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Contents lists available at ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

Biostratigraphy and paleoenvironmental characterization of the Middle Ordovician from the Sierras Subandinas (NW Argentina) based on organic-walled microfossils and sequence stratigraphy

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ARTICLE INFO

Article history:

Received 23 January 2010

Accepted 17 July 2010

Keywords:

Biostratigraphy
Paleobiogeography
Paleoenvironment
Palynomorphs
Middle Ordovician
Northwestern Argentina,

ABSTRACT

Middle Ordovician acritarchs, including enigmatic, spore-like microfossils, are recorded from the Labrado and Capillas formations, of the Sierras Subandinas (Capillas River Section, Sierra de Zapla), northwestern Argentina. The Sierras Subandinas represent the outermost exposures of the Central Andean Basin that display an alternation of shallow-marine deltaic systems and estuarine environments, where relative sea-level fluctuations are frequent. The scarcity of fossils in the section, due to the marginal marine settings and frequent subaerial exposures, hinders the biostratigraphic constraining of these sedimentary successions. Based on the palynological assemblages, a probably Dapingian age is interpreted for the upper Lagunilla Member of the Labrado Formation, whereas the lower part of the Capillas Formation is assigned to the Darriwilian. Acritarchs from the lower part of the Capillas Formation indicate clear affinities with the “peri-Gondwana province”. However the lack of *Frankea*, a marker taxa for the Middle Ordovician, could be related either to the intermediate paleolatitudinal position of the Central Andean Basin or to local paleoenvironmental conditions. The facies analysis and the distribution of palynomorph assemblages throughout the studied section, suggest that organic-walled microfossils are influenced by local paleoenvironmental conditions. A probable non-marine origin is proposed for the spore-like microfossils co-occurring within the acritarch assemblages.

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1. Introduction

The usefulness of organic-walled microfossils (e.g., acritarchs and chitinozoans) has been widely recognized for age-dating and correlation of Early Paleozoic sediments, being especially useful in areas devoid of other fossils or in subsurface cored stratigraphic sections where macrofossils are more difficult to find (Molyneux et al., 1996; Paris, 1996).

Many acritarch taxa show a global distribution, hence allowing long-distance correlation among different paleocontinents; however, it is also well known that differences do exist among acritarch assemblages from different paleogeographic domains (Vavrdová, 1974; Cramer and Díez, 1977; Martin, 1982; Li, 1987;

Colbath, 1990; Brocke et al., 1995; Playford et al., 1995; Tongiorgi et al., 1995; Servais et al., 2003). It has been also recognized that within a single paleogeographic unit, differences in acritarch composition may reflect variations in local paleoenvironmental conditions such as along an inshore-offshore trend (Staplin, 1961; Jacobson, 1979; Dorning, 1981; Vecoli, 2000; Li et al., 2004; Stricanne et al., 2004; Le Hérisse et al., 2007), variations of substrate type or different water-masses (Colbath, 1980; Le Hérisse and Gourvenec, 1995) or differences in tectonic setting (Achab et al., 2006).

In this paper, we analyze the organic-walled microfossil content of Middle Ordovician rock sequences preserved in the inliers of the southern Central Andes (NW Argentina) and discuss its value in terms of biostratigraphy and paleoenvironmental interpretation, as well as in the context of the paleogeographic history of western Gondwana.

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The study area is regarded as one of the most spectacular in the world for the study of Gondwanan Ordovician sequences, showing thickness of >5000 m and continuous exposures of thousands of square kilometers. After the amalgamation of Gondwana, continuous subduction took place along the Proto-Andean margin, partly responsible for development of wide retroforeland basins (Astini, 2003; Astini and Marengo, 2006), part of which have been considered “pericratonic areas” within South America (cf. Harrington, 1962).

