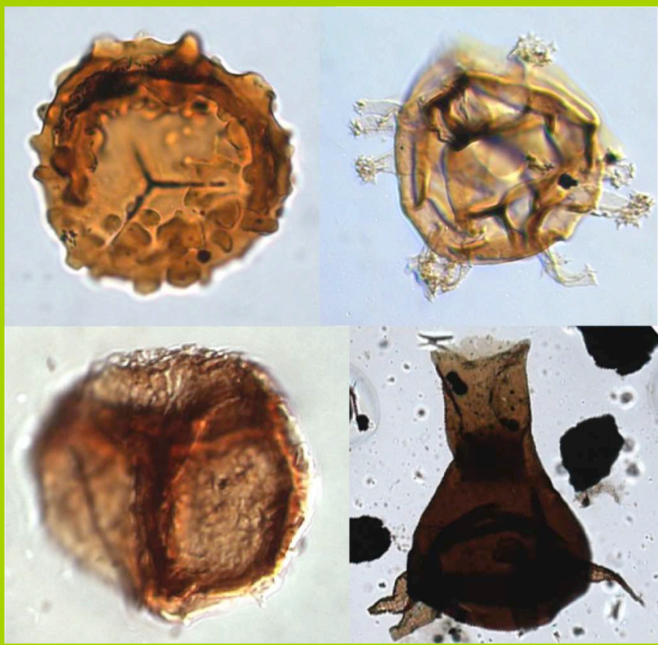
Les palynomorphes du Paleozoïque Inferieur: applications en paleobiologie (evolution des ecosystemes oceaniques et terrestres) et en geologie (biostratigraphie et paleogeographie)

Early Palaeozoic palynomorphs: applications to palaeobiology (evolution of oceanic and terrestrial ecosystems) and to geology (biostratigraphy and palaeogeography)



Mémoire présenté en vue de l'obtention de l'Habilitation à Diriger des Recherches

Marco Vecoli

Chargé de Recherche au CNRS

UMR 8157 du CNRS - Géosystèmes

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LES PALYNOMORPHES DU PALEOZOÏQUE INFERIEUR: APPLICATIONS EN PALEOBIOLOGIE (EVOLUTION DES ECOSYSTEMES OCEANIQUES ET TERRESTRES) ET EN GEOLOGIE (BIOSTRATIGRAPHIE ET PALEOGEOGRAPHIE).

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EARLY PALAEOZOIC PALYNOMORPHS: APPLICATIONS TO PALAEOBIOLOGY (EVOLUTION OF OCEANIC AND TERRESTRIAL ECOSYSTEMS) AND TO GEOLOGY (BIOSTRATIGRAPHY AND PALAEOGEOGRAPHY)

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III - Curriculum Vitae

Les palynomorphes du Paléozoïque Inférieur: applications en paléobiologie (évolution des écosystèmes océaniques et terrestres) et en géologie (biostratigraphie et paléogéographie)

Résumé

Trois groupes principaux de palynomorphes (microfossiles à paroi organique) se retrouvent en abondance dans des roches sédimentaires du Paléozoïque Inférieur (Cambrien – Silurien): les acritarches, les chitinozoaires, et les miospores (incluant les spores trilètes et les cryptospores). Bien que les affinités biologiques de ces palynomorphes ne sont pas connues avec précision, il existe un consensus général pour considérer les acritarches (qui apparaissent au Protérozoïque et atteignent leur maximum de diversité au cours du Paléozoïque Inférieur) comme l'enregistrement fossile du phytoplancton océanique. Les chitinozoaires (Ordovicien – Dévonien) sont interprétés comme les restes microscopiques d'organismes marins zooplanctoniques. Le terme de "cryptospore" est généralement utilisé pour décrire les spores les plus primitives produites par les premières plantes terrestres. Si on accepte cette définition, les cryptospores les plus anciennes datent de l'Ordovicien Moyen. Cependant, des palynomorphes semblables à des spores d'origine non-marine ont été observés depuis le Cambrien Moyen; ces microfossiles font l'objet de débats et de controverses quant à leurs affinités et leurs implications évolutives.

Dans ce travail, j'illustre l'application des palynomorphes du Paléozoïque Inférieur aussi bien en géologie (pour la datation des roches sédimentaires, les reconstitutions paléogéographiques et paléoenvironnementales, et la modélisation géodynamique) qu'en paléobiologie (pour l'étude de l'évolution du plancton, des relations trophiques dans les écosystèmes marins au cours du Paléozoïque Inférieur, et des premiers écosystèmes terrestres).

Une première partie des études présentées ici concerne l'analyse palynologique de nombreuses coupes en sondages et à l'affleurement en Afrique du Nord (Algérie, Libye, Tunisie) et en Moyen-Orient (Turquie, Arabie, Iran). Ces investigations ont permis des analyses taxonomiques détaillées sur des assemblages phytoplanctoniques fossiles d'âge Cambrien Moyen à Ordovicien terminal ainsi que les datations et les corrélations précises de séquences sédimentaires antérieurement inexplorées, avec des améliorations substantielles des zonations palynologiques antérieures. De plus, les analyses des fluctuations d'abondance relative de groupes morphologiques d'acritarches et de leur diversité en fonction des conditions de dépôt ont été appliquées à des reconstitutions paléoenvironnementales.

Early Palaeozoic palynomorphs: applications to palaeobiology (evolution of oceanic and terrestrial ecosystems) and to geology (biostratigraphy and palaeogeography)

Abstract

Three main groups of palynomorphs (organic walled microfossils) are abundantly preserved, and often co-occur, in Lower Palaeozoic (Cambrian through Silurian) sedimentary rocks: the acritarchs, the chitinozoans, and the miospores (including trilete spores and cryptospores). Although the precise biological affinities of these palynomorphs are still the subject of considerable debate, a general consensus exists in considering the acritarchs (appearing in the Proterozoic and attaining their diversity maximum in the Early Palaeozoic) as the fossil record of Palaeozoic oceanic phytoplankton. The chitinozoans (Ordovician - Devonian) are generally interpreted as the microscopic remains of small marine zooplanktonic organisms. The term "cryptospore" is predominantly used to indicate the most primitive dispersal spores produced by earliest land plants; accepting this definition, the oldest cryptospores occur in the Middle Ordovician. However, spore-like palynomorphs of probable non-marine origin are observed since the Middle Cambrian; these microfossils are currently the subject of much controversy as to their affinities and evolutionary implications.

In this work, I illustrate the application of Early Palaeozoic palynomorphs in geology, for the dating of sedimentary rock bodies, palaeogeographic and palaeoenvironmental reconstructions, and geodynamic modelling; in palaeobiology, for the study of the evolution of oceanic plankton, the trophic relationships in the marine ecosystems during Ordovician times, and the evolution of the earliest terrestrial ecosystems.

