postulated a possible pelagic mode of life for both the Ordovician odontopleurid genus *Selenopeltis* and the earliest Tremadocian olenid *Jujuyaspis*. According to Hamman *et al.* [1986], the early stages (meraspids and early holaspids) of *Selenopeltis* could have been pelagic, whereas adults became nektobenthic active swimmers (with the exception of two possible epibenthic species restricted to SW Europe). Similarly, Tortello and Clarkson [2003] stated that small meraspids of *Jujuyaspis* were pelagic, whereas holaspids may have had a nektobenthic mode of life.

In addition, some authors have suggested that agnostoids (Cambrian-Ordovician) were pelagic [Robison, 1972] based on their small size, functional morphology, widespread palaeogeographical distributions and usual occurrence in deep water, fine-grained sediments. Based on a complete study of the Upper Cambrian *Agnostus pisiformis*, Müller and Walossek [1987] confirmed that these organisms had the capacity to swim, but also claimed that this cannot be taken as conclusive evidence for a pelagic mode of life, suggesting that many agnostoids could have been able to

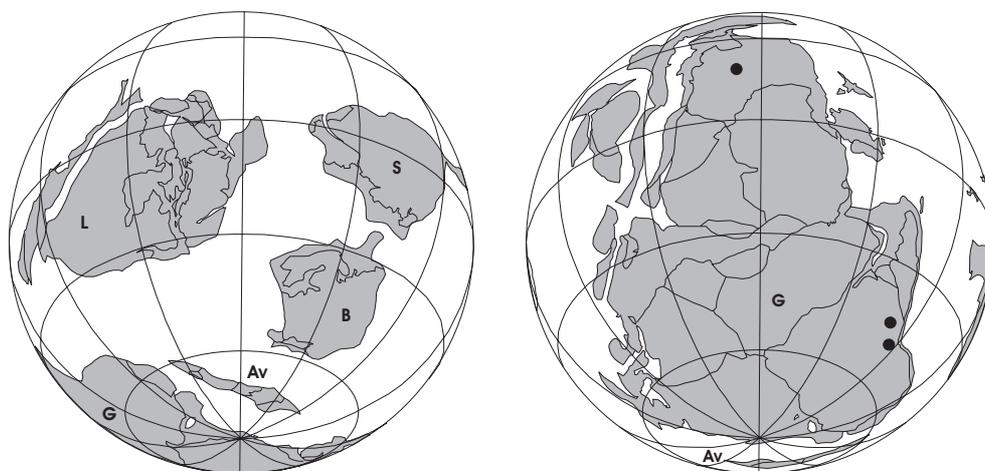


FIG. 4. – Early Ordovician reconstruction (for legend see figure 1) illustrating the distribution of the Arenig-Llanvirn (Arenig-Darriwilian) arandaspid agnathans (vertebrates) recovered from the Gondwanan supercontinent; data adapted from Young in Webby *et al.* [2000], *Sacabambaspis* fauna; and Turner *et al.* [2004], Gondwanan Endemic Assemblage GEA.

FIG. 4. – Reconstitution paléogéographique de l'Ordovicien inférieur (pour la légende voir fig. 1), avec la représentation de la distribution des assemblages des agnathes arandaspides (vertébrés) retrouvés sur le supercontinent Gondwana; données de Young in Webby *et al.* [2000], faune à *Sacabambaspis*; et Turner *et al.* [2004], Gondwanan Endemic Assemblage GEA.

swim or float around a flocculent seabed, rich in detrital matter. On the other hand, other authors have postulated that agnostoids were widespread, benthic inhabitants of deep, cold water environments [Nielsen, 1995; Chatterton, 2001]. Since different species or genera may have had different modes of life [e.g., Jago, 1973; Fortey, 1980], further studies are needed to discuss this subject in a more complete context [Nielsen, 1997]. Recently, Tortello and Esteban [2003a] have provided evidence in favour of a possible nektobenthic habit of an agnostoid community adapted to low-oxygen environments.

Fortey and Mellish [1992] noted that epipelagic trilobites are not good tools for palaeogeographical discrimination. Cocks and Fortey [1990] plotted the occurrences of two telephinid genera (*Carolinites* and *Opipeuter*) on an Early Ordovician palaeogeographical map. These organisms show a pan-equatorial distribution, denoting sensitivity to palaeotemperature and palaeolatitude. Since most species have wide distributions in association with different benthic assemblages (e.g., *Carolinites genacinaca* has been described from all Ordovician continents [McCormick and Fortey, 1999]), they do not add conclusive information for the definition of palaeocontinents [Cocks and Fortey, 1990].