The Central Andean Basin, located in northwest Argentina and extending into Chile, Bolivia and Perú, includes extensive outcrops of Ordovician fossiliferous rocks. Several Andean geological provinces (e.g., Puna, Cordillera Oriental and Sierras Subandinas) show part of the stratigraphy of this formerly continuous basin that extended farther east into the subsurface of the Chaco plains (Fig. 1). Various authors provided interpretations in the context of modern plate tectonics for the Central Andean Basin (Coira et al., 1982; Ramos, 1988, 2000; Bahlburg and Hervé, 1997). Present-day knowledge allows refinement of the formerly suggested foreland systems model that considered sedimentary dispersal to the fore-deep largely derived from the western Puna arc (Bahlburg and Furlong, 1996). There is now enough evidence to support a doubly feed system with an extremely important input from the east, related to major deltaic complexes sourced from the craton (Astini and Marengo, 2006) that accounted for additional loading and active flexure within the back-bulge depozone (Fig. 2).

Basin-wide correlation across the proto-Andean foreland basin is difficult due to the subtle and frequent paleoenvironmental changes and to the poorly known biostratigraphic resolution. Thus,

high-resolution sequence stratigraphy based on detail sedimentological-ichnological observations and palynological work is fundamental to understand the peri-Gondwana settings. In this work we focus into the outermost exposures of the Central Andean basin, in what is known as the Sierras Subandinas, in order to learn about the Ordovician settings and rock equivalents to the better known platform and deep-water facies outcropping in the Cordillera Oriental and Puna, respectively. In this interdisciplinary study we focus into the Ordovician-earliest Silurian successions of the Sierras Subandinas, where significant relative sea-level fluctuations have occurred. We present new data on the Middle Ordovician (Dapingian?–Darriwilian) palynomorphs from the Labrado and Capillas formations that allow establishing a high-resolution stratigraphy for this interval and complements paleoenvironmental, paleoecological and paleobiogeographical aspects.

This study also permits to test the models of palynomorph distribution in relation to changing paleoenvironmental conditions (changes in sea level and transition from a tide-dominated estuary to fully marine setting).

2. Geological setting and stratigraphy

The study area is specifically located within the Sierras Subandinas (“Subandean Ranges”), that represents a typical thin-skinned Andean foreland thrust and fold belt, wherein most of the Andean shortening has occurred largely from 12 Ma to present (Kley et al., 1999). It is a relatively narrow belt (~100 km), with several major east-vergent thrust sheets that accommodates >100% shortening resulting in a steep wedge taper with great