A first part of the studies presented here concerns the palynological analyses of numerous subsurface and outcrop sections in North Africa (Algeria, Libya, Tunisia) and the Middle East (Turkey, Saudi Arabia, Iran). These investigations have permitted detailed taxonomical analyses of Middle Cambrian to Late Ordovician microphytoplankton fossil assemblages and the accurate dating and correlation of previously unexplored stratal sequences, with substantial refinements of previously available palynozonations. Moreover, the analysis of relative abundance fluctuations of acritarch morphological classes and assemblage diversity relatively to the depositional environments have been applied to palaeoenvironmental reconstructions.

The large database of stratigraphic occurrences of acritarch species in the Early Palaeozoic formations of the North Sahara Platform and adjacent regions has formed the basis for the analysis

La base de données des occurrences stratigraphiques des espèces d'acritarches établie à partir de l'étude des formations d'âge Paléozoïque Inférieur de la plate-forme nord-saharienne et des régions voisines a été utilisée pour analyser les mécanismes, les facteurs de contrôle et la signification paléobiologique de la diversification du microphytoplancton au cours de l'Ordovicien. Cette étude a montré que l'évolution des acritarches à l'Ordovicien a été contrôlée principalement par les changements paléogéographiques et paléocéanographiques. Les courbes de diversification des acritarches ont été comparées avec celles de groupes majeurs d'invertébrés marins, montrant qu'une augmentation importante de la production primaire dans les océans constituerait un des principaux facteurs responsables de la "Grande Biodiversification Ordovicienne".

L'étude palynologique de plusieurs sondages dans le socle Paléozoïque en Europe Centrale (Allemagne, Danemark, Pologne) a permis de confirmer l'utilité des acritarches et des chitinozoaires pour tracer les limites entre les principales unités tectonostratigraphiques à travers la zone de suture trans-européenne. Les palynomorphes ont également été utilisés comme indicateurs de provenance sédimentaire et ont permis de dater avec précision la collision entre les microcontinents Avalonia and Baltica et la fermeture de l'Océan Tornquist.

Une étude multidisciplinaire, incluant les données de la palynologie (acritarches, miospores, chitinozoaires), des palynofaciès et de la géochimie isotopique et organique, a été effectuée sur des successions sédimentaires d'âge Ordovicien terminal – Silurien en Afrique du Nord. Cette étude a permis la reconstitution d'une courbe isotopique du $\delta^{13}C$ dans le Paléozoïque Inférieur de l'Ouest Gondwana, de proposer un modèle de dépôt des couches d'argiles noires riches en matière organique, et de préciser leur géométrie à l'échelle du bassin de sédimentation. Les événements isotopiques Ireviken et Lau, liés à des modifications globales dans le cycle du carbone, ont été identifiés pour la première fois dans l'Ouest Gondwana; l'étude de la dynamique du phytoplancton à travers ces événements a montré une corrélation entre extinctions, excursions isotopiques et dépôts de sédiments riches en matière organique. Les miospores, bien représentées dans les successions marines de plate-forme, ont été extrêmement utiles pour les datations des séquences siluriennes. Elles vont fournir un cadre chronostratigraphique de référence pour établir une biozonation silurienne à acritarches. En outre, les rapports d'abondances entre spores triletes et cryptospores ont été analysés pour tester des modèles d'évolution de végétation primitive terrestre proposés par différents auteurs.

of the diversification of marine microphytoplankton during Ordovician, its palaeobiological meaning and its controlling factors. This study showed that the primary controls on acritarch evolution during the Ordovician were the palaeogeographical and associated palaeoceanographical changes. The patterns of acritarch diversification have been compared to those of the main groups of marine invertebrates, showing that a manifold increase in oceanic primary productivity was among the principal driving factors of the "Great Ordovician Biodiversification Event".

The palynological study of subsurface sections in the Palaeozoic basement of Central Europe (Germany, Denmark, Poland) confirmed the utility of acritarch and chitinozoans in the mapping of the major terrane boundaries across the Trans European Suture Zone. The palynomorphs were also used as sediment provenance indicators and permitted to place chronostratigraphic constrains to the timing of collision between the Avalonia terrane and the palaeocontinent Baltica, following the closure of the Tornquist Ocean.

The more recent works presented here concern a multidisciplinary study, including palynology (acritarchs, miospores et chitinozoans), palynofacies, and organic and isotope geochemistry of predominantly marine latest Ordovician – late Silurian sequences in North Africa. These studies have permitted the reconstruction of the first $\delta^{13}C$ isotope curve for the Early Palaeozoic of West Gondwana, to propose a model of deposition of oil-prone, organic-rich black shale horizons in early Silurian times, and to better constrain the geometry of the black shale deposits at the sedimentary basin scale. The Ireviken and Lau events have been recognized for the first time in West Gondwana, and the fossil phytoplankton dynamics across these events described, showing extinction events correlated to isotopic excursions and onset of organic-rich sedimentation. Miospores, abundantly present in the platformal marine successions have been extremely useful for the precise dating of the Silurian sequence, and provide a solid chronostratigraphic framework for the establishment of a Silurian acritarch biozonation. Moreover, cryptospores vs. trilete spore abundance fluctuations have been analyzed in order to test previously proposed models of evolution of early terrestrial vegetation.

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A la mémoire de mon père

Early Palaeozoic palynomorphs: applications to palaeobiology (evolution of oceanic and terrestrial ecosystems) and to geology (biostratigraphy and palaeogeography)

1. Introduction

Three main groups of palynomorphs (organic walled microfossils) are abundantly preserved, and often co-occur, in Lower Palaeozoic (Cambrian through Silurian) sedimentary rocks: the acritarchs, the chitinozoans, and the miospores (including " cryptospores" and "trilete spores"). Although the precise biological affinities of these palynomorphs are still the subject of considerable debate, a general consensus exists in considering the acritarchs (appearing in the Proterozoic and attaining their maximum diversity in the Early Palaeozoic) as the fossil record of Palaeozoic oceanic phytoplankton, or at least an important part of it (Tappan, 1980; Colbath and Grenfell, 1995; Servais et al., 1997; Riegel, 2008; Strother, 2008). The chitinozoans are generally interpreted as the microscopic remains of small marine zooplanktonic organisms: they first appear in the fossil record in the basal Ordovician (earliest Tremadocian) and suffer a complete extinction at the end of the Devonian (Paris, 1981, 1996; Jaglin and Paris, 1992; Miller, 1996). Miospore is a general descriptive term used to identify all fossil plant spores smaller than 200 m (Steemans, 2000). Dispersed spores showing archaic and/or unusual morphological characters, and supposed to have been produced by coastal and/or continental primitive land plants, are generally identified with the term of "cryptospores" (Wellman, 1999; Steemans, 2000). Their unanimously accepted oldest occurrence is the Middle Ordovician (Strother et al., 1996). Recently, some reports of enigmatic sporomorphs (spore-like palynomorphs) from Middle Cambrian sediments in North America (Strother et al., 2004; Taylor and Strother, in press) and North Africa (Vecoli et al., 2007a, b) have animated a debated about a possible much earlier appearance of land plants than currently considered.

