Llandovery miospore biostratigraphy and stratigraphic evolution of the Paraná Basin, Paraguay – Palaeogeographic implications

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Key words. – Miospore, Paraguay, Llandovery, Palaeogeography, Phytogeography.

Abstract. – The Paraná Basin covers 1,600,000 km^2 including parts of southern Brazil, Paraguay, Uruguay and Argentina. It contains rocks ranging from the Ordovician to Tertiary in age. The present study is focused on the Itacurubí Group, of Llandovery age, from Paraguay. The sedimentology and palynology have been studied in three boreholes from the central part of Paraguay. The Itacurubí Group consists of the Euzébio Ayala, Vargas Peña and Cariy Formations. It corresponds to a complete transgressive – regressive cycle with maximum flooding in the Vargas Peña Formation. The sediments of the group were deposited in a glacio-marine regime and are included in the second order sequence.

The palynofacies are dominated by acritarchs and chitinozoans, with miospores rare. Among the latter, cryptospores are most abundant and trilete spores very rare. The miospore assemblages are typical of the Llandovery. The presence of *Laevolancis divellomedia* and the successive first occurrence of the trilete spore genus *Ambitisporites,* followed by *Archaeozonotriletes*, allow the recognition of three biozones : *divellomedia I, divellomedia II* and *chulus-nanus*. Correlations between the three boreholes based on miospore biostratigraphy and sequence stratigraphy techniques are similar.

The miospore assemblages have important palaeogeographic implications :

(1) Ordovician / Silurian miospore assemblages, identified in South America are similar to those described in palaeogeographically distinct regions such as China, UK, Belgium, USA etc. This suggests that the phytogeographical differentiation proposed by Gray *et al.* [1992], with a Malvinokaffric Realm characterised by smooth tetrads and an extra-Malvinokaffric Realm characterised by ornamented tetrads, has to be reconsidered. Clearly, the same miospores are recovered from both regions, no matter if they are close to the palaeo-equator or the palaeo-pole, as is the case in Paraguay. These findings suggest that the same vegetation could survive under various climates.

(2) In theory, large oceans could be impassable geographic barriers for land plant miospores larger than 25 μm in diameter. As similar miospore assemblages occur, around the Ordovician – Silurian boundary, on the Gondwana, Avalonia and Laurentia plates, it seems likely that these palaeo-continental plates were in close proximity permitting the expansion of the vegetation through these continents. Therefore, palaeogeographic reconstructions with narrow oceans between the continents better explain early miospore biogeographies in early Silurian times.

(3) Maps produced by Dalziel *et al.* [1994] better explain the diachronism of trilete spore first appearances : Hirnantian in Turkey, Rhuddanian in Saudi Arabia, early Aeronian in Libya, late Aeronian in Paraguay, latest Aeronian in UK, and possibly Telychian in USA.

(4) The Baltica plate could possibly have been isolated by a geographic barrier during the Ashgill and the Llandovery, as only simple naked tetrads are known from that plate. The first appearance of the trilete spores in Götland during the early Wenlock could correspond to the end of this geographic isolation. This apparent isolation of the Baltica plate could be due to a lack of data.

Les miospores au Llandovérien du Paraguay – implications paléogéographiques

Mots clés. – Miospore, Paraguay, Llandovérien, Paléogéographie, Phytogéographie

Résumé. – Le bassin du Paraná est le plus vaste d'Amérique du Sud. Il représente une superficie de plus de 1 600 000 km^2. Il couvre une partie du sud du Brésil, de l'est du Paraguay, de la partie centrale de l'Uruguay et du nord est de l'Argentine. Il est composé de roches datées depuis l'Ordovicien jusqu'au Tertiaire. Les couches étudiées ne concernent que le Groupe Itacurubí, d'âge llandovérien, au Paraguay. Trois sondages de la partie centrale du Paraguay, à l'ouest d'Asunción, font l'objet d'une étude tant sédimentologique que palynologique, où seules les miospores sont étudiées. Les résultats obtenus sur la base des chitinozoaires ont déjà été publiés [Grahn *et al.*, 2000]. Le groupe Itacurubí correspond latéralement à la formation de Vila Maria, au Brésil. Il est composé, stratigraphiquement de bas en haut, des formations de Euzébio Ayala, de Vargas Peña et de Cariy. Elles représentent un cycle sédimentaire transgressif – régressif complet, où les sédiments de la formation de Vargas Peña correspondent à la période d'immersion maximale. La succession sédimentaire est étudiée en termes d'analyse stratigraphique séquentielle. Cette analyse permet de corréler les trois sondages entre eux. Les sédiments du groupe Itacurubí, ainsi que ceux de la formation de Vila Maria se sont déposés dans un contexte glacio-marin.