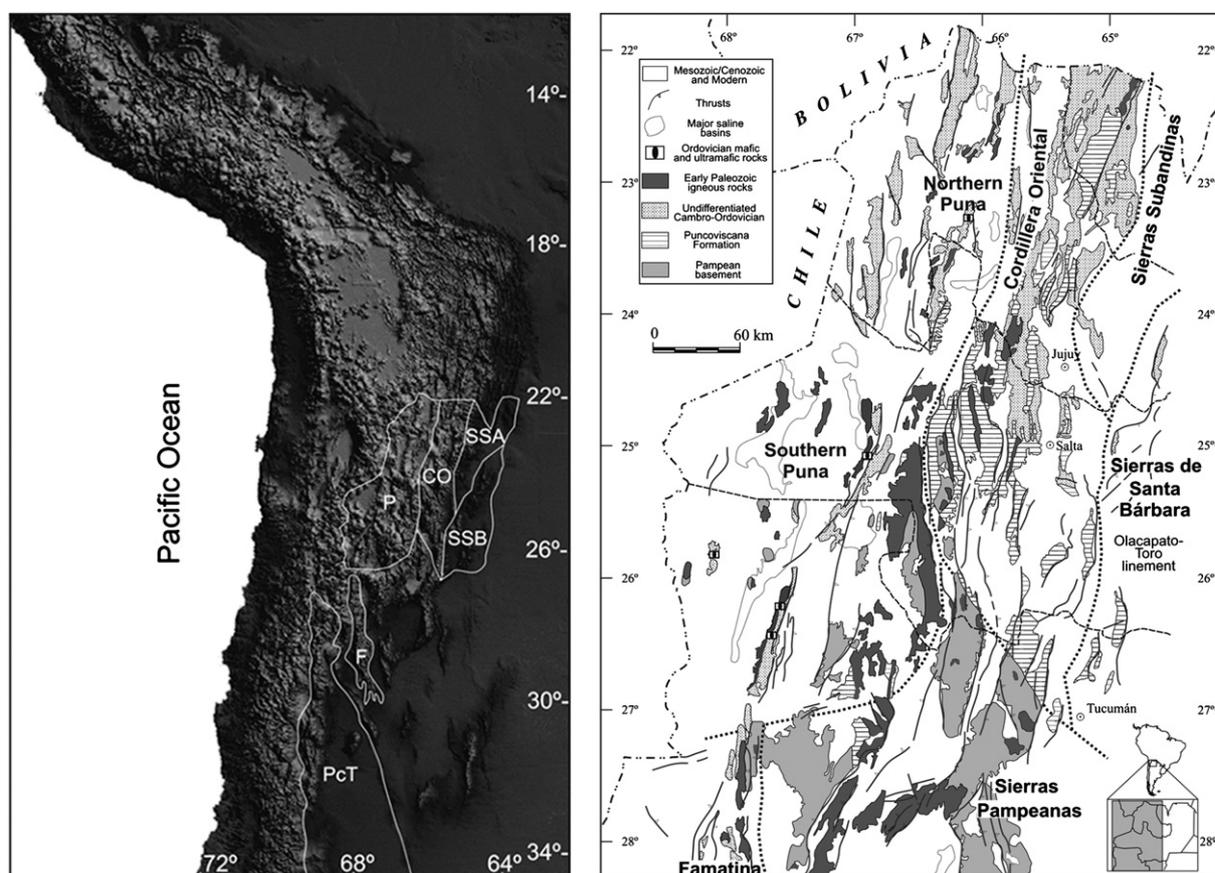


Fig. 1. Relief image showing topography of the Central Andes, indicating the different Ordovician basins located in western Argentina. P: Puna; CO: Cordillera Oriental; SSA: Sierras Subandinas; SSB: Sierras de Santa Bárbara; F: Famatina; PcT: Precordillera terrane (on the left). Geological and geographical map of the Central Andean Basin (modified from Coira et al., 1999 and Astini, 2003). The Puncoviscana Formation and the Pampean basement are assigned to the Neoproterozoic-Eopaleozoic (on the right).

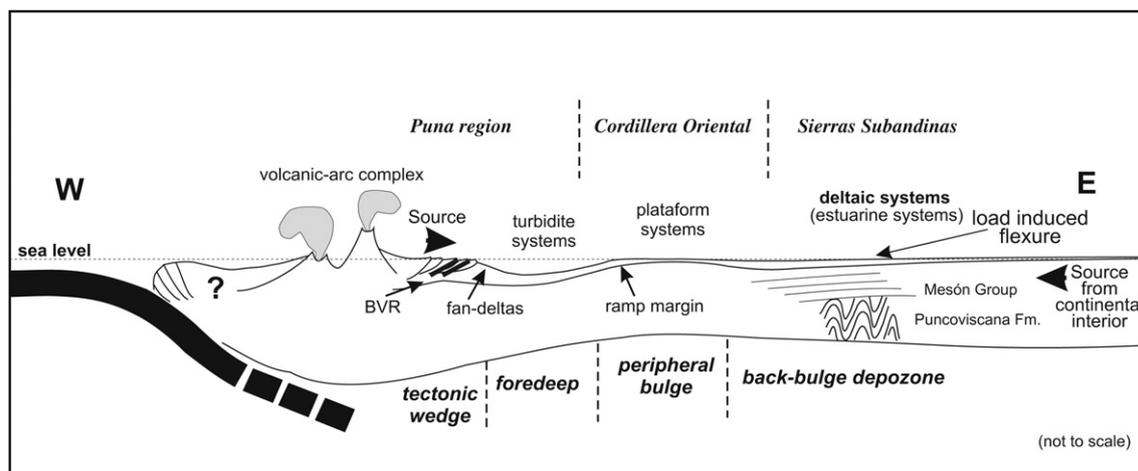


Fig. 2. Schematic Middle Ordovician E–W cross section of the northern region (northern Puna) of the Central Andean Basin, northwestern Argentina, showing the tectonic setting and distribution of adjacent regions in a foreland basin system (modified from Astini, 2003). BVR: bimodal volcanic rocks recording a previous back-arc stage, now thrust within the thrust belt.