Early Palaeozoic palynomorphs are generally present and in large numbers in many different kinds of fine-grained, chemical or detrital sedimentary rocks, often even surviving low-grade metamorphism (**Vecoli et al., 2008b**). They are geographically widespread, and their distribution within a given sedimentary basin reflects both their ecological requirements as a function of local palaeoenvironmental conditions, as well as their *post-mortem* hydrodynamic transport by sedimentary processes. Observed patterns of extinctions and radiations along a vertical profile can be related either to abrupt changes in the palaeoenvironment, or to evolutive events of the biocenosis. Accordingly, the study of Palaeozoic palynomorphs can be applied to a wide range of topics crossing the boundary between geology and palaeobiology, including biostratigraphy, palaeobiogeography and palaeogeographic reconstructions, palaeoenvironmental analysis, evolution of oceanic and terrestrial ecosystems.

In this memoir, I will present the main results of my research activity since the obtaining of my PhD degree at the University of Queensland, Brisbane, Australia, in July 1999. My PhD Thesis mainly concerned the taxonomic, biostratigraphic, and palaeoenvironmental analysis of Cambrian-Ordovician acritarch assemblages from North Africa. During a first two-year post-doc funded by the European Community "Training and Mobility of Researches" Programme, which I conducted in Germany (Martin-Luther Universität Halle/Wittenberg, Halle an der Saale), I applied the study of palynomorphs (acritarchs and chitinozoans) for palaeogeographic reconstructions and sediment provenance analysis in the framework of a multidisciplinary project: "Palaeozoic Amalgamation of Central Europe". This involved collaboration with nine research institutes in Europe and more than twenty postdoctoral students specialists in different fields of geology (geophysics, geochemistry, petrology, etc.). A second two-year postdoctoral project (conducted at the "Domaines Océaniques" unit of the CNRS in Brest, France) was funded by a Marie Curie Individual Fellowship, to investigate on the relationships between microphytoplankton evolution and palaeogeographical changes during Cambrian-Ordovician times in high-latitude peri-Gondwana (North Africa, southern Europe, and Middle East). Following this I first obtained as short-term postdoc at the Palaeontological Laboratory in Lille (UMR 8014 research unit of CNRS) before my recruitment as permanent researcher in the same institution (now UMR 8157), starting from October 2004. This gave me the opportunity of enlarging the range of my investigations and to develop the study of miospores and their application to the analysis of the terrestrialization process, spanning a stratigraphic range from Cambrian through Lower Devonian.

2. Taxonomical studies and biostratigraphical applications of Early Palaeozoic acritarchs and chitinozoans

Taxonomy is often perceived by non-specialists as an unattractive, time-consuming, arid exercise which simply consists in attaching a name to an object. In the more and more competitive "market" of sciences where value is often associated simply with number of publications per year, spending months in trying to understand, describe, and formally classify fossils may seem "out of fashion". However, one soon realizes that good taxonomy is simply fundamental to any meaningful interpretative analysis of a fossil assemblage. Loeblich (1970) noted that the statement sometime expressed by workers that one "is not interested in nomenclature but only in the organism", shows little concern of real understanding or scientific communication.

In the past, many palynomorph taxa have been poorly described and not adequately figured and indeed some even merely named, and this is particularly true for the acritarchs. In addition, many published old studies fail to give adequate locality data or stratigraphic detail so that comparative material cannot be easily obtained. It is evident that in order to develop a meaningful biostratigraphic scheme or biozonation which may be confidently used for long distance correlation, the index taxa must be carefully described and their full stratigraphic range well documented. In fact, the long stratigraphic ranges exhibited by many acritarch genera and species as currently understood may simply signify that general, probably polyphyletic features of morphology have assumed disproportionate emphasis in classification. Hence, there is often a need for studies focusing on the taxonomic revision of published taxa in order to better define, and adequately illustrate the morphological variation of a given taxon, and subsequently its stratigraphical and geographical distribution. Highly detailed morphological descriptions –at the base of good taxonomy and systematics- have also a bearing on our understanding of the palaeobiology and phylogenetic relationships of the different kinds of palynomorphs. As noted by Tappan and Loeblich (1971), for example, gross morphology of acritarchs may reflect convergent adaptations for a planktonic existence and might be unreliable to infer natural relations, while the vesicle wall microstructure might be considered as not to be environmentally affected and hence to best reflect relationships. Similar arguments are obviously valid for chitinozoans and miospores.

Taxonomic work is thus a basic activity which underlies the research in palaeontology. Biostratigraphy is also among the more fundamental and direct applications of palaeontology for field geology, aiming at a comprehensive appreciation of the spatio-temporal distribution of fossil taxa. Recently, there has been an obvious return of interest in Palaeozoic (and pre-Cambrian) palynostratigraphy, mainly driven by a revived concern of oil companies for exploration in the deepest sedimentary sequences of intracratonic basins worldwide and particularly in many parts of the late Neoproterozoic to Early Palaeozoic Basins of peri-Gondwana (South America, North Africa, Middle East, India: e;g., Bezan, 2004; Dardour et al., 2004; Vecoli et al., 2004; Craig and Said, 2008; Underdown and Redfern, 2008).

In the first part of the present memoir, I present some selected examples of taxonomic description and revision of acritarch taxa and their bearing on biostratigraphy and palaeobiogeography. While the largest part of my research into acritarch taxonomy and classification was conducted mainly during my PhD Thesis; the systematic evaluation and description of palynomorph assemblages continues to represent a fundamental aspect of all palynological investigations. Some of the most recent work on palynostratigraphy in the Early Palaeozoic of North Africa and Iran are also presented.