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Les assemblages de palynomorphes observés dans les échantillons sont dominés par les acritarches et les chitinozoaires, d'origine marine, alors que les miospores, d'origine terrestre, sont rares. Parmi ces dernières, les cryptospores sont nettement plus abondantes que les spores trilètes. En dépit de la pauvreté en miospores, il est possible de reconnaître les assemblages typiques du Llandovérien tels qu'ils sont connus dans de nombreuses localités de par le monde. Trois biozones peuvent être distinguées, stratigraphiquement de bas en haut : *divellomedia I, divellomedia II, chulus – nanus*. Les principales caractéristiques sont la présence de *Laevolancis divellomedia*, l'apparition des premières spores trilètes (*Ambitisporites*) à la base de la Biozone *divellomedia II* et l'apparition des premiers *Archaeozonotriletes* à la base de la Biozone *chulus – nanus* sus-jacente.

Les assemblages définis permettent de réaliser des corrélations entre les sondages. Ces corrélations confirment parfaitement les corrélations basées sur l'analyse séquentielle.

Les observations réalisées ont également plusieurs implications paléogéographiques.

1 – On retrouve ici les mêmes assemblages de miospores qu'au Brésil ou en Argentine dans des couches d'âge similaire, mais aussi dans des régions plus éloignées comme en Chine, en Arabie Saoudite, au Royaume-Uni , en Belgique, aux USA etc. Ceci indique que, contrairement à ce qui avait été suggéré auparavant [Gray *et al.,* 1992], il n'existe vraisemblablement pas de différenciation phytogéographique au Silurien inférieur. Ces auteurs distinguaient un domaine Malvinokaffric où les tétrades sont lisses, d'un domaine extra-Malvinokaffric où les tétrades sont ornementées. Cependant, quelles que soient les régions étudiées les mêmes tétrades sont observées. Les plantes, à cette époque, devaient donc être capables de supporter des climats très différents puisque leurs miospores sont les mêmes depuis des régions proches du paléo-équateur jusqu'à des régions proches du paléo-pôle, comme le montre les résultats obtenus ici.

2 – En théorie, de larges océans pourraient constituer des barrières géographiques difficilement franchissables pour des miospores de plus de 25 µm de diamètre. Comme les mêmes assemblages en miospores sont connus, au Silurien inférieur, dans les régions nord et ouest du Gondwana, en Avalonia et Laurentia, ces continents devaient être très proches les uns des autres, avec des connexions terrestres entre eux. Ces déductions sont contraires à la plupart des reconstitutions paléogéographiques. Les cartes publiées par Dalziel *et al.* [1994] correspondent le mieux à nos observations.

3 – De plus, les reconstitutions proposées in Dalziel *et al.* [1994] permettent de visualiser plus clairement le diachronisme des niveaux d'apparition des premières spores trilètes qui sont datées de l'Hirnantien en Turquie, du Rhuddanien en Arabie Saoudite, de l'Aéronien inférieur en Libye, de l'Aéronien supérieur au Paraguay et de l'Aéronien le plus supérieur au Royaume-Uni. Les données stratigraphiques aux USA ne sont pas suffisamment précises, mais il se pourrait que les spores trilètes n'y soient pas connues avant le Telychien.

4 – La plaque baltique semblerait être isolée au moins au cours de l'Ashgillien et du Llandovérien car les miospores y sont seulement représentées par de rares tétrades d'une seule espèce [Le Hérissé, 1989]. Les premières spores trilètes y apparaissent pour la première fois au cours du Wenlockien inférieur. Cet événement pourrait correspondre à la fin de l'isolement de cette plaque tectonique par une barrière géographique, ce qui aurait permis aux plantes de coloniser ce continent depuis les plaques continentales Laurentia et Avalonia. Cependant, le manque de données sur les miospores en provenance de Baltica pourrait être la cause de cet apparent isolement.