topographic relief. Its most internal part (~20–50 km) has been called the Inter-Andean zone in its northern continuation to Bolivia (Roeder, 1988). This abrupt region correlates with the greatest rainfall and the highest erosion rates in Central Andes (Masek et al., 1994) and has a very dense green coverage. Toward the south, the Subandean belt dies out across the Salta Province and is replaced by a different relieve, represented by the Sierra de Santa Bárbara (Ramos, 1999). Ordovician outcrops are only known from the innermost thrusts and associated anticlines, as it is the case of the Zapla anticline in Jujuy, which shows the most complete exposed section through this region. Excellent quality exposures along the Río Capillas traversing the Sierra de Zapla allow high-resolution work and careful palynologically oriented sampling that is the matter of this work.

The best and most complete palynologically constrained Ordovician section across the Sierras Subandinas crops out in the southern part of the Sierra de Zapla along the Río Capillas (Sierras Subandinas, Jujuy Province) that shows a ~450 m thick shallow marine and marginal marine succession (Fig. 3). This stratigraphy is exposed in both flanks of a fold propagation anticline. Frequent subaerial exposures and largely marginal marine settings explain the scarcity of invertebrates throughout the section. Based on a detailed facies analysis aided with geometry and paleocurrent measurements, and recognition of key surfaces, four 3rd order depositional sequences with different internal arrangements were identified (Fig. 4). The Zanjón Formation, with unexposed base (core of the anticline), initiates the stratigraphic section and is characterized by a thoroughly bioturbated muddy interval with alternations of heterolithic facies associations and subordinated storm layers, represented by thin-bedded phosphate-rich microconglomerates and broken inarticulate-rich shell lags within some more laterally continuous sandy beds with sharp erosive contacts at their base. The Zanjón Formation (sequence 1) yields a mixed *Skolithos-Cruziana* ichnofacies, intimately associated to the heterolithic facies and particularly well recorded in the prominent and continuous sandy beds. Toward the top of the unit, thin sandy beds with interference ripple patterns, truncated ripple tops and superimposed wrinkle marks indicate periodical emergence strongly suggesting tidal flat environments. Moreover, horizons affected by pervasive mudcracking (up to 10 cm depth) are well developed indicating clear subaerial exposure. The Zanjón Formation has been assigned to the upper part of the Floian and probably Dapingian stages. Above, a ~35–40 m of the stratigraphic section

shows a gradual increase in color mottling and a broad gradual change into dominant purplish-red colors (Laja Morada Member of the Labrado Formation) indicating a more protracted subaerial emergence during a most likely Dapingian relative sea-level drop (sequence 2, comprising low system tract to transgressive system tract). During this regressive interval, strong influence of a fluctuating water table, characteristic of interfluvial is interpreted, contributing to degradation of organic matter and thus, reducing preservation of organic-walled microfossils. This red interval is sharply truncated by cross-bedded sandstones with mud chip, phosphate-rich and quartz-pebble lags suggesting development of composite fluvial incisions, characterizing the overlying Lagunilla Member (basal part of sequence 3, comprising the transgression system tract) of the Labrado Formation (Fig. 4). This gray to greenish color unit shows stacking patterns of meter-scale amalgamated sandy beds with superbly recorded tidal bundling, frequent reactivation surfaces with mud drapes and mud couplets suggesting strong tidal influence (Astini and Marengo, 2006), alternating with thoroughly bioturbated muddy packages. Sandy fluvial to tide-dominated estuarine fills and subtidal heterolithic intervals are interpreted for the Lagunilla Member that distinctly overlie the subaerially exposed Laja Morada Member. Thus, the boundary between them is interpreted as a major sequence boundary recording bypassing and later retrogressive stacking representing a typical transgressive systems tract. Development of surfaces with dense vertical millimeter to centimeter-scale in diameter *Skolithos*-like forms filled with very mature coarse sandstones are interpreted as representing *Glossifungites* ichnofacies (Astini and Marengo, 2006), typically indicating firm-ground development and by-pass erosion and filling contemporaneous with interfluvial exposure and previous to subaqueous reworking during advancing ravinement surfaces (e.g., McEachern and Pemberton, 1992; McEachern et al., 1999).