The Ordovician acritarch genus *Frankea* has attracted considerable interest of Palaeozoic palynologists because of its characteristically simple and elegant morphology, easily recognizable at generic level. Several authors have previously investigated into the morphological attributes, taxonomy and potential for stratigraphic correlation of this genus (e.g., Colbath, 1986; Servais, 1993; Fatka et al., 1996). Exceptionally well preserved specimens of *Frankea* occur in Middle Ordovician strata of North Africa, but their taxonomic attributions at species levels and stratigraphic significance proved problematic in the light of the existing literature. For this reason, a series of detailed observation by S.E.M. and biometric study with statistical data analysis were performed on material not only from the North African area, but also from the type area (Belgium) and Spain with the aims of better describe the morphology and improve the knowledge on First Appearance Datum and the stratigraphic extension of some of the most commonly occurring *Frankea* species (**Vecoli et al., 1999**). The study permitted to detail the nature and distribution of microsculptural elements of the vesicle walls, to quantitatively define the morphological variation ranges of the three species *F. breviuscula*, *F. longiuscula*, and *F. sartbernardensis*, and finally to establish their stratigraphic ranges against independent stratigraphic control provided my co-occurring macrofossils in various localities.

Two other widely cited Ordovician acritarch genera of distinctive morphology but characterized by very complex taxonomic statuses and not fully appreciated biostratigraphic value are *Veryhachium* Deunff 1954 and *Coryphidium* Vavrdová 1972. In the recently published paper by **Servais et al. (2008)**, I participated to the review of all published data concerning the genus *Coryphidium*, in order to rationalize its taxonomy and to understand its relationship to other acritarch genera of similar morphology. The study also attempted to review the biostratigraphical distribution of the genus in order to better evaluate its potential for international correlation; stratigraphic data from North Africa based on my previous studies and new subsurface material constituted a critical input to this work. The plotting of all known *Coryphidium* occurrences on a recent palaeogeographical reconstruction permitted finally to in order to clarify the palaeobiogeographical distribution of this important genus. A similar study was conducted on the genus *Veryhachium* (**Servais et al., 2007**); in this case the complete revision of all published data (with more than 250 species and subspecies described in the literature) was not undertaken, but we focused on the proposition for the use of a simple classification scheme for the triangular and rectangular forms of the genus which were grouped under the informal grouping of *Veryhachium trispinosum*, and *Veryhachium lairdii* morphotypes, respectively. In this study, the oldest known occurrence of *Veryhachium lairdii* (earliest Tremadocian) was documented based on personal unpublished data from the subsurface of

North Africa. Moreover, a detailed analyses of the first occurrences of *Veryhachium* in different localities from different palaeocontinents (peri-Gondwana, Baltica, Laurentia) allowed to describe the palaeobiogeographical radiation of the genus, suggesting that *Veryhachium* first appeared in the Tremadocian at high latitudes before it radiated to lower latitudes of the Gondwanan margin (China and Argentina) and Baltica during the Floian, to become cosmopolitan only by Middle Ordovician times (Vecoli et al., 2007c).

Notwithstanding the problems highlighted in the above discussion, the acritarchs, and more in general all Palaeozoic palynomorphs, undoubtedly remain very important tools for detailed biostratigraphic investigations in the Palaeozoic sedimentary successions. Indeed, in many cases the palynomorphs are the only identifiable fossils present in Palaeozoic sediments, and this is even more evident in the case of cored subsurface sequences, where only small amount of samples are available for biostratigraphic analyses. Some examples are shown here which demonstrate the use and significance of acritarchs and chitinozoans in Early Palaeozoic biostratigraphy.

A palynological (acritarchs) analysis of a previously undated pre-Ordovician clastic succession of northwestern Algeria cored by borehole MG-1 resulted in the first biostratigraphic evidence of Middle to Late Cambrian sedimentation in the subsurface of the whole Algerian Sahara (**Vecoli et al., 2008a**). The results have provided the basis for an improved correlation with the Cambrian outcrop successions in Morocco and in the Ougarta Range of Algeria, contributing to the sequence stratigraphic interpretation of these sequences at a regional scale (e.g., Ghienne et al., 2007).

Acritarchs and chitinozoans have proved extremely useful for the dating and correlation of Cambrian-Ordovician clastic sedimentary successions in Iran. Here, Palaeozoic rocks occur vastly both in outcrop and in the subsurface and represent a primary target for oil exploration. A collaboration with Dr. Ghavidel-syooki of the National Iranian Oil Company provided the opportunity of starting the palynological investigation of the main Palaeozoic Basins in the North (Alborz Range) and in the South (High Zagros Mountains) in order to improve the knowledge of the Lower Palaeozoic stratigraphy of these areas, which are still largely unexplored, with fundamental implications for future planning of exploration strategies (**Ghavidel-syooki and Vecoli, 2007**; and **in press**). The data collected are also important as contribution towards a more detailed knowledge of the palaeobiogeographic distribution and diversification trends of the Early Palaeozoic oceanic microplankton (acritarchs and chitinozoans).

The two papers by **Raevskaya et al.** (**2003**, **2004**) are the result of a collaborative study conducted during a 6-month stay at the University of Pisa, Italy, in 2001, focusing on Middle Ordovician strata from the Baltic area (St. Petersburg region, northwestern Russia). Palynological analyses were conducted on Hunneberg to Billingen sediments (Baltic regional stages *grosso modo* equivalent to the Tremadocian and Floian Stage of the Global Ordovician Series, respectively) of the Baltic Ladoga-Glint area. These analyses revealed well preserved and diverse acritarch associations, inlcuding the morphologically distinct acritarch species *Rhopaliopora*? *asymmetrica* which was newly established and proposed as a potential index species for the recognition of the base of the Floian (previously indicated as "Stage 2") in the Baltic region (**Raevskaya et al., 2003**). Furthermore, the biogeographical significance and palaeogeographic and palaeoclimatic implications of the Tremadocian through Floian acritarch assemblages were discussed in **Raevskaya et al.** (**2004**). This indicated that acritarch assemblages had a fairly undifferentiated "cold water" oceanic character along the whole margin of peri-Gondwana as well as on the South Chinese and Baltic Platform (Mediterranean Oceanic Realm). However, the occurrence of very typical high latitude acritarch taxa only in South China suggested a prevailing warmer climate in Baltica than in South China although the two palaeocontinents occupied the same palaeolatitudinal position.

Finally, the paper by **Vecoli et al.** (**2008b**) consists in a re-evaluation of an acritarch-based biostratigraphic dating of an assemblage recovered from the "Col di Foglia" schists in the metamorphic basement of the Italian Eastern Alps, which was first described by Kalvacheva et al. (1986). This re-evaluation permitted to improve the previous age assignment, indicating that the Col di Foglia assemblage represents indeed the oldest biostratigraphic age of the entire Alps and adding precious information on the poorly known depositional age of the sedimentary protolith of the metamorphic units comprising the Alpine chain.