GEOLOGICAL SETTING

Introduction

The Silurian rocks of the Paraná Basin, in Paraguay, have been studied since the early geological works of Harrington [1950], Eckel [1959] and Wolfart [1961] based on outcrop information from the central part of eastern Paraguay (fig. 1).

The first subsurface information on Palaeozoic rocks of Paraguay was published in 1982 in an internal report of the Shell-Pecten Company, describing two boreholes : Asunción-1 and Asunción-2. Zalán *et al.* [1987] correlated these boreholes with a purportedly coeval section in the Paraná Basin in Brazil. However, this correlation was based only on lithology and was not sustained by any biostratigraphic control. Milani and Daemon [1992] restudied these boreholes and prepared a preliminary biostratigraphic subdivision of the Ordovician – Devonian interval, based on chitinozoans and other palynomorphs, but strongly controlled by lithostratigraphy. More accurate Silurian biostratigraphic dates in eastern Paraguay were presented by Wood and Miller [1991, 1997], Gray *et al.* [1992] and Grahn *et al.* [2000]. In this paper, a new interpretation of the Silurian rocks of the boreholes Asunción – 1, RD – 116 and RD – 115 has been undertaken on a north – south section located in the central part of eastern Paraguay (fig. 2).

Silurian stratigraphic framework

The Paraná Basin is the largest sedimentary basin in South America, covering approximately 1,600,000 km^2, including parts of south Brazil, east Paraguay, central Uruguay and northeast Argentina. It contains sediments deposited from the Ordovician through Tertiary periods. In Brazil, the pre-Carboniferous strata of this basin occur in two distinct sub-basins : the Alto Garças Sub-basin in the north and the Apucarana Sub-basin in the south (fig. 1). Recently, Grahn *et al.* [2000] introduced the term East Paraguay Sub-basin to define a new compartment of the Paraná Basin, characterised by sedimentological and biostratigraphical aspects of the pre-Carboniferous sediments in Paraguay. The three sub-basins had different sedimentological histories during this time interval. There are more lithological similarities between the Alto Garças and East Paraguay Sub-basins, than between these sub-basins and the Apucarana Sub-basin.

The Silurian sequence in the East Paraguay Sub-basin is composed, in lithostratigraphic terms, of the Itacurubí Group [Harrington, 1972], which is equivalent to the Vila Maria Formation in the Alto Garças Sub-basin [Pereira, 2000]. This group overlays beds of the Caacupé Group that are Llanvirn to late Ashgill in age [Wiens, 1995].

The Itacurubí Group consists of three formations. The lowest is the Euzébio Ayala Formation. The predominant li-
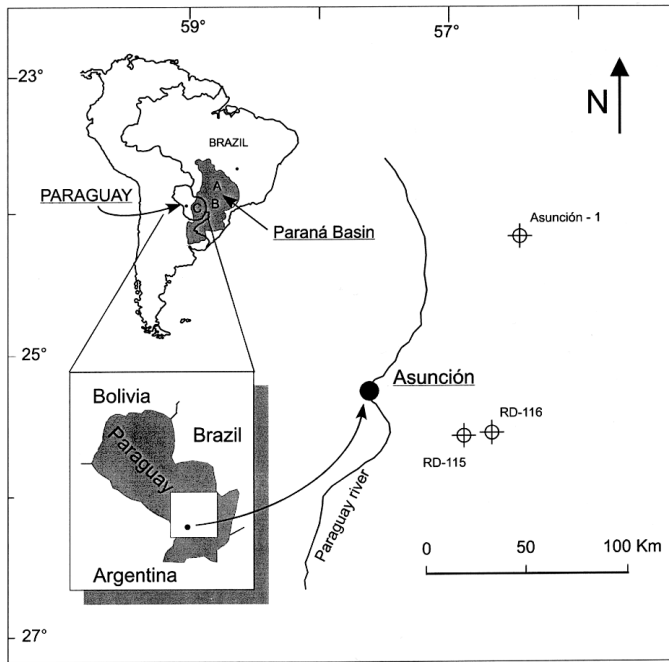
FIG. 1. – Locality map showing the location of the Paraná Basin ; the Alto Garças Sub-basin (A), the Apucarana Sub-basin (B) and the east Paraguay sub-basin (C) ; boreholes RD-115, RD-116 and Asunción-1.
FIG. 1. – *Position du bassin du Paraná en Amérique du Sud et de ses sous unités de Alto Garças (A), de Apucarana (B) et de l'est du Paraguay (C). Localisation des sondages RD-115, RD-116 et Asunción-1 au Paraguay.*