Above the composite estuarine fill represented by the Labrado Formation, a sharp non-erosive boundary to a fine-grained laterally continuous fully marine interval indicates a rapid transgressive shift, compatible with development of a maximum flooding surface. This constitutes the boundary between the Labrado Formation (top of the Lagunilla Member) and the Capillas Formation (sequence 3, transgressive system tract, starting from the maximum flooding surface 3). The Capillas Formation, formerly assigned to the Darrivilian to possibly Katian stages, sharply levels the previous estuarine complexes and represents a fine-grained shelfal facies

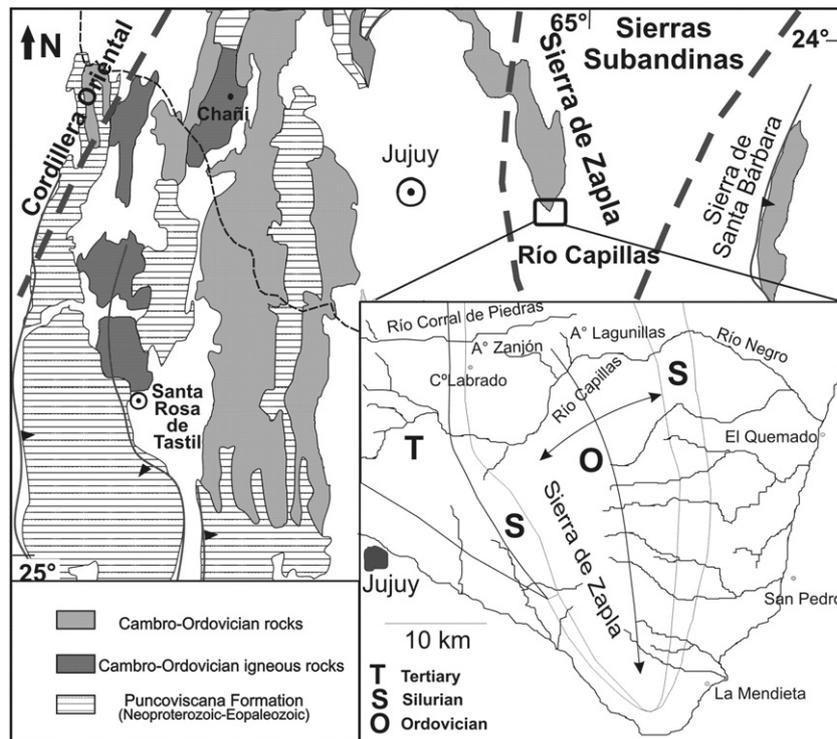


Fig. 3. Regional geological map and location map of the studied area.