3. Acritarchs as palaeoenvironmental tools

In addition to biostratigraphic correlation, palynomorphs can be applied to palaeoenvironmental reconstructions which in turn can form the basis for characterization of systems tracts in sequence stratigraphic studies (Poumot, 1989; Gregory and Hart, 1992). While such applications have proved successful in Mesozoic and younger sedimentary strata, the use of palynomorphs as palaeoenvironmental analysis of Lower Palaeozoic sequences is somewhat hindered by the absence of obvious palynological indicators of terrestrial provenance, and by the relatively limited knowledge of the palaeoenvironmental distribution of Palaeozoic organic-walled microphytoplankton compared, for example, to the level of detail reached in the understanding of dinoflagellate cyst-ecology (e.g., Wall et al., 1977; Dale, 1996; De Vernal et al., 1998). One reason for this is the low number of detailed investigations devoted to the mapping of acritarch distributional patterns in areas where independent palaeoenvironmental control is available.

Various authors have proposed general models linking the composition of Palaeozoic microphytoplankton cyst communities to specific palaeoenvironmental conditions (e.g., distance from shore and/or increasing water depths; Staplin, 1961; Jacobson, 1979; Dorning, 1981; Colbath, 1980; Li et al., 2004; Stricanne et al., 2004). Criticism regarding such models pointed to the difficulty of their testing in the more general situations (Strother, 1996), and the lack of present-day analogues for such models. Undoubtedly, the palaeoecological distribution of acritarchs was influenced by many factors (e.g., salinity, light, oxygen availability, nutrient supply, pH, water turbidity), and at this time, there is limited information on the relative importance of these factors in determining the characteristics of specific acritarch assemblages. In my two papers dealing with palaeoenvironmental interpretation of acritarch diversity changes along a given vertical profile (**Vecoli, 2000, 2004**), I have however assumed that most of the palaeoecological factors determining marine microphytoplankton distribution (e.g., the amount of land-derived nutrients, salinity, temperature, turbidity of the water), were indeed related principally to distance from shore. The underlying concept is that (as it seems to be supported by sufficient observational data) acritarch diversity and relative abundance of certain genera or morphotypes show consistent distributional patterns on a inshore-offshore profile, similar to what is observed within dinoflagellate cyst communitites (e.g., maximum acritarch diversity in offshore, open shelf environments). If this approach might be considered as an over-simplification, it does provide a working hypothesis upon which one can further develop and gradually improving palaeoecological models. Further advance in the knowledge of the palaeoenvironmental distribution of Palaeozoic palynomorphs (especially acritarchs), obviously rely on future detailed studies focusing on the description and comparison of acritarch assemblages from stratigraphic sections in which independent palaeoenvironmental information can be obtained (e.g., from sedimentology, macrofossil content, isotopic analyses, etc.), like it has been recently done in the case of the Late Silurian of Gotland (Stricanne et al., 2004, 2006).

In the Ordovician of the Sahara Platform, some trends of variation in acritarch diversity and in relative abundance of morphotypes appear to be significantly related to palaeoenvironmental signals. High specific diversity is characteristic of outer shelf to shelf margin conditions and correlate with maximum abundance of diacromorph, herkomorph ("galeates"), and acanthomorph acritarchs. Conversely, leiospherid, netromorph, and veryhachid acritarchs characterize low-diversity assemblages, relatable to nearshore, shallow marine conditions. A distinction into eurytopic, highly tolerant taxa from facies-sensitive forms can be proposed (**Vecoli, 2000, 2004**). In particular, one of the species frequently cited as possible index-taxon for the base of the Tremadocian, *Acanthodiacrodium angustum* (Downie 1958) Combaz, 1967 only occur in shallow-water marine, marginal to inner neritic situations, together with thin-walled, discoidal forms (e.g., *Saharidia fragilis* Combaz, 1967), and the "spore-like" enigmatic palynomorphs *Attritasporites* Combaz, 1967, and *Virgatasporites* Combaz, 1967. The recognition of the facies-controlled distribution of some acritarch taxa has implications for acritarch biostratigraphy in that in a given section, a significant number of acritarch species' First Appearance Datum (FAD) may be concentrated at an abrupt lithostratigraphic boundary associated with a shift in depositional facies. In **Vecoli** (**2004**), I demonstrated in detail that two previously established palynological zones in the Tremadocian of the Ghadamis Basin, North Africa ("Zone A" and "B" of Combaz, 1967, considered as early and late Tremadocian age, respectively) most probably have a palaeoenvironmental rather than a biochronological meaning: this has fundamental implications for biostratigraphic correlation of the various Tremadocian formations in the subsurface of the Ghadamis Basin.

The study of acritarch distributional patterns in a Middle Ordovician sedimentary succession in Saudi Arabia (Qasim Formation: **Le Hérissé et al., 2008**) further confirmed some trends observed in the previous analyses. In this localities, the occurrence of cryptospores and chitinozoans was useful in order to better constrain the palaeoenvironmental analyses. Sedimentological features were also used for determining the sedimentary environment. Cryptospore-dominated palynomorph assemblages were found in a fluvio-marine sedimentary body (the Saijr Member of Qasim Fm.), where the associated acritarchs were largely represented by abundant thin-walled spaheromorph acritarchs. Diversity of the acritarchs increased markedly in correspondence of a lithological transition towards the Hanadir Mb. of the Qasim Fm., paralleling an increase in chitinozoan abundance, and a significant decrease in the cryptospore abundance. The Hanadir unit consists of bioturbated shales and was interpreted as representing a deepening in depositional environment following a general transgressive trend. This trend was interrupted cyclically by the incursion of more proximally derived sediments, probably as a consequences of high-frequency sea level oscillation. This was reflected in the palynological spectrum by the presence of distinct intervals characterized by cryptospore-dominated palynomorph assemblages, with low-diversity acritarch associations rich in sphaeromorphs. Further palynological signals, such as the relative abundance variations of *Veryhachium* and *Frankea* were interpreted as possibly reflecting temperature or salinity changes within the Hanadir Mb.