thologies in this formation are yellowish to brownish sandstones with intercalated mudstones. Recently, diamictites, sandstones and shales, attributed to a transgressive glacial-marine environment, were decribed by Borghi *et al.* [1997]. In the boreholes, the formation is composed of fine to coarse sandstones and siltstones. The fine sandstones are laminated and wave-cross stratifications are frequent. The coarser sandstones are normally massive and their original lamination is rarely preserved. Convoluted beds, pillar and dish sedimentary structures are present in the deformed beds. The siltstones are inserted between the sandstones and show different bioturbation rates. Wavy-linsen structures are frequent in the siltstones.

The Vargas Peña Formation overlays the Euzébio Ayala sediments. The sediments of the Vargas Peña Formation crop out in a large area of central east Paraguay. The sediments consist of micaceous shales that are strongly weathered in the outcrops. In the boreholes, this formation is defined by a thick and monotonous succession of black shales and siltstones. Wavy-linsen structures and hummocky cross stratification are abundant and some levels are strongly bioturbated.

The youngest sediments of the group belong to the Cariy Formation. This unit is basically composed of sandstones. In outcrop and the boreholes hummocky cross stratification is the most abundant sedimentary structure. In the boreholes, the formation is unconformably overlain by younger glacial sediments of the Coronel Oviedo Formation of post Frasnian age, or locally by early Devonian sediments in central east Paraguay.

Sedimentological evolution of the Itacurubí Group

The north-south section (fig. 2) shows a stratigraphic correlation of the Silurian rocks in central Paraguay. This section was constructed using the transgressive surface located at the base of the Vargas Peña Formation as a datum.

The sediments of the Itacurubí Group represent a complete transgressive – regressive cycle. The sandstones of the Euzébio Ayala Formation mark the base of this cycle. These sandstones are organised in a coarsening and thickening upward succession. The sandstone facies association indicates that the sediments were deposited in a deltaic environment. The Euzébio Ayala sediments are overlain by the transgressive surface. In borehole RD-116, this surface is characterised by the presence of oolites (Fe $^{++}$). Shales and siltstones of the Vargas Peña Formation have been deposited above this surface. The facies association of this unit registered the maximum flooding in the Silurian. Pereira [2000], using total organic carbon analysis, identified the maximum flooding surface in the interval between 210 – 230 meters in borehole RD-116. Offshore conditions are predominant in the whole thickness of the Vargas Peña Formation. The sandstones associated with the Cariy Formation define the top of the transgressive-regressive cycle. This sandstone was deposited in shoreface conditions, defined by the frequent presence of hummocky cross stratification. These sediments are unconformably overlain by younger successions.

The sedimentary succession of the Itacurubí Group can be analysed in terms of the genetic stratigraphy. All the sediments are included in a second order sequence of Silurian age. The lower sandstones in this section probably represent the lowstand system tract of this sequence. The transgressive surface delimits the transgressive system tract, represented by the siltstones and rare sandstones of the lower part of the Vargas Peña Formation. The pelitic section of this unit includes the maximum flooding surface of the Silurian sequence. The shallow marine sandstones of the Cariy Formation represent the highstand system tract.

The sedimentary framework is very similar to the sedimentary evolution of the Vila Maria Formation described in the Alto Garças Sub-basin. This Silurian unit was deposited in the glacial-marine context in which three phases are recorded [Pereira *et al.*, 1998]. The first represents the glacial maximum, the second defines the post-glacial phase, and the third marks the isostatic post-glacial phase. In this sense, the facies association observed in the Itacurubí Group may be considered as accumulating in a peri-glacial position in relation to the Silurian deposits of the Paraná Basin in Brazil.

PALYNOLOGICAL RESULTS

Introduction

Silurian miospores from the Paraná Basin have been described from a number of different localities, mainly located in Brazil [Gray *et al.,* 1985 ; Melo, 1997 ; Mizusaki *et al.,* 2002], but also in Paraguay from boreholes and outcrops close to area studied herein [Gray *et al.*, 1992].