On the other hand, a similar plot of Early Ordovician cyclopygid trilobites shows that this family was mainly distributed in high-latitude marginal regions of Gondwana [Cocks and Fortey, 1990]. Recent findings of primitive cyclopygids (*Prospectatrix*, *Degamella*, *Sagavia*) in the Tremadocian of China and Argentina [Zhou *et al.*, 1994; Esteban, 1996; Tortello and Esteban, 2003b] have greatly improved the knowledge of the distribution of this group. The oldest occurrences of the genera cited above are late early Tremadocian – late Tremadocian in age. Since they involve China (Tarim), England (Shropshire, Lake District), Argentina (Famatina System), and possibly southern France, they can be regarded as distinctive elements of peri-Gondwana. In addition, the recent discovery of a *Prospectatrix genatenta* – *P. brevior* morphological intermediate form in Argentina [Tortello and Esteban, 2003b] links high- and mid-latitude areas of the supercontinent. On the other hand, the cyclopygids (*Prospectatrix*, *Degamella*, *Sagavia*, *Cyclopyge*, *Aspidaeglina*, *Novakella*, *Microparia*, *Circulocrania*, *Pricyclopyge*, *Ellipsotaphus*, and *Psilacella*) are more diverse in the Arenig of different localities of Gondwana and associated blocks (Wales, Shropshire, southern France, Bohemia and Turkey), whereas they are widespread during the late Llanvirn and the later Ordovician. It must be pointed out that the isolated records of *Cyclopyge* in the Lower Ordovician of Baltica (southern Sweden) are attributed to particular sea level rises and possible changes of palaeocurrents [Nielsen, 1995]. Since the mesopelagic cyclopygids have a predominantly peri-Gondwanan distribution in the Tremadocian-Arenig [Fortey and Owens, 1987], crossing lines of latitude, they can be regarded as having close relationships to the continental configurations during the first few million years of their evolution.

Selenopeltis (Arenig-Ashgill) is a similar example, although it occurs in high latitudes only. This genus is the most characteristic ‘Mediterranean’ element (see *Selenopeltis* Province of Whittington [1966]) in a wide area comprising the Anglo-Welsh area, France, Germany, Portugal, Spain, North Africa (Morocco), Bohemia, Turkey and Iraq. It appears in different environments and biofacies, associated with

different benthic communities. Although *Selenopeltis* is especially represented in the Middle – Upper Ordovician, its first records are from the Arenig of Shropshire (England) and the Montagne Noire (southern France).

The geographic distributions of other possible pelagic or nektobenthic trilobites have proved to be wide, which *a priori* limits their value as palaeobiogeographical tools. However, some taxa do provide valid information or, in some cases, permit a check of palaeogeographical configurations based on benthic organisms. Nielsen [1997] compiled a review of Ordovician agnostids, indicating that they were more diverse in cold and temperate continental areas, although several genera are found also at the fringes of palaeoequatorial continents. It is interesting to note that some taxa are restricted to Gondwana and associated blocks during the Tremadocian-Arenig (*Anglagnostus*, *Lotagnostus* (*Semagnostus*), *Corrugatagnostus* and *Dividuagnostus*), providing valuable evidence in favour of provincialism during that time (see fig. 5). On the other hand, other Early Ordovician agnostoids occur in relatively high-latitude areas of both Gondwana and Baltica, the cosmopolitan genera *Geragnostus* (*Geragnostus*) and *Arthrorhachis* are also recorded in Laurentia and North China and other genera seem to be typical of temperate and warmer areas (and rare or absent at high latitudes) in peri-Gondwana, Baltica and Laurentia.

Among the olenids, the species of the cosmopolitan genus *Jujuyaspis* have proved to have distinctive distributions during the earliest Tremadocian. *Jujuyaspis borealis* KOBAYASHI has been described from different localities of Laurentia, whereas *J. kelleri* (BALASHOVA) and *Jujuyaspis sinensis* ZHOU characterize Kazakhstan and North China/Korea, respectively. In addition, *Jujuyaspis angusta* HENNINGSMOEN is restricted to the clastic lowest Ordovician of southern Norway, whereas *J. keideli* has a wide distribution in high to moderate latitudes (South America and Baltica), predominantly in olenid biofacies (Baltic Province of Shergold [1988]). Low latitude paleocontinents have particular *Jujuyaspis* species, suggesting that the distributions of these taxa were influenced by latitude and, also, by the palaeogeographical configuration of the continents.

DISCUSSION AND CONCLUSIONS

The trilobites and brachiopods were the two fossil groups that allowed construction of the first palaeogeographical maps for the Early Palaeozoic. It is evident that together with some bivalves and ostracodes, the benthic elements of these fossil groups have proved to be of great palaeobiogeographical importance, that cannot be ignored. However, does this necessarily mean that these groups are ‘better’ fossils for inferring palaeogeography?