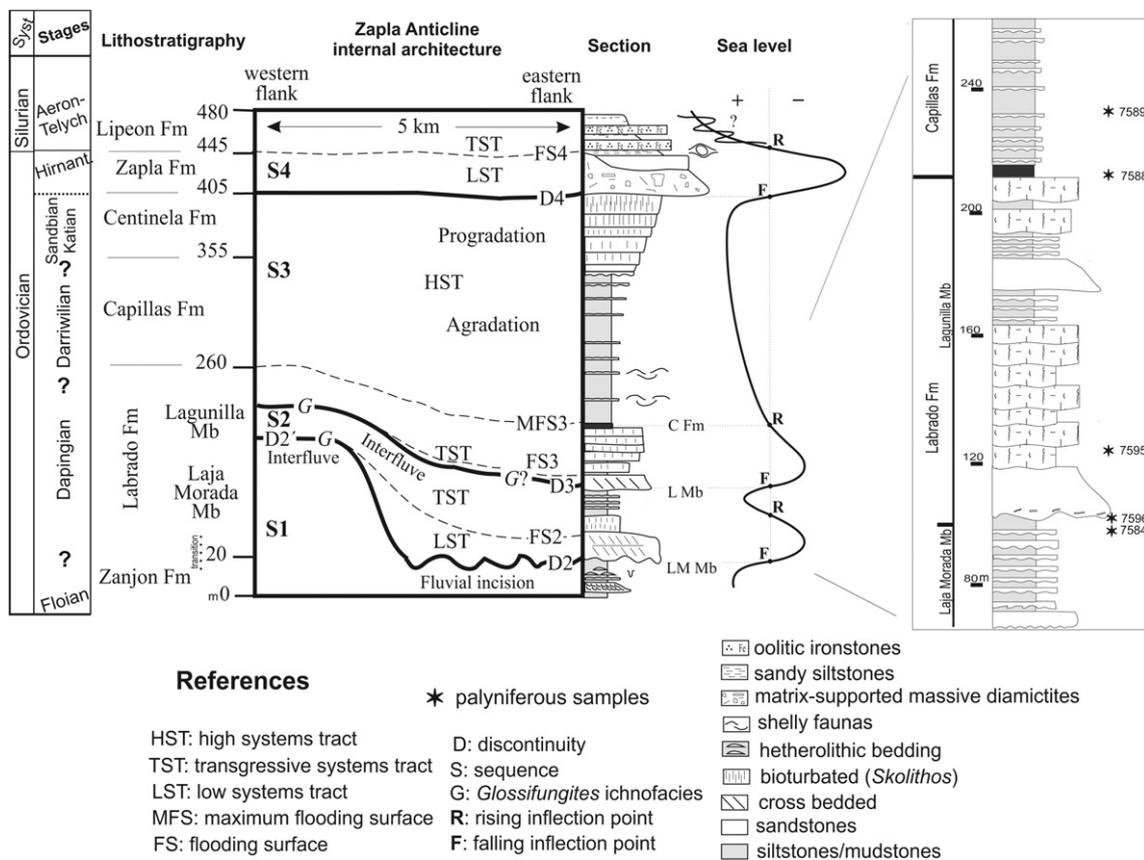


Fig. 4. Ordovician columnar section exposed in the Río Capillas showing units with asymmetries in their outcrops between both flanks, lithology, sequence stratigraphy, sea-level curve and location of samples (modified from Astini et al., 2003). LM Mb, L Mb and C Fm indicate the bases of the Laja Morada and Lagunilla members, of the Labrado Formation, and of the Capillas Formation respectively.