The present study utilised 53 palynological samples from boreholes RD-115, RD-116 and Asuncion 1 (fig. 1). Few miospores have been observed. Marine palynomorphs, acritarchs and chitinozoans are abundant. Chitinozoans
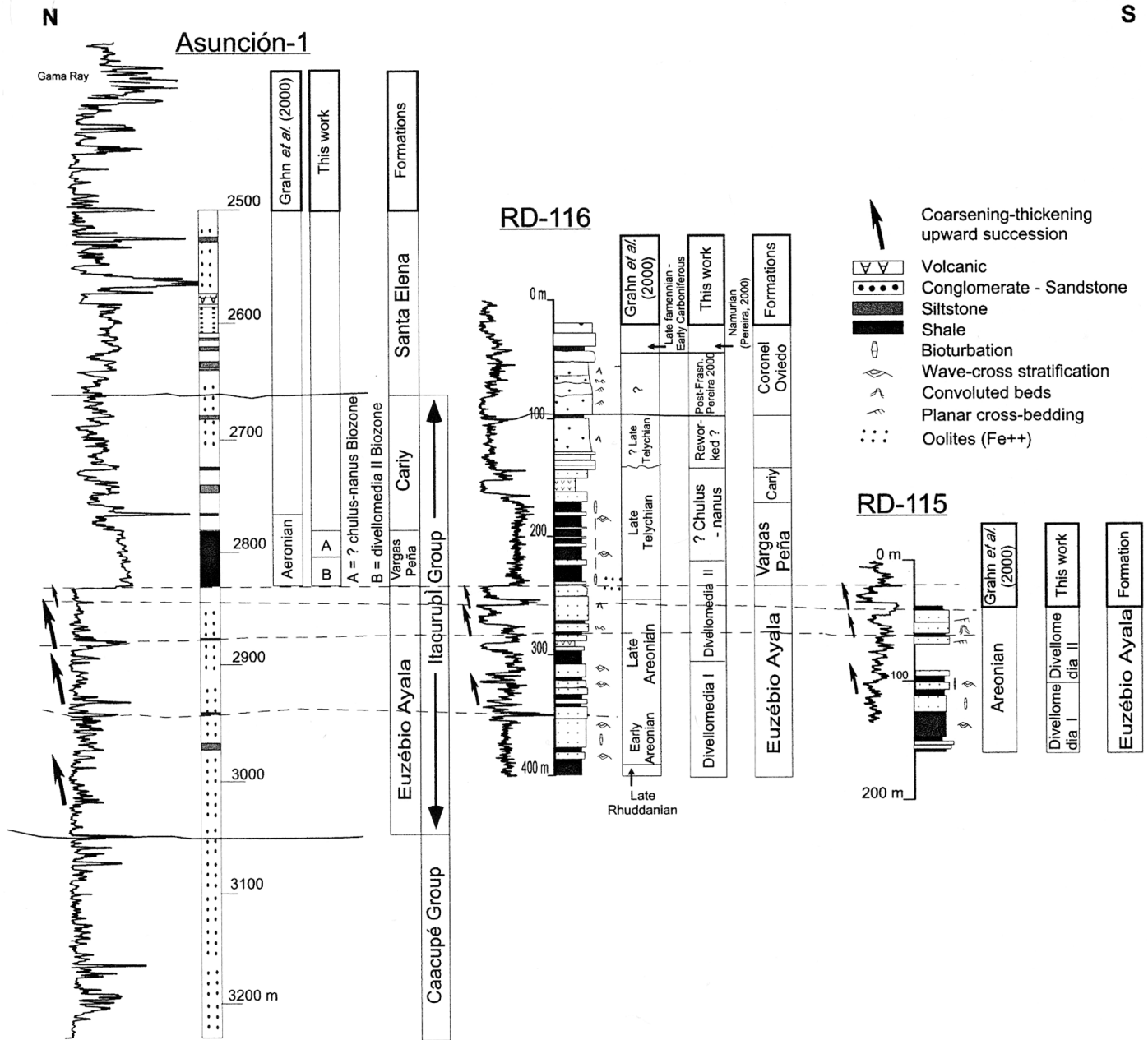
FIG. 2. – North-south stratigraphic section of Ordovician and Silurian sediments from the Paraná Basin, Paraguay. Without horizontal scale. For borehole location see figure 1.
FIG. 2. – *Coupe stratigraphique nord-sud dans les sédiments de l'Ordovicien et du Silurien du bassin du Paraná, Paraguay. Sans échelle horizontale. Localisation des sondages voir figure 1.*

from the same samples have been studied by Grahn *et al.* [2000]. They concluded that all the samples belong to the Llandovery. They defined two total range zones and three concurrent range subzones from the Rhuddanian to the Telychian.