Although we acknowledge that selected benthic fossils may be ‘good’ palaeogeographical indicators, our study indicates that planktic and nektic fossil groups should not be neglected. The plots on a palaeogeographical reconstruction of some planktic fossil groups, presented in this study, indicate that their distribution, at least that of the organic-walled microfossils (acritarchs and chitinozoans), appears in part surprisingly similar to that of the trilobite faunas selected by Cocks and Fortey [1990].

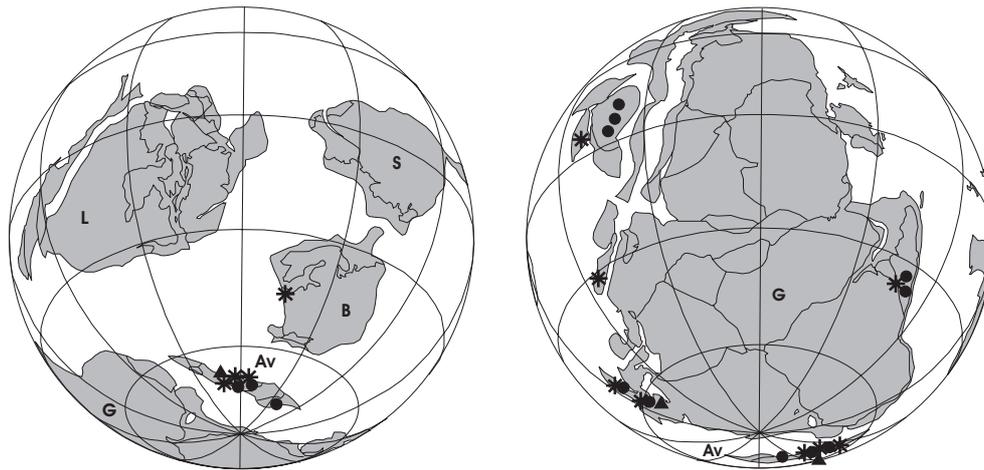


FIG. 5. – Early Ordovician reconstruction (for legend see figure 1) illustrating the distribution of palaeogeographically significant pelagic trilobite taxa (data from M. F. Tortello, unpublished): Tremadocian-Arenig occurrences of the Cyclopygidae (stars), Arenig occurrences of *Selenopeltis* (triangles), and Tremadoc-Arenig agnostoid plots of *Anglagnostus*, *Lotagnostus* (*Semagnostus*) and *Corrugatagnostus* (black dots).

FIG. 5. – Reconstitution paléogéographique de l'Ordovicien inférieur (pour la légende voir fig. 1), avec la représentation de la distribution des assemblages de trilobites pélagiques significatifs (données de M. F. Tortello, inédit) : présence de Cyclopygidae au Trémadocien-Aréniq (étoiles), présences de *Selenopeltis* à l'Aréniq (triangles), et présences au Trémadocien-Aréniq des agnostoïdes *Anglagnostus*, *Lotagnostus* (*Semagnostus*) et *Corrugatagnostus* (points noirs).

A great 'disadvantage' of the two planktic microfossil groups is the fact that, in comparison with some of the 'classical' Ordovician fossil groups, acritarchs and chitinozoans are fairly 'young' groups, because they have been investigated in detail only for less than half a century. A comprehensive picture of their global distribution is thus far from established at the moment.

The data for the radiolarians and for the different groups that can be attributed to the nekton (vertebrates and nautiloid cephalopods) is even sparser and it is too early to discuss palaeogeographical scenarios of these groups, although it is probable that all may eventually show useful palaeogeographical patterns.

The critical re-evaluation of the distribution of 'pelagic' trilobites indicates that palaeobiogeographical useful taxa can also be detected among this group.

Even the graptolites, that are generally considered to be of low palaeogeographical significance, show distributional scenarios that may be useful to interpret palaeogeography or palaeoclimate.

The review of the different fossil groups in this paper also indicates that it is very important to carefully select the 'good' palaeogeographical indicators, in most cases from a large number of taxa. Within the lists of genera and species of the different planktic fossil groups, only few morphotypes indicate clear endemism, while most of the other forms seem to have pandemic or cosmopolitan distributions.

It is thus extremely important that each fossil group is well understood, not only from a taxonomic point of view, but also regarding its distributional mechanisms in terms of both palaeoecology and palaeogeography, in order to isolate the 'good' palaeogeographical taxa. Cluster analysis and parsimony methods of biogeographical analysis, as used by Fortey and Mellish [1992], Fortey and Cocks [1992] or Lees *et al.* [2002], must be critically evaluated by specialists of each fossil group in order to avoid misinterpretations. Quantitative palaeontology can only provide significant results if the data in the datasets come from palaeontologists with expertise in the group concerned.

Finally, it appears that almost all fossil groups include some 'good' palaeobiogeographical 'markers'. It would thus be wiser to look for the 'better' taxa within each fossil group, instead of asking which are the 'better' fossil groups.

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