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Ordovician acritarchs of China and their utility for global palaeobiogeography

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Key-words. – Acritarchs, Ordovician, China, Palaeobiogeography

Abstract. – Since the 1970s, acritarch workers have recognized two distinct geographic acritarch assemblages in the Ordovician. The first assemblage occurs in the late Tremadoc in low latitude areas. This assemblage, recently redefined by Volkova [1997], has been attributed to warm-water environments. A second "Mediterranean" or "peri-Gondwanan" province, attributed to high latitudes in the southern hemisphere, can easily be recognized in late Tremadoc to Arenig acritarch assemblages. This second palaeogeographic "province", defined by Li [1989] is distributed around the border of Gondwana in a zone reaching from Argentina through northern Africa and peri-Gondwana up to Iran, Pakistan and southern China. In the present work we propose an initial simplified, tentative model of the latitudinal distribution of selected early to middle Ordovician acritarchs. Both "provinces" are plotted on the recent palaeogeographical reconstruction of the early Ordovician of Li and Powell [2001]. It appears that the first "province" is limited to low and intermediate latitudes, i.e., to warmer water environments. However, the generally adopted interpretation that the so called "Mediterranean" or "peri-Gondwanan" geographical assemblage is principally controlled by palaeolatitudes and is considered to be typically "cold-water" has to be revised, because the distribution of this "province" appears related more to the continental arrangement along the Gondwana border than to latitudes. This distribution shows some similarities with recent investigations in Silurian acritarch palaeogeography [Le Hérissé and Gourvennec, 1995] that provides evidence that the global distribution of Silurian acritarchs is under the interdependence of continental arrangement, latitudinal position, environmental conditions and oceanic currents, and that it is not simply latitudinally controlled as previous interpretations have suggested. The Yangtze Plaform of southern China presents elements of both early to middle Ordovician "provinces", i.e., from both the "warm-water" and the "peri-Gondwanan" geographic assemblages. The South China Plate is therefore one of the areas that shows typically mixed assemblages. Although it remains difficult to define clearly a "Baltic" province, it is important to note that between the latest Tremadoc and the early Llanvirn a clear distinction of the acritarch assemblages between peri-Gondwana and Baltica is possible.

Les acritarches de l'Ordovicien de la Chine et leur utilité pour la paléobiogéographie globale

Mots clés. – Acritarches, Ordovicien, Chine, Paléobiogéographie

Résumé – **Introduction**. – Depuis les années 1970, plusieurs auteurs proposent des modèles paléobiogéographiques séparant les acritarches de l'Ordovicien en deux "provinces", une première province localisée dans des basses latitudes présentant des conditions intertropicales et une deuxième province interprétée comme étant typique des milieux tempérés à froids de hautes latitudes dans l'hémisphère sud.

La paléogéographie de la Chine à l'Ordovicien. – Malgré une évolution géotectonique assez complexe, il existe actuellement un consensus parmi les paléogéographes pour séparer la Chine au cours du Paléozoïque en trois entités majeures : les plaques du Nord de la Chine, du Sud de la Chine (plate-forme Yangtze) et de Tarim. Au cours de l'Ordovicien ces continents étaient localisés à des latitudes différentes. Le Nord de la Chine se trouvait dans des basses latitudes de l'hémisphère nord, tandis que la plate-forme Yangtze et la plaque de Tarim se trouvaient sur l'équateur et dans l'hémisphère sud. Ces régions, et particulièrement le paléocontinent du Sud de la Chine, jouent un rôle majeur dans la compréhension de la distribution globale des acritarches dans l'Ordovicien.

La modélisation de la distribution des acritarches. – Le microphytoplankton actuel (formé majoritairement par les dinoflagellés et d'autres groupes d'algues unicellulaires) montre des schémas de distribution assez complexes. Néanmoins, on peut identifier dans les océans actuels des espèces de kystes de dinoflagellés qui indiquent clairement un signal climatique, c'est-à-dire latitudinal. L'étude de la distribution des acritarches de l'Ordovicien devrait donc théoriquement aussi livrer certains taxons qui indiquent la paléolatitude.

La base de données de l'Ordovicien et les modèles de distribution publiés. – Plus de 700 références bibliographiques, plus de 250 genres et plus de 1300 espèces d'acritarches ordoviciens ont été publiés, permettant la délimitation de plusieurs paléoprovinces. Certains auteurs proposent jusqu'à sept provinces, mais la révision critique de la littérature montre que seulement deux provinces peuvent être maintenues pour l'instant.