Despite the low thermal alteration, the miospores are poorly preserved. The miospore assemblages are dominated by cryptospores, with trilete spores very rare. Because the material is badly preserved, the number of true trilete spores could be underestimated. Indeed, the first genus of trilete spores, *Ambitisporites* HOFFMEISTER 1959, is very similar to the cryptospore genus *Imperfectotriletes* STEEMANS *et al.* 2000. The proximal face of the latter has an imperfect trilete structure that is in fact a tear, resulting from

the physical disruption of a permanent cryptospore tetrad [Steemans *et al.,* 2000]. Therefore, it is difficult in this material to differentiate torn specimens of true trilete spores, from isolated specimens of cryptospores with a pseudo trilete mark.

RD-116 borehole

Laevolancis divellomedia (CHIBRIKOVA 1959) BURGESS & RICHARDSON 1991 is present in all samples except the last six which are very poor. Envelope-enclosed cryptospores are only present in the lower part of the borehole up to 236.85 m. The first trilete spore *Ambitisporites avitus* MORPHON *sensu* STEEMANS *et al.* 1996 occurs at 300.39 m,

and is present but very rare in all samples. Through the entire borehole, only one specimen of *Archaeozonotriletes chulus* MORPHON *sensu* STEEMANS *et al.* 1996 has been observed, occurring at 224.20 m.

RD-115 borehole

Very few miospores have been observed. Two possible specimens of trilete spores are observed at 101.35 and 64.40 m. Rare envelope-enclosed cryptospores are present at 150.35 and 99.20 m. *Laevolancis divellomedia* is present in all samples from level 139.45 m.

Asunción-1 borehole

Very few miospores are present. No envelope-enclosed cryptospores have been identified. One specimen of *Ambitisporites* and one specimen of *Archaeozonotriletes* have been identified at 2,815 m. *Laevolancis divellomedia* is present in the lowest sample at 2,835 m.

Biostratigraphic interpretations

In the Llandovery, the miospore zonation scheme [Steemans *et al.,* 2000] is subdivided into two assemblage zones. The first is subdivided in two interval zones, each of which is subdivided in two sub-zones. This biostratigraphic scheme is based on the first occurrence of certain species, the first occurrence of trilete spores, and the relative abundance of envelope-enclosed cryptospores.

The first appearance of true trilete spores (*Ambitisporites*) marks the base of the *Imperfectotriletes* β sub-biozone. The boundary between the *divellomedia* α and β sub-biozones is marked by the end of abundant envelope-enclosed cryptospores and the beginning of abundant trilete spores (*Ambitisporites*).

However, the first appearance of the oldest trilete spores seems to be diachronous from the latest Ordovician to the Llandovery. Indeed, the oldest trilete spores are Hirnantian in age from Turkey [Steemans *et al.,* 1996], Rhuddanian in age from Saudi Arabia [Steemans *et al.,* 2000], upper Aeronian from Libya [Richardson, 1988], and uppermost Aeronian from UK [Burgess, 1991]. In northern Brazil, the first trilete spores (*Ambitisporites*) appear in the upper Aeronian, as dated by chitinozoans and acritarchs, from the Tiangua Formation, Serra Grande Group [Le Hérissé *et al.,* 2002]. Stratigraphic data on the first trilete spores are not accurate on the Laurentia plate. Specimens of *Ambitisporites* have been reported by Pratt *et al.* [1978] from the early Silurian of Virginia. However, Gray *et al.* [1992] consider that trilete spores only become dominant in the Telychian. In Gotland, Sweden, the first trilete spores are observed in the earliest Wenlock [Le Hérissé, 1989].