4. The application of acritarchs and chitinozoans for palaeogeographic reconstructions: PACE – Palaeozoic Amalgamation of Central Europe

PACE was a Research Training Network project funded by the European Commission during 1999-2001. It provided opportunity for research training of more than 20 postdoctoral students working on a multidisciplinary research environment, in nine different European Universities. The principal scientific objectives of the PACE Network were twofold: to provide the surface correlation to the shallow and deep lithospheric structures across the Trans European Suture Zone (The huge fault system bounding the East European Craton and extending from the Danish North Sea to the Black Sea) and to gain an understanding of the processes and timing of amalgamation of the various central European terranes to the East-European Craton. A subsidiary objective was to gain an insight into the controls on accumulation of mineral and hydrocarbon resources which accompanied these processes. The principal research of the PACE network comprised geophysics, geochronology, petrography, structural geology, and palaeontology (principally palynology). In order to gain insights into the surface structure of the Trans European Suture Zone, one of major challenges was to determine the Gondwanan versus East European Craton palaeogeographical affintity of tectonostratigraphic terranes and microcontinents. I participated to the PACE project with a two year postdoc position at the Martin Luther Universität in Halle an der Saale, Germany. My research activity was to determine the sedimentary provenances of rock sequences from the subsurface of northern Germany, the Black Sea basement of Danemark, and the Pomerania region of Poland, using an integrated approach involving sedimentary petrography, zircon geochronology and palynology, to establish from which microcontinent originated the different Palaeozoic sedimentary sequences. In this research, I collaborated mostly with the Palaeontological Laboratory of the Geology Department of the University of Ghent, Belgium where Dr. Joakim Samuelsson (postdoc) and Professor Jacques Verniers were also involved in the PACE research network.

The PACE-related scientific publications selected herein mainly concern comprehensive palynological (acritarchs and chitinozoans) investigations of the Lower Palaeozoic rocks of the area comprising the eastern sector of the Norwegian-Danish Basin, the southern Baltic Sea (area of Bornholm Island) and northwestern Poland (Pomerania) in order to: 1) establishing a refined biostratigraphic subdivision of the Cambrian through Silurian subsurface sedimentary successions; 2) facilitating palaeogeographic reconstruction; and 3) increasing the knowledge of the Palaeozoic geodynamic evolution of the northern section of the Trans European Suture Zone.

We demonstrated that not only was it possible to obtain precise biostratigraphic datings of the several subsurface sections (e.g., the Rügen boreholes: **Samuelsson et al., 2000, 2001**), but that acritarchs and chitinozoans were most useful in order to determine the palaeogoegraphical affinity of the tectonostratigraphic terranes (e.i., Gondwanan vs. Baltican) and its evolving character during the convergent migration of these terranes during Ordovician times (**Vecoli and Samuelsson 2001a, b**; **Samuelsson et al., 2002**). Palynological evidence was provided for the first time of early Silurian ages in the Lower Palaeozoic basement of the Danish sector of the North Sea (**Vecoli and Samuelsson, 2001a**); additionally, these early Silurian assemblages were characterized by the presence of reworked acritarchs of Late Cambrian and Ordovician ages which gave clear indications of sediment provenance from a Perigondwanan detrital source. We suggested (**Vecoli and Samuelsson, 2001a, b**) that these reworked acritarchs were transported onto the south-western margin of the East European Platform (EEP) from a corrugated and eroding area, formed during the start of the Avalonia-Baltica collision, which definitely established the timing of Avalonia-EEC amalgamation as Ashgill. This timing was crucially important for determining that the basement to the southern North Sea was likely to have had Avalonian affinity, despite the presence of the Anglo-Brabant Deformation Belt (Verniers et al., 2002). The PACE postdoc was most successful in clearly showing that palaeontological analyses are can play a fundamental role in developing and constraining geodynamic-structural models by integration of chronostratigraphical and palaeobiogeographical information provided by the fossils. This is clearly demonstrated in the collective paper which summarized the main results obtained by the PACE Research Network teams by **Winchester et al.** (**2002**).

5. The biodiversity dynamics of Ordovician microphytoplankton and its palaeobiological significance

The palynological investigations carried out in the Upper Cambrian through Ordovician sedimentary successions in the Sahara Platform (Algeria, Tunisia, Libya) and in southern and central Europe during my PhD Thesis (Vecoli, 1996, 1999) and my postdoctoral stay in Germany (Halle) permitted to build up an extensive database of Ordovician acritarch occurrences. Compared to existing databases of Ordovician acritarch occurrences which were mainly derived by the simple and often uncritical compilation of published data, my personal database had the advantage of being taxonomically consistent: redundancies due to misidentification and synonymies were greatly reduced and virtually all stratigraphic occurrences were based on actual observations within actual sedimentary successions. This database has been at the origin of a diversity curve of the acritarchs for the latest Cambrian through Ordovician time interval for the so called "northern Gondwana region", that portion of peri-Gondwana located in high-latitudes during Ordovician times and corresponding to North Africa and the various southern-central European and Middle East terranes. This was also a contribution to the international project IGCP 410 "The Great Ordovician Biodiversification Event" (1997-2003) which had the objective of compiling all existing data on the Ordovician biodiversity dynamics of all fossil groups (Vecoli in **Servais et al., 2004**). This publication presented a preliminary diversity curve: data from the stratigraphic interval corresponding to the Caradoc Series (equivalent to Sanbdyan and early Katyan Global Stages) were still incomplete and were not shown.

Further developing the analysis of acritarch diversification patterns during latest Cambrian through Ordovician times, my postdoc at Brest, France (2002-2004), under the mentorship of Alain Le Hérissé, funded by a Marie Curie Individual Fellowship (European Commission) was meant to investigate into the "Evolution of organic-walled microphytoplankton in relation to the palaeogeographical changes of the northern Gondwana margin during Ordovician – Early Silurian times".

The project included new palynological studies of outcrop and borehole sections in Saudi Arabia (later published in **Le Hérissé et al., 2008**) and Turkey (Paris et al., 2008), and a revision of previously published material (palynological slides) from several European sections, which improved the database of "northern Gondwanan" Ordovician acritarch occurrences, namely by adding new data on Caradoc (Sandbyan-early Katyan) occurrences. The results are detailed in the paper by **Vecoli and Le Hérissé (2004)**, indicating that the most important Cambro-Ordovician acritarch bio-events are short periods of diversification, which also correspond to introduction of morphological innovations, observed in latest Cambrian and earliest Tremadoc, late Tremadoc, early Arenig (early Floian), basal Llanvirn (early Darriwilian), and latest Ashgill (Hirnantian), and a marked extinction phase in the earliest Caradoc (basal Sandbyan). These events have also a clear biostratigraphic value, and our publication included a series of range charts illustrating the known stratigraphic range of 245 acritarch species, plotted against the chitinozoan zonation and Global Ordovician stratigraphic chart. Overall, acritarch diversity is found to increase from the basal Ordovician up to the middle Darriwilian, and then to decline in Sandbyan times (early-middle Caradoc). During Ashgill times (late Katyan – Hirnantian), the assemblages are characterized by relatively low generic diversity (probably as a result of a combined effect of sea level drawdown and onset of glacial conditions), but no major extinction event was observed in connection with the end-Ordovician biotic crisis. The peak in acritarch diversity during Middle Ordovician times appeared to be correlated to maximum spread of palaeogeographical assembly. Acritarch dynamics appeared largely uncorrelated to second order sea-level oscillations, and the primary abiotic controls on acritarch evolution were assumed to be the palaeogeographical and associated palaeoceanographic changes (especially during Middle Ordovician), and the end-Ordovician (Hirnantian) palaeoclimatic change. Although the acritarch fossil record potentially provides important information on the evolution of oceanic primary producers, analyzing the relationships between acritarch diversity, oceanic productivity, and evolution of invertebrate animals proved complex. In particular, the hypothesis of a causal relationship between changes in acritarch diversity and metazoan evolution in the Palaeozoic, which had been proposed in many previous publications by several workers, remained unsupported by our data.