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La paléobiogéographie des acritarches dans l'Ordovicien inférieur et moyen. – Dans ce travail, nous proposons pour la première fois un modèle simplifié et expérimental qui pourrait expliquer la distribution latitudinale de certains taxons d'acritarches sélectionnés de l'Ordovicien inférieur à moyen qui sont probablement dépendant de la température.

Les deux assemblages retenus ici, c'est-à-dire la "province d'eau chaude" du Trémadocien terminal de Volkova [1997] et la "province méditerrannéenne" de l'Arénigien définie par Li [1989] sont positionnées sur une reconstruction paléogéographique récente de l'Ordovicien inférieur publiée par Li et Powell [2001]. Si la première province semble bien limitée aux latitudes basses, la "province méditerranéenne", aussi appelée "province péri-gondwanienne", n'est pas limitée aux hautes latitudes de l'hémisphère sud. Elle est présente dans toute la périphérie de la partie sud du continent de Gondwana, de l'Argentine à l'Afrique du Nord, et s'étend de l'Europe du Sud, l'Iran et le Pakistan jusqu'en Chine du Sud. Cet assemblage, présent ainsi du pôle sud jusqu'à l'équateur, ne peut donc plus être qualifié de typique des eaux froides des hautes latitudes dans l'hémisphère sud.

Conclusions. – Ces résultats montrent des similitudes avec les résultats de l'étude des acritarches du Silurien dans lequel Le Hérissé et Gourvennec [1995] ont montré que la distribution des assemblages géographiques n'est pas simplement réglée par la paléolatitude, mais qu'elle est le résultat de l'interaction de l'arrangement des continents, de la position latitudinale, des conditions environnementales et de courants océaniques de surface. La plate-forme Yangtze, présentant des éléments des deux provinces dans l'Ordovicien inférieur et moyen, peut être considerée comme une région clé pour comprendre la paléobiogéographie des acritarches de l'Ordovicien.

Malgré le fait qu'il est difficile de définir une "province baltique", il est important de signaler qu'il existe une nette distinction entre les assemblages d'acritarches de la bordure de Gondwana et ceux de la Baltique entre le Trémadocien supérieur et le Llanvirnien inférieur.

INTRODUCTION

The Ordovician palaeogeography of China has been discussed in many papers. A general consensus exists today that China consists of a series of palaeocontinents, of which the three major elements were the North China (Sino-Korean Plate), Tarim, and the South China plates [e.g. Li, 1998].

Since the early 1970s, several authors have proposed various Ordovician palaeobiogeographical models, in which two major acritarch "provinces" were recognized : a first "province" containing species only present in high latitude southern hemisphere areas ("cold"-water forms), and another region considered to host warmer-water taxa located at lower latitudes and around the equator.

The position of the different palaeocontinents that later came together to form modern China is essential in understanding the palaeogeographic distribution of Ordovician acritarchs. More than 50 publications deal with Ordovician acritarchs from China [Li *et al.*, 2002]. Although most papers concern Arenig deposits of the South China Plate (Yangtze Platform), acritarchs have been described from all Ordovician stages in most areas of China, i.e., from all major tectonostratigraphical units. Because it was located at intermediate latitudes during the early and middle Ordovician, the Yangtze Platform is of particular importance, as this area shows assemblages with a mixture of taxa considered as "cold" or "warm" water indicators.

South China is thus a key element for not only understanding the global distribution of Ordovician acritarchs, but also for stratigraphical correlations at the global scale, because stratigraphic index taxa can be correlated with most other areas in the world [e.g., Brocke *et al.*, 1995].

The objective of this paper is to place described Ordovician Chinese acritarch assemblages into a global geographic context, by plotting them on the palaeogeographic reconstruction by Li and Powell [2001].

Of particular interest is understanding the global distribution of the "warm-water" assemblage redefined by Volkova [1997] in the late Tremadoc (based on the occurrence of the acritarch genera *Aryballomorpha, Athabascaella, Lua*), and the Arenig "cold-water" assemblage defined by Li [1989] (based on the occurrence of the acritarch taxa *Arbusculidium filamentosum*, *Coryphidium,* and *Striatotheca*).

THE ORDOVICIAN PALAEOGEOGRAPHY OF CHINA

The Palaeozoic geotectonic evolution of China is fairly complex. Because this paper is not a comprehensive review of the different published models, the reader can be referred to a series of general papers cited below.