Local biozonation schemes are required because of the diachronism of trilete spore first occurrences in the Llandovery. In Paraguay, the first occurrence of *Ambitisporites* is dated as late Aeronian in age by chitinozoans from borehole RD-116. The *divellomedia* interval biozone is here subdivided into a *divellomedia* I sub-biozone without trilete spores and a *divellomedia* II sub-biozone with rare *Ambitisporites*, below the first occurrence of *Archaeozonotriletes* that characterises the overlying assemblage biozone. The boundary between the *divellomedia* I and II sub-biozones is within the late Aeronian, as dated by chitinozoans (fig. 3).

The base of the *chulus-nanus* assemblage biozone is Telychian in age in borehole RD-116. The first occurrence of *Archaeozonotriletes* is also dated as Telychian in age in Libya [Al-Ameri, 1980 ; Richardson, 1996] and, probably, also in Saudi Arabia [Wellman *et al.,* 2000]. However, no *Archaeozonotriletes* has been found below the Wenlock in the UK [Burgess and Richardson, 1991]. No information is available from the Laurentia plate.

PALAEOGEOGRAPHIC IMPLICATIONS

The earliest miospore-producing land plants were of small size (a few millimetres to a few centimetres tall). They probably thrived in wet habitats, nearshore or inland. Cryptospores and the earliest trilete spores can be dispersed by wind but only over short distances (a few meters to a few kilometres) as most of them are larger than 25 μm in diameter [Gray, 1985 ; Streel *et al.,* 1990 and therein]. The main agents of dispersal are the rivers and the sea currents. Rivers may transport the miospores to the lakes or to the seas where they are deposited a short distance from the shoreline. Because of miospore size and weight, the currents cannot also transport all of them over long distances. Sea currents may transport some at a larger distance from coasts, but never over very long distances. The same is true for the distribution of marine palynomorphs like acritarchs and chitinozoans which can show clear provincialism [Paris, 1995 ; Le Hérissé *et al.,* 1997]. Because these marine palynomorphs are not transported over long distances, the assemblages are not mixed together (consequently, this indicates that the sea currents probably cannot transport miospores over long distances either). Even if, by chance and with a long time available, a few miospores would be disseminated over long distances, studies on isolated islands [Tryon, 1970, 1972], endemic areas, and geographic speciation in modern tropical American ferns demonstrate that long-distance (e. g. 1,600 km) migration normally induces genetic isolation in the new colony. In consequence, differences in assemblages appear progressively. All these

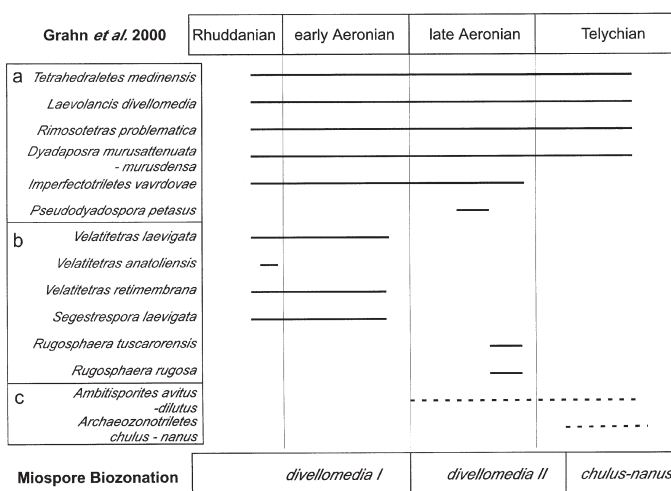| Grahn *et al.* 2000	Rhuddanian	early Aeronian	late Aeronian	Telychian
a *Tetrahedraletes medinensis*				
Laevolancis divellomedia				
Rimosotetras problematica				
Dyadaposra murusattenuata - murusdensa				
Imperfectotriletes vavrdovae				
Pseudodyadospora petasus				
b *Velatitetras laevigata*				
Velatitetras anatoliensis				
Velatitetras retimembrana				
Segestrespora laevigata				
Rugosphaera tuscarorensis				
Rugosphaera rugosa				
c *Ambitisportes avitus -dilutus*				
Archaeozonotriletes chulus - nanus				
Miospore Biozonation	*divellomedia I*		*divellomedia II*	*chulus-nanus*

FIG. 3. – Miospores stratigraphic ranges compared with the chronostratigraphic scale published in Grahn *et al.* [2000]. Naked cryptospores (a), envelope-enclosed cryptospores (b), trilete miospores (c).
FIG. 3. – *Extension stratigraphique des miospores comparées à l'échelle chronostratigraphique publiée par Grahn* et al. [2000]. *Cryptospores nues* (a), *cryptospores entourées d'une enveloppe* (b), *spores trilètes* (c).

facts indicate that if similar miospore assemblages are found on different continental plates, then, the areas of land were probably geographically close.