The fundamental question whether the fossil record of organic walled microphytoplankton could be used as a proxy for levels of primary production in the oceans and consequently be put in relation with patterns of diversifications among the invertebrates was further developed during my six-month postdoctoral position at the Laboratoire de Paléontologie et Paléogéographie at the University of Lille, (March-August 2004) and through the collaboration to the "Phytopal" project (2003-2006) funded by a Leverhulme Trust and led by Gary Mullins of the University of Leicester which was intended to document the global biogeographical and stratigraphical distribution of Palaeozoic phytoplankton. This research was also carried out in the framework of the participation at the IGCP 503 "Ordovician Palaeogeography and Palaeoclimate" (2004-2007). The evident decoupling of acritarch diversity from marine invertebrate diversity in the Ordovician of peri-Gondwana documented by **Vecoli and Le Hérissé** (**2004**) had already been described at a larger scale by Strother et al. (1996) for the entire Phanerozoic record of acritarch diversity. The analysis published in **Vecoli (2008)** on microphyoplankton dynamics across the Ordovician-Silurian boundary, corroborates the view that acritarch and marine invertebrate diversities are uncorrelated not only in peri-Gondwana, but also globally: no obvious evidence for a mass extinction in the Hirnantian exist for the microphytoplanktonic assemblages. Further detailed analyses of phytoplankton assemblages from Ordovician-Silurian boundary beds from Laurentia (Antiscoti Island, Québéc, Canada), and Baltica (Estonia) are currently conducted for a PhD Thesis (M. Aurélien Delabroye) which I supervise. The lack of correlation between the Palaeozoic fossil diversity curves of acritarchs and marine invertebrates is not surprising. Acritarchs presumably represent only a fraction of the total Palaeozoic phytoplankton, which should have included (as in today's oceans) picoplanktonic and nannoplanktonic organisms and for which there is only extremely limited evidence in the fossil record (Munnecke and Servais, in press). In modern oceans, marine phytoplankton density is a unimodal function of diversity, which reaches maximum values at intermediate levels of phytoplankton biomass and minimum values during massive blooms (Irigoien et al., 2004). No relation was found to exist between phytoplankton and zooplankton diversity in a study of diversity-productivity patterns in modern oceans (Irigoien et al., 2004). Even the absolute abundance of the organic-walled microfossils in the sediments is a complex function of many variables such as cyst production, hydrodynamic sorting, preservation of the organic matter, thus giving no direct information on microphytoplankton density in the water column. Tongiorgi et al. (2003), for example, showed that the number of acritarchs per gram of rock in Middle Ordovician strata of the Yangtze Platform, China, was strictly controlled by lithology, and that no definite meaning could be attached to the distribution of palynologically barren samples.

In the paper by **Lehnert et al. (2007)** we considered the possibility that indirect evidence for past levels of oceanic primary production (and evolution of oceanic microphytoplankton) could be obtained by analyzing the patterns of biodiversification of consumers at different levels of the trophic chain. This concept is further developed in a recent paper by Servais et al. (in press). The database used in this study was mainly derived from the fossil diversity compilation of the IGCP 410 project (Webby et al., 2004). The considerable radiations observed in different zooplanktonic groups (e.g., first appearance and radiation of graptolites and chitinozoans as well as diversification of radiolarians) and in primary and secondary consumers (for example reflected by the development of planktotrophy in molluscs larvae) during Early Ordovician times should have been paralleled by a higher primary production and availability of phytoplankton to sustain the increasingly complex marine ecosystem. The obvious “explosion” in the diversity of filter feeders and the development of different complex reef communities, especially during Middle and Late Ordovician times, is another fact to argue for an increase in primary production. Even considering plate tectonic evolution and associated continent dispersal a major factor for promoting speciation events, these must have been also associated with an increase in the level of nutrients available for the marine biotas. Accordingly the dramatic radiation of all major groups might have been promoted by a marked increase in the level of primary production during Early to Middle Ordovician times.

6. The application of Early Palaeozoic palynomorphs for the study of the Terrestrialization process: current projects and perspectives

The invasion of the land by plants is one of the most significant evolutionary events in the history of life on Earth, and correlates in time with periods of major palaeoenvironmental perturbations (“terrestrialization”: Ordovician - Devonian). The development of a vegetation cover on the previously barren land surfaces impacted the global biogeochemical cycles and the geological processes of erosion and sediment transport. The terrestrialization process includes the rise of major new groups of animals, such as arthropods and tetrapods. Mass extinction and radiation events observed in the marine fossil record correlate significantly with bioevents recorded in the terrestrial realm, providing evidence of strong terrestrial-marine connections. The evolution of early land plants also correlates with a dramatic decline in CO_2 concentration in the atmosphere, testifying to a first-order disturbance in the global carbon cycle. The onset of the end-Devonian glaciation after a protracted period of “greenhouse” climatic conditions appears also to be causally linked to the invasion of the continents by land plants.

The miospores (cryptospores and trilete spores), occur abundantly in many types of sediments and are the only direct evidence of the earliest phases of land plant evolution in sediments older than Middle Silurian. The study of miospores provide therefore the means for tracking the evolutionary steps of the primitive vegetation and the patterns of their progressive diffusion onto the continents.

Since the my recruitment as permanent researcher at the CNRS, I have started to develop the study of Palaeozoic spores (mainly Ordovician and Silurian cryptospores, Ordovician through Devonian trilete spores, Devonian megaspores) in the framework of a broad and multidisciplinary research project focusing on the study of the terrestrialization process. This project also involve the collaborations with palaeobotanists, specialists of early terrestrial vertebrates, sedimentologists and geochemists.

The development of a totally new research project requires the building up of new competences (miospore taxonomy and biostratigraphy, but also carbon isotope analyses in this case), the setting up of fundraising strategies, the establishing a new network of collaborators, and access to suitable study material.