According to Shen [1994], China can be divided into five geotectonic regions. These five regions are, from north to south (fig. 1) :

(I) The Tianshan – Xing'an Region, composed of post-Neoproterozoic active continental-margin belts with several stable microblocks;

(II) the Tarim – North China Region, built up by stable palaeoblocks with a pre-Sinian basement;

(III) the Kunlun – Qinlin Region, that forms active continental margin belts with the exception of the Qaidam microblock;

(IV) the Chuan (Sichuan) – Dian (Yunnan) – Qing (Qinghai) – Zang (Tibet) Region, that represents mainly several active continental margin belts and suture belts with several incorporated microblocks; and

(V) the South China Region, that includes the Yangtze Platform, the South Hainan microblock, the South China active belt, and the Taiwan island arc.

According to the present geographical understanding, the above mentioned regions I, II, and III are located in northern China and regions IV and V occur in southern China.

In terms of plate tectonics, China has generally been divided into three major units, the Sino-Korean (North China) Plate, the Tarim Plate, and the Yangtze Platform, as well as several additional minor terranes [e.g., Scotese and McKerrow, 1990; Burrett *et al.,* 1990; Li, 1998]. During the

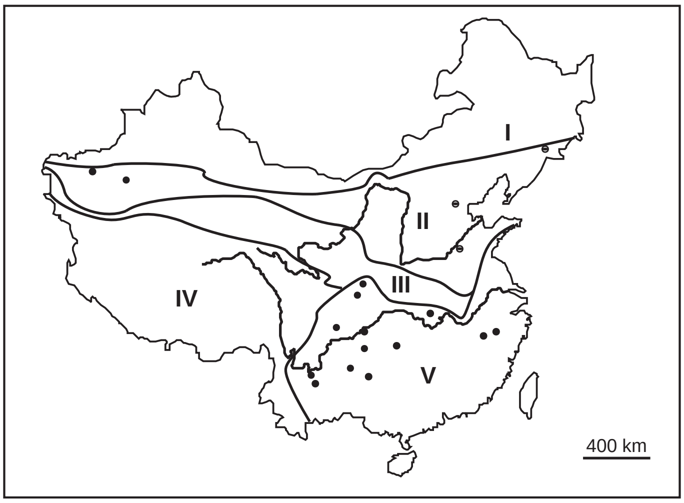

FIG. 1. – Map of China showing the five major geotectonical regions according to Shen [1994] and major localities from which Ordovician acritarchs have been reported (represented by round dots).
I = Tianshan – Xing'an Region ; II = Tarim – North China Region ; III = Kunlun – Qinlin Region ; IV = Chuan – Dian – Qinq – Zang Region ; V = South China Region.

FIG. 1. – *Carte de la Chine montrant les cinq régions géotectoniques majeures d'après Shen [1994] et les localités majeures dans lesquelles des acritarches de l'Ordovicien ont été décrits (représentées par des points ronds).*
I = *Région de Tianshan – Xing'an ;* II = *Région de Tarim – North China ;* III = *Région de Kunlun – Qinlin ;* IV = *Région de Chuan – Dian – Qinq – Zang ;* V = *Région de South China.*

early Palaeozoic, these plates were separated from each other and were located in different latitudes. According to different palaeogeographic reconstructions [e.g., Li, 1998; Torsvik, 1998], the North China Plate along with Laurentia, Baltica and Siberia, was one of the major plates independent from Gondwana. Various palaeogeographic studies show that, during the early Ordovician, the North China Block was dominated by warm-water carbonates, and was located near the equator and/or in low latitutes in the northern hemisphere. The South China Block and Tarim Plate were located further south, with South China occupying a position close to the equator or in low latitudes in the southern hemisphere. Palaeobiogeographically, the Tarim Block shared similar geographic provinces with the South China Block from the Cambrian until the Carboniferous [Zhou and Chen, 1990]. Biogeographic affinities with eastern Gondwana suggest that South China was located near Australia during most of the Palaeozoic [Scotese and McKerrow, 1990]. It appears that Tarim collided with Siberia and Kazakhstan during the late Palaeozoic, whereas North China and South China did not join Asia until the Indosinian Orogeny (Triassic-Jurassic) [Nie *et al.*, 1990].

In the present study, we plot our acritarch data on the recently published early Ordovician palaeogeographic reconstruction of Li and Powell [2001]. This reconstruction has the advantage of providing an excellent view of the position of the different Chinese plates in relation to Gondwana (including Australia), as well as Laurentia, Baltica and Siberia.

ACRITARCH DISTRIBUTION AND PALAEOBIOGEOGRAPHY

What are/were acritarchs ?

Before considering various interpretations of global acritarch distribution patterns, it is important to review the definition and interpretation of the term acritarch. Evitt [1963] defined the informal group Acritarcha as a polyphyletic "group" of organic-walled microfossils of uncertain or unknown biological affinities. According to his definition, the group thus includes palynomorphs of which the attribution to a biological entity remains questionable or unknown. The interpretation of what acritarchs are/were indicates that during the Palaeozoic, most acritarchs probably represented the cysts of diverse marine microplankton groups. Thus, the acritarchs, very probably, can be considered as the ancestors or equivalents of such phytoplankton groups as the dinoflagellates, and the prasinophycean and chlorophycean algae [for a more detailed discussion, see Servais *et al.*, 1997].