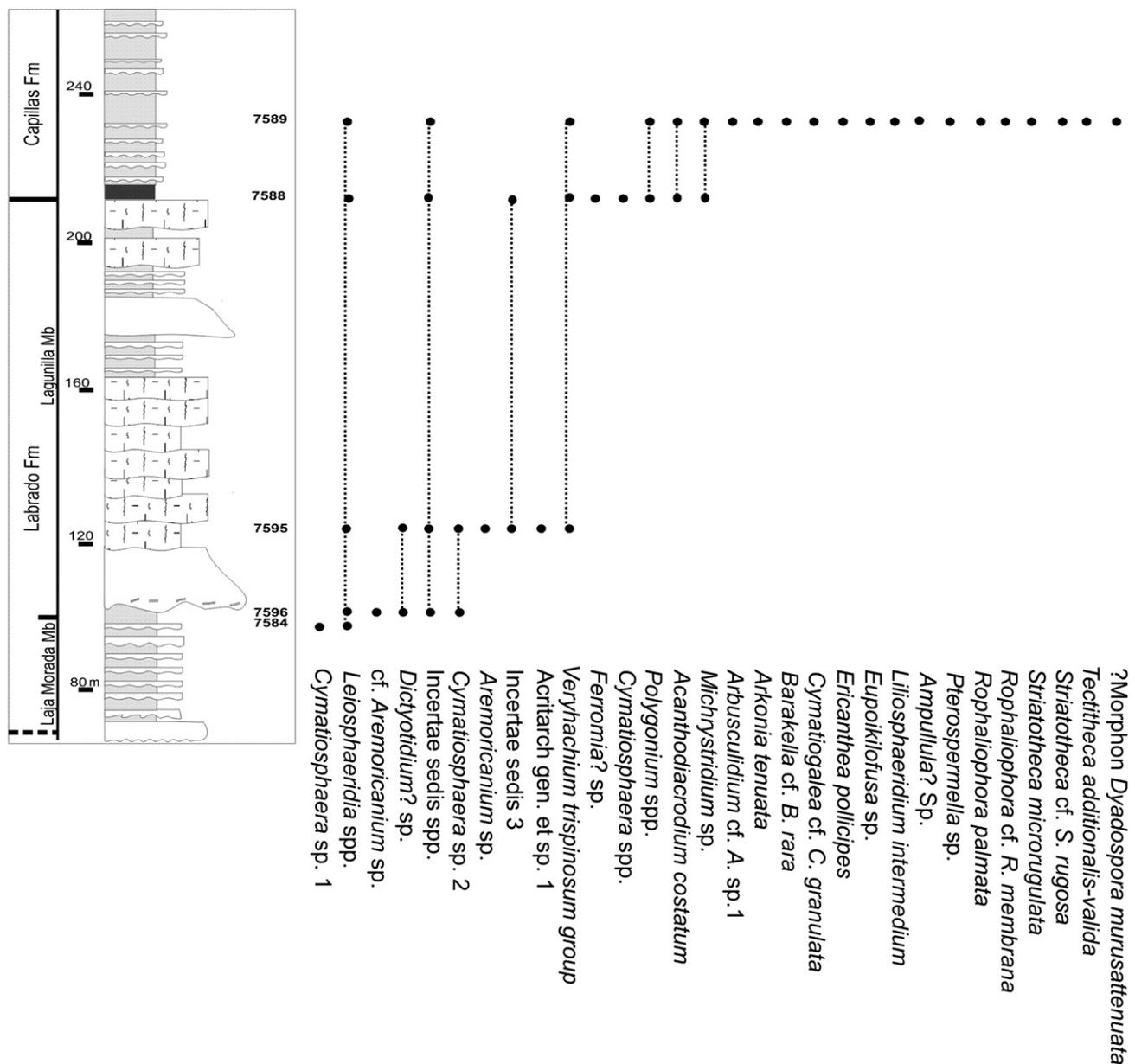


Fig. 5. Stratigraphic distribution of palynomorphs taxa throughout the studied section.

association that gradually coarsens and thickens up. This unit contains the only truly marine shelly fauna concentrated in few storm beds above the fine-grained interval that characterizes a maximum flooding stage. This interval is the only one that can be positively correlated with sections in the Cordillera Oriental to the west (base of Santa Gertrudis Formation and Sepulturas Formation) and Bolivia (Anzaldo and Coroico Formations) (Astini, 2003; Astini et al., 2003; Astini and Marengo, 2006). Albanesi et al. (2007) have recently confirmed an age not younger than late Darriwilian for the upper section of the Capillas Formation, based on its conodont fauna. Their analysis has also allowed correlation with the Santa Gertrudis Formation in the Cordillera Oriental. A gradual coarsening-thickening upward trend into silty sandstones and the replacement of *Cruziana* by *Skolithos* dominated ichnofacies suggest a shallowing-upward section, capped by the thick-bedded, high-energy quartz sandstones with pipe-rock structures of the Centinela Formation (of probable Sandbian to Katian age). The recorded shallowing-upward trend in the Capillas Formation indicates the

progradation of a deltaic complex during a highstand systems tract. Truncation in its top is correlated with erosion during a major eustatic sea-level drop associated with the waxing stage of the Hirnantian ice cap that rapidly spread out across Gondwana during uppermost Ordovician. The Zapla Formation (Hirnantian) or Zapla glacial horizon covers the unconformity and, in turn, is drowned by a major flooding surface initiating a separate supercycle with deposition of several oolitic ironstones developed within the Silurian. The Silurian deposits (Lipeón Formation) record high frequency sea-level fluctuations after repeated Gondwanan glacial waning stages and isostatic rebounds that contributed to truncation of Fe⁺² saturated estuaries, favouring the deposition of oolitic ironstones. The more restricted estuarine facies are regionally succeeded by the development of a *Zoophycos* dominated muddy shelf.

This outermost region of the