Applications to research grants have been successful in obtaining a two-year funding for a project titled "The terrestrialization process: modelling complex interactions at the biosphere-geosphere interface", in the framework of the programme "ECLIPSE: Environment et Climat du Passé: Histoire et Evolution" of the Institut National des Sciences de l'Univers of the CNRS; and a further two-year grant awarded by the University of Lille 1 under the BQR (Bonus Qualité Recherche) scheme for the project: "Variations à long terme du cycle du carbone au Paléozoïque (542-251 Ma) ; implications sur la biosphère et le climat" ("Long-term variation in carbon cycle during the Palaeozoic; consequences on biosphere and climate").

The ECLIPSE funding was important to establish a network of collaborations, by funding several sub-projects including several specialists in palynology and palaeobotany, sedimentologists, and organic geochemists, and also to finance fieldwork, and laboratory analyses costs. The BQR grant was used to cover costs of geochemical analysis of whole rock and organic concentrates (see below). A two-year travel grant (2006-2007) has been also obtained under the "Alliance" scientific exchange programme of the “Programme d’Actions Intégrées franco-britannique", financed by the British Council and Ministère des Affaires Étrangères, which allowed the collaboration with Dr.

Charles Wellman of the Department of Animal and Plant Sciences of the University of Sheffield, U.K.

In addition, one PhD Thesis (Ms. Maria Fernanda Romario Sarmiento), and one 12-month postdoctoral project (Dr. Amalia Spina) have been financed and are currently in progress. Both projects are related to the analysis of palynology, palynofacies and organic geochemistry (carbon isotopes and biomarkers) of Silurian-Devonian sedimentary successions of the subsurface of North Africa.

Current investigations focusing on the terrestrialization process are briefly summarize herein, with reference to published papers or presentations in international meetings of the current results. A palynological study concerns problematic sporomorphs from Cambrian sediments from Algeria and Libya. The preliminary results have been presented at the last Palaeontological Annual Meeting held in Uppsala (**Vecoli et al., 2007b**). The Cambrian sporomorphs occurr in dyads and pseudo-tetrads, have much thicker walled than sphaeromorph acritarchs and consistently occur in fluvial-influenced estuarine proximal sediments (the acritarch flora occurring in the same sedimentary sequence is detailed in **Vecoli et al., 2008a**). These findings resemble similar material recovered from Middle Cambrian sediments in the U.S.A. (Strother and Beck, 2000; Strother et al., 2004), which has been tentatively attributed to embryophyte cryptospores, in this case pushing back the oldest stratigraphic record of embryophyte spores of more than 40 million years. An alternative explanation is that these palynomorph represent freshwater algae (e.g., Wellman, 2003). The study, even very detailed, of gross morphology alone is not likely to provide a definite answer concerning this dilemma. Analyses of palynomorph wall ultrastructure (e.g., Taylor and Strother, in press) and carbon isotope chemical composition could provide more insight into the nature of these microfossils. A collaboration with the "Ion Probe Group" of the CRPG (Centre de Recherches Pétrographiques et Géochimiques) of the CNRS at Nancy, France has been established in order to develop a method for carbon (and possibly oxygen) isotopic analysis of single palynomorph specimens. An application to get access to the ion microprobe has been submitted, and the analyses will take place in late 2008 – early 2009. Additionally, new material of Cambrian sediments sampled from subsurface sections in North Africa are being treated for palynological extraction and microscopy analyses.

Combined observation techniques, namely Light Microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM) were applied to Early Carboniferous megaspore specimens in a collaborative study with Dr. Charles Wellman of the University of Sheffield ("Alliance" program). The study provided much new information on the gross morphology and wall ultrastructure of a megaspore taxon which was characterized by confused taxonomy and uncertain palaeobotanical affinity (**Wellman et al., accepted**). The morphological/ultrastructural analyses suggested that it probably derived from a large arborescent lycopsids of the type that went on to dominate the Euramerican Coal Measure forests, revealing an interesting insight into vegetation ecology at a still poorly understood time in plant history.

A further project currently in progress is the coupled geochemical and palynological study of Silurian through early Devonian subsurface sedimentary successions in Tunisia and Libya. These predominantly marine successions yield extremely well preserved palynomorph assemblages including acritarchs, chitinozoans, cryptospores, and trilete spores. Potentially, this permits to analyze at the same time the evolution of the terrestrial vegetation cover and that of the oceanic microplankton communities, and thus to investigate into relationships between the evolving marine and terrestrial ecosystems during the critical time in Earth History corresponding to the transition of life from the sea into the continents and the sub-aerial environment. The palynological analyses of the Siluro-Devonian succession of borehole MG-1, Ghadames Basin, southern Tunisia, is currently in progress and is the subject of the 12-month postdoctoral project conducted by Dr. Amalia Spina. In addition to providing crucial and high-resolution biostratigraphy, the analysis of the miospore assemblages (cryptospores and trilete spores) give insights into the rapidly evolving terrestrial flora in Gondwana and its palaeophytogeography (**Spina and Vecoli, 2008**). Geochemical and biomarkers analysis of marine and terrestrially-derived organic matter from the North African successions are a major objective of my future research activity as they have the potential to contribute much to our understanding of the impact of the terrestrialization not only on ecosystem structure but also on global biogeochemical cycling and ultimately on palaeoclimate. The PhD Thesis currently conducted by Ms Maria Fernanda Romario Sarmiento starting from October 2007, which I co-supervise together with Prof. Nicolas Tribovillard and Dr. Armelle Riboulleau, has the objective of isolating and identify fossil molecules (biomarkers) from sedimentary organic matter of the North African Silurian samples in order to shed light on its biological origin and possibly to relate the fossil molecules to the organic-walled microfossils which co-occur in the sediments. A first integrated palynological (acritarchs, chitinozoans, miospores) and geochemical investigation of a Silurian sequence (borehole Tt1, Ghadames Basin, southern Tunisia) has demonstrated the utility of such an approach (**Vecoli et al., in press**). In this study, we have provided for the first time a carbon isotopic curve for the Silurian of northern Gondwana and evidenced some of the more prominent isotopic excursions which were thought to be global in extent but were previously undetected in main Gondwanaland, and in particular the early Wenlock positive δ^{13}C-excursion (associated with the "Ireviken Event") and the late Ludlow positive δ^{13}C-excursion. These isotopic events are related to changes in rates of carbon burial and also to turnover in the marine phytoplanktonic communities. In addition, the Ludfordian excursion is peculiar in the fact that it correlates with an abrupt and significant increase in abundance of miospores in the palynological content, evidencing increased sedimentary input from a terrestrial sources. It is evident that a comprehensive understanding of global processes need a multidisciplinary approach; organic geochemistry is the most logical complement of palynological investigations, and it is in this direction that I plan to orientate my future research activities.

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