Palaeozoic acritarchs should therefore show a global distribution pattern comparable to that of other planktonic groups, such as, for example, the graptolites. Such a distribution pattern should basically follow latitudinal belts.

Modeling modern phytoplankton distribution

The conditions reflecting the Palaeozoic global acritarch distribution should be compared to those acting on the distribution of modern phytoplankton, and in parti- cular, the cysts of modern dinoflagellates.

A series of environmental signals can be recognised in the distribution pattern of modern dinoflagellate cysts : temperature, salinity, water depths, nutrient supply, water chemistry, etc. One of the more important parameters is the climatic signal that is mainly related to latitude. Published models on Recent dinoflagellate distribution patterns show that selected dinoflagellate species occupy different climatic zones (e.g., arctic to cool-temperate, temperate, cool-temperate to tropical), i.e., some modern taxa are restricted to polar waters, while others are only found in warm-waters in tropical zones [e.g., Edwards and Andrle, 1992; Dale, 1996]. It appears evident then that Ordovician acritarchs should also reflect a similar distribution pattern.

Other important environmental signals in recent cyst assemblages are the coastal/oceanic signal and the salinity signal, which provide evidence in modern associations of an inshore/offshore trend. Several published models, both from modern oceans and from Mesozoic sequences, clearly show that some selected microphytoplankton taxa occupy different environments (from estuarine to outer neritic, estuarine to oceanic, inner neritic to oceanic, etc.) [e.g., Brinkhuis, 1994; Dale, 1996]. Although not yet fully understood, it appears that during the early Palaeozoic, inshore/offshore trends mirrored those observed in modern phytoplankton [e.g., Dorning, 1981].

Several distribution maps of modern microphytoplankton have been published. Mudie and Harland [1996], for example, published a global map of modern dinocyst-acritarch geographic assemblages from surface sediments of the oceans. This map showed that some "provinces" are clearly latitudinally controlled, while others are partly located along the margin of a continent. These authors also discuss the importance of surface water currents, which partly control the distribution of modern "provinces."

The Ordovician dataset

Acritarch research only seriously began with the development of the oil industry during the 1960s, leading to the publication of a large number of scientific articles. An annotated bibliographical review of Ordovician acritarchs was published by Servais [1998], who listed some 700 references and about 250 genera from the Ordovician. The acritarch clade-team of the IGCP project no. 410 "The Great Ordovician Biodiversification Event" recently compiled a complete index of more than 1300 acritarch species described in the Ordovician Series [Servais *et al*., 2002].

The review of the Chinese literature shows that more than 50 publications deal with Ordovician acritarchs [Li *et al*., 2002], some 100 new species have been described from the Chinese Ordovician. Most of the publications concern investigations of the Yangtze Platform, and, in particular the early and middle Ordovician of this area. Nevertheless, the other Chinese palaeocontinents have also been investigated. Some papers document in detail the investigations of the early Ordovician of the North China Plate, while other publications are concerned with the Upper Ordovician of the Tarim Block. Unfortunatelly, Lower and Middle Ordovician sediments from the Tarim Block have not yet been investigated for acritarchs.

Published models of the palaeobiogeographical distribution of Ordovician acritarchs

Following the publication of a global distribution model of Silurian acritarchs, where several large-scale acritarch assemblages were interpreted as being controlled by palaeolatitude, Cramer and Díez [1974] were also the first to present a global distribution model for Ordovician acritarchs. They distinguished two major provinces, the "cold African" and the "warm American Palynological Unit." Vavrdová [1974], by comparing the European assemblages, came to a similar conclusion and also distinguished two "provinces" : the Baltic (Boreal) and the Mediterranean provinces. This two province model was largely used in subsequent papers and the terms Baltic and Mediterranean provinces were commonly employed despite the absence of a clear definition between these units.

In documentating Arenig acritarchs from the Meitan Formation of the Guizhou Province, south-west China (Yangtze Plaform), Li [1987] noted the presence of taxa, that were typically considered to have a "cold-water" distribution, in an area supposedly located in lower latitudes. Li [1987] therefore extended the Mediterranean province eastwards to include southern China. In the same paper Li mentioned the presence of a "fairly homogeneous Arenig assemblage extending from east Newfoundland through the Mediterranean area and the middle-east to south-west China."

In a subsequent paper Li [1989] redefined the so-called "Mediterranean" Province of Vavrdová [1974] by basing its recognition on the occurrence of the three genera *Arbusculidium*, *Coryphidium,* and *Striatotheca*. This definition of the "Mediterranean" Province, which was also called the "Peri-Gondwana Province" [e.g., Martin, 1982] has subsequently been widely used in the literature by most authors. The province was later recognized from other areas, such as Argentina [e.g., Ottone *et al.,* 1992], Pakistan [e.g., Tongiorgi *et al*., 1994], and Iran [e.g., Ghavidel-Syooki, 1997], so that, until recently, it has been considered to be a cold-water province extending from Argentina on the border of northern Gondwana to the Yangtze Platform [e.g., Vecoli, 1999].

In order to interpret the presence of "cold-water" forms in lower latitudes in South China, Li [1991] proposed a model of oceanic surface currents plotted on the palaeogeographic map of Scotese and McKerrow [1990]. This follows similar models used for other planktonic fossil groups, such as the graptolites [Finney and Chen Xu, 1990] and the chitinozoans [Paris, 1991]. Subsequently, Tongiorgi *et al.* [1995] published a similar model, by proposing that the extension of the Mediterranean province up to South China can be attributed to "a cool peri-Antarctic (peri-Gondwanan) oceanic current flowing along the subpolar margin of Gondwana and rising northwards up to South China."

Playford *et al.* [1995] subdivided the number of biogeographic provinces into seven units : North America, Baltica, Perigondwana (which was divided into three subprovinces : South America, Mediterranean, South China), North China and Australia. This model, however, has not been adopted by other authors. It basically has two major problems : (1) the provinces defined by Playford *et al.* [1995] are not the same age; (2) the different provinces are based on the presence/absence of individual morphotypes of the genus *Peteinosphaeridium*. Since the late Tremadoc, this extremely variable taxon is present world-wide [Servais and Mette, 2000]. However, although different morphotypes are reported from different localities, there is so far no evidence that the intraspecific variability reflects palaeogeographical differences rather than local environmental effects. For the same reason, it is difficult to define a "Baltic acritarch province," based only on the distinction of selected *Peteinosphaeridium* species, as proposed by Tongiorgi and Di Milia [1999]. Detailed investigations on the variability of *Peteinosphaeridium* and its related genera are needed to fully understand the palaeoecological and palaeogeographical distribution of this complex acritarch plexus.

Servais and Fatka [1997] noted that a model of two provinces can be retained for a time interval between the Tremadoc and the early Llanvirn. These authors stated that the "cold-water" assemblages at the northern border of Gondwana in the southern hemisphere include the diagnostic morphotypes *Arbusculidum filamentosum, Arkonia, Aureotesta, Coryphidium-Vavrdovella, Dicrodiacrodium, Frankea* and *Striatotheca*. The presence/absence of these taxa clearly delimits a boundary in Europe, that can be correlated with the Trans-European suture zone. None of the above mentioned taxa have indeed been recorded from Baltica.

Until recently, the warm-water province, used by many authors since the early 1970s, has never been adequately defined. Vavrdová [1974] noted a prevalence of acanthomorphic acritarchs in this province, which cannot be considered a distinctive parameter. It was Volkova [1997] who first defined this warm-water province on the basis of the presence of the distinctive genera *Aryballomorpha, Athabascaella,* and *Lua*.

These morphotypes are described from lower latitude areas [e.g., Martin and Yin, 1988], but never from locatities of southern Gondwana or adjacent continents. This province can also be recognized in the late Tremadoc, a time interval for which data exist for areas in both the low and middle to high latitudes of the southern hemisphere.

PALAEOBIOGEOGRAPHY OF EARLY TO MIDDLE ORDOVICIAN ACRITARCHS

A tentative model of biogeographic zones

The dataset of the Ordovician acritarch literature [Servais, 1998; Servais *et al*., 2002] clearly shows that many areas and time intervals are not yet adequately covered. It is almost impossible to present a global acritarch distribution scenario for the late Ordovician, because only limited data are available world-wide, excepted for the continent Laurentia. On the other hand, it is also highly speculative to define provinces (for example : Australia) from areas that have not yet been investigated in great detail. However, the dataset for the early and middle Ordovician is more complete allowing a tentative model of global acritarch distribution to be constructed.