The data on Llandovery miospores reported herein confirm that the assemblages observed in Brazil, Paraguay and Argentina [Rubinstein and Vaccari, 2001] are similar to many others from coeval strata in other regions of the world [Steemans 1999a, 1999b, 2000 ; Wellman, 1996].

Because of the continental origin of the miospores, and because large oceans are impassable geographic barriers for them, it seems likely that at the Ordovician-Silurian boundary palaeo-continents were close to each other, with continental bridges linking them. Similar conclusions have been reached on the basis of the palaeogeographic distribution of vertebrates [Blieck *et al.*, 2001]. On the contrary, palaeogeographic reconstructions such as those from Cocks [2001] or Scotese and McKerrow [1990] show large oceans between Avalonia, Laurentia and Gondwana. Evidence from miospores favours palaeogeographic models more like those published by Dalziel *et al.* [1994] that show a close proximity between Gondwana and Laurentia from the Ordovician to the Devonian. Avalonia was probably still connected with the northern part of the western Gondwana as it was during the Tremadoc-Arenig period [Servais and Mette, 2000]. In addition, such a map could explain how the first trilete spore-producing plants migrated from the southwest to the northeast, from Turkey, passing through Saudi Arabia, Libya, South America, UK and finally to North America. On the basis of the data from Gotland [Gray *et al.*, 1974 ; Le Hérissé, 1989], Baltica would be geographically isolated, because only simple naked tetrads are known around the Ordovician-Silurian boundary. The incoming of trilete spores in Gotland during the earliest Wenlock suggests the disappearance of that geographic barrier. More data are required to be more precise.

Based on data from Paraguay, Africa, Saudi Arabia, etc. Gray *et al.* [1992] defined two phytogeographic regions. They considered that tetrad assemblages available from the Malvinokaffric and extra-Malvinokaffric realms show significant differences. The tetrads from the Malvinokaffric Realm are always naked and smooth. However, tetrads from the extra-Malvinokaffric Realm include forms that are enclosed within an envelope that may be ornamented. Recent results [Steemans *et al.,* 2000 ; Wellman *et al.,* 2000, Mizu-saki *et al.*, 2002] and the present study, from regions close to the area studied by Gray [1985, 1988, 1991] and Gray *et al.* [1985, 1992], show clearly that miospore assemblages from Malvinokaffric and extra-Malvinokaffric Realms are very similar. This implies that the same parent-plants lived in regions close to the palaeo-equator, such as China [Wang *et al.,* 1997], and regions close to the palaeo-pole, such as South America.

CONCLUSIONS

Three biozones based on miospores have been recognised. The biostratigraphic correlation confirms correlations based on sequence stratigraphy. The stratigraphic succession shows that the coarsening-thickening upward cycles from the base of the sequence are limited by the transgressive surface which is late-Aeronian-early Telychian in age. Thus the palynological data allow one to compare this transgressive episode with the Llandovery rising sea level proposed in the coastal onlap curve of Ross and Ross [1988]. This curve suggests that the most important Silurian sea-level rise took place in the Llandovery. In the present study, the maximum flooding surface of the Silurian sequence was dated as early Telychian. These results are in accordance with the global sea-level change curve.

Observations on the material from Paraguay confirm previous results obtained from South America and suggest a uniformity of vegetation from Avalonia, Gondwana and Laurentia. These findings are in contradiction with the phytogeographic provinces described by Gray in these regions around the Ordovician-Silurian boundary. The parent-plants of the first trilete spores could have migrated from the eastern part of the Gondwana to the western part and to the Laurentia plate.

Palaeogeographic reconstructions with narrow oceans separating the continents better explain the uniformity of the vegetation in these times. Baltica, however, may have been isolated until the Wenlock.

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