If one considers that Ordovician acritarchs probably showed a similar distribution scheme as modern dinoflagellate cysts do, it seems reasonable to assume that a limited number of Ordovician acritarch morphotypes may indicate temperature-related affinities. Many taxa may indicate specific ecologic conditions, while others may be useful for the interpretation of inshore-offshore trends. Only a few taxa may indicate possible climatic belts, that may be primarily related to palaeolatitudes. Some widespread taxa, such as, for example, *Baltisphaeridium*, *Goniosphaeridium*, and *Micrhystridium* are recorded in most environments and from all parts of the world. They are thus not very useful for palaeogeographic reconstructions. Other taxa, however, may reflect colder or warmer environments.

Figure 2 illustrates a tentative distribution model of selected morphotypes of the early to middle Ordovician, that have been considered in the literature to be palaeogeographically important : *Arbusculidium filamentosum*, *Coryphidium-Vavrdovella*, and *Arkonia-Striatotheca* are early to middle Ordovician morphotypes that so far have only been recorded from areas considered to be located at higher latitudes (more common in latitudes between 60º S and the south pole, but also present to a lesser extend at latitudes between 30º and 60 ºS). These taxa are always absent from Baltica, Laurentia, and North China. The galeate and diacromorph taxa, which are very common in the early Ordovician seem to be more abundant in areas of higher latitudes, although they are also found at lower latitudes, such as the Baltica continent. On the other hand, typical warm-water forms, considered to be diagnostic for the Tremadoc warm-water province by Volkova [1997] (*Aryballomorpha, Athabascaella, Lua*) are taxa typical of the areas located around the equator (reaching from ± 20º N to 30º S, rarely to 60º S). The genus *Rhopaliophora* appears to be more common at low latitudes, but can also be found in higher latitudes. However, it appears to be almost absent from localities of the northern rim of Gondwana in the southern hemisphere.

It is important to consider that this first model of climate-related morphotypes in the early Ordovician presented in figure 2 is only tentative. Future studies will show if some

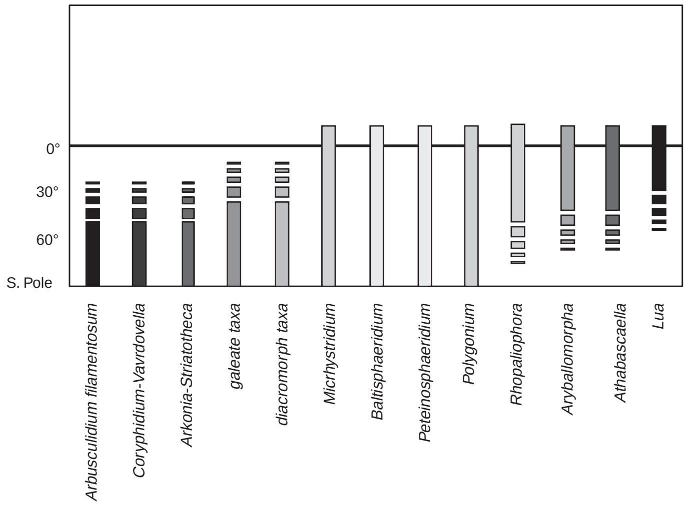

FIG. 2. – An initial simplified, tentative model to explain the latitudinal distribution of selected Early to Middle Ordovician acritarchs that are possibly related to temperature. For an explanation, see text.
FIG. 2. – *Un premier modèle simplifié et expérimental qui pourrait expliquer la distribution latitudinale d'une sélection de certains taxons d'acritarches de l'Ordovicien inférieur à moyen possiblement liés à la température. Pour des explications voir le texte.*

of these taxa have a restricted geographical distribution and thus occupied different climatic zones (e.g., arctic to cool-temperate, temperate, cool-temperate to tropical).

The palaeogeographic distribution of acritarchs plotted on the most recent Ordovician reconstruction

Although many authors have used a two "provinces" subdivision, only a few publications have illustrated the plotting of available acritarch data on palaeogeographic reconstructions. Among these papers, Vavrdová [1990] illustrated the distribution of a selection of acritarch species characterizing the high-latitude peri-Gondwanan sea, whereas Servais and Fatka [1997] plotted *Arbusculidium filamentosum*, *Dicrodiacrodium,* and *Frankea* on a palaeogeographical reconstruction.

However, it has not been attempted to plot on a global reconstruction both the distinctive taxa of the late Tremadoc "warm-water" assemblage defined by Volkova [1997] (the genera *Aryballomorpha, Athabascaella,* and *Lua*) and the morphotypes indicating the Arenig "cold-water" assemblage defined by Li [1989] (the taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca*).

In the present study, all available data from the literature have been used to plot the occurrence of the taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* (peri-Gondwanan taxa) and the genera *Aryballomorpha, Athabascaella,* and *Lua* (warm-water taxa) on one of the most recently published reconstructions, the global reconstruction at the early Ordovician (± – 480 Ma) of Li and Powell [2001].

The datasets used for the plotting are the following : *Arbusculidium filamentosum* has recently been reviewed in detail by Fatka and Brocke [1999], whereas the distribution of all elements of the genus *Striatotheca* is based on the detailed review of Servais [1997]. The distribution of *Coryphidium* is based on the genus revision of Servais [1993]. The warm-water genera *Aryballomorpha, Athabascaella,* and

Lua are recorded from much fewer localities. Their distribution is documented by Volkova [1997] and adopted here.

Figure 3 illustrates the distribution of both the late Tremadoc "warm-water" assemblage defined by Volkova [1997] and the Arenig "cold-water" assemblage defined by Li [1989]. This latter assemblage can partly be recognised in the late Tremadoc, because species of the genera *Coryphidium-Vavrdovella* and *Arkonia-Striatotheca* already appear during this time interval [Servais and Mette, 2000].

According to the distribution of taxa on the reconstruction, the "warm-water" taxa *Lua, Athabascaella,* and *Aryballomorpha* are found in areas situated between latitudes 30^{o} N and 45 ^{o}S. They are reported from Alberta, Canada ; Texas, USA ; Hunjiang, North China ; Yichang, South China, as well as from Öland and Estonia on the Baltica continent. However, these genera are not recorded in the southern part of Gondwana nor from peri-Gondwana. The distribution of the "cold-water" taxa is more complex. Described from many areas of Gondwana and peri-Gondwana (Argentina, Brazil, Bolivia, Newfoundland, Ireland, United Kingdom, Belgium, Germany, France, Spain, Portugal, Morocco, Algeria, Tunisia, Lybia, Sardinia, Bohemia, Hungary, Bulgaria, Turkey, Saudi-Arabia, and Jordan), these distinctive morphotypes are also reported from Pakistan, Iran and southern China. They have not yet, however, been recorded from Australia and North China. It therefore seems that this "province" is, as has previously been mentioned, distributed along the margin of Gondwana in the southern hemisphere. However, it is difficult to continue to attribute this geographical assemblage to a "cold-water" environment, as this "province" apparently extends from the south pole to the equator.

This result of the plotting of a large "province" along the margin of Gondana shows some similarities with recent results in Silurian acritarch palaeogeography. Le Hérissé and Gourvennec [1995] showed that Cramer and Díez's [1974] provincialism model, which was largely used for over 25 years by most acritarch workers, has to be modified. Instead of being simply latitudinally controlled, the Silurian acritarch bioprovinces seem to be the result of a complex interrelation of many parameters such as continental distribution, latitudinal position, environmental conditions, and oceanic currents. Therefore, it appears that the early to middle Ordovician "Meditterranean" province is probably partly related to continental arrangement (facies-controlled) as well as being climatically controlled.

The Ordovician acritarch palaeobiogeography of China

Figure 3 illustrates that the different Chinese plates, and in particular the South China Plate, occupied palaeogeographical positions that are essential for the understanding of the global distribution of Ordovician acritarchs.

While the early Ordovician acritarchs of North China can be compared with the sequences from other localities at lower latitudes (e.g. with the Tremadoc of Texas and of Alberta) [Martin and Yin, 1988], the material from the Yangtze Platform, described in various publications and investigated in detail in three PhD theses [Li, 1991; Xu, 1995; Brocke, 1998], includes elements considered to be of "warm-water" affinity in the late Tremadoc and the taxa with a "cold-water" affinity in the Arenig. It is beyond the scope of the present paper to review in detail the palaeoecology and palaeogeography of the acritarchs of this continent, from which some authors reported changing affinities

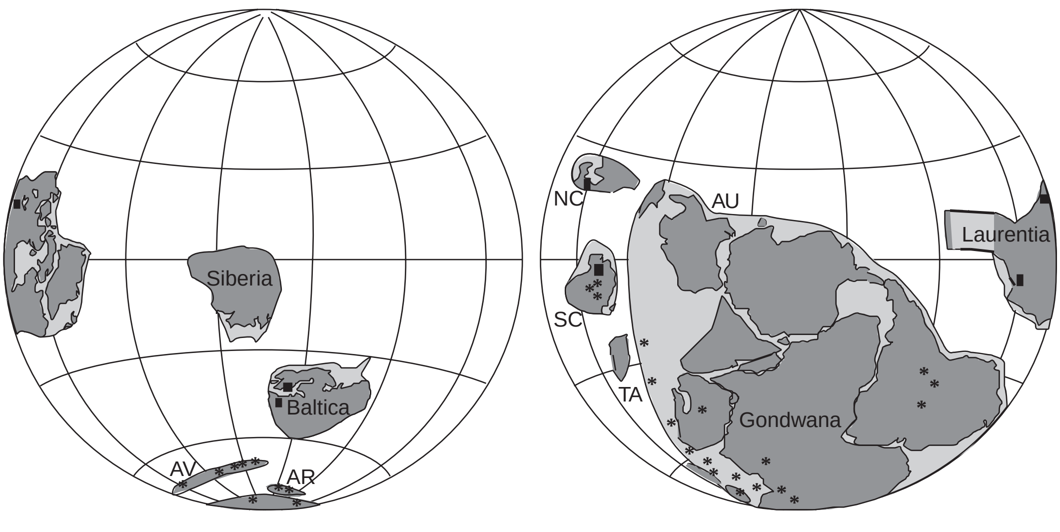

FIG. 3. – Distribution of the distinctive acritarch taxa of the two early to middle Ordovician "provinces" on a palaeogeographical reconstruction of Li and Powell [2001]. Black squares represent the occurrences of the genera *Aryballomorpha*, *Athabascaella*, and *Lua*, typical of the "warm-water province" of Volkova [1997]. Stars represent the occurrences of the taxa *Arbusculidium filamentosum, Arkonia-Striatotheca,* and *Coryphidium-Vavrdodella*, that are characteristic of the "Mediterranean" or "peri-Gondwanan province" defined by Li [1989]. For further explanation see text.

FIG. 3. – *Distribution des taxons distinctifs des deux "provinces" de l'Ordovicien inférieur à moyen sur une reconstruction paléogéographique de Li et Powell [2001]. Les carrés noirs représentent la présence des genres* Aryballomorpha, Athabascaella *et* Lua*, qui sont typiques de la "province d'eaux chaudes" de Volkova [1997]. Les étoiles réprésentent la présence des taxons* Arbusculidium filamentosum, Arkonia-Striatotheca, *et* Coryphidium-Vavrdodella, *qui sont caractéristiques de la " province méditerranéenne" ou "péri-Gondwanienne" definie par Li [1989]. Pour d'autres explications, voir le texte.*

in the upper Arenig [Tongiorgi *et al.*, 1998]. The important result, however, is to confirm the presence of the taxa *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* in South China at very low latitudes, around the equator and possibly reaching 30° S.

Acritarchs from the Tarim Plate are so far known only from the Upper Ordovician [e.g., Li, 1995; Li and Wang, 1997]. Clear palaeogeographical affinities cannot be identified for this period. Nevertheless, the assemblages from the late Ordovician of Tarim show greatest similarities with the material of the same age described from Baltica.

CONCLUSIONS

Although the Ordovician acritarch dataset remains incomplete, it appears evident that selected acritarch morphotypes show a recognizable distribution pattern. A tentative latitudinal distribution model can be proposed for the interval between the late Tremadoc and Arenig. The taxa *Arbusculidium filamentosum*, *Coryphidium-Vavrdovella,* and *Arkonia-Striatotheca* are morphotypes that appear more common at high latitudes (cold to temperate waters), while *Aryballomorpha, Athabascaella, Lua* are taxa typical of areas located around the equator and at low latitudes, and thus, they possibly represent warm water indicators. Many acritarch genera, such as *Baltisphaeridium*, *Goniosphaeridium*, *Micrhystridium* and *Peteinosphaeridium* have a limited palaeogeographical potential, as they occur in all areas and distributed through all latitudes. They therefore appear less temperature sensitive.

Since the 1970's, two different geographical acritarch assemblages have been identified. In this work they are plotted for the first time on a recent palaeogeographical reconstruction [Li and Powell, 2001].

The "warm-water" assemblage which can be identified in the late Tremadoc is reported from areas of low to intermediate latitudes.

The late Tremadoc to Arenig "Mediterranean" or "peri-Gondwana" province can easily be distinguished. This palaeogeographic assemblage is distributed around the border of Gondwana in a zone reaching from Argentina through northern Africa and peri-Gondwana up to Iran, Pakistan, and southern China. The generally adopted interpretation that this geographical assemblage is controlled by palaeolatitudes and that it can be considered as typically "cold-water" has to be revised, as the distribution of this "province" appears to be more related to the continental arrangement of the border of Gondwana, rather than to latitudes.

South China shows both "warm-water" elements and the typical taxa of the"peri-Gondwana" province. It is therefore one of the areas that shows typically mixed assemblages. Although it remains difficult to clearly define a "Baltic" province, it is important to note that between the latest Tremadoc and the early Llanvirn a clear distinction of the acritarch assemblages between peri-Gondwana and Baltica is possible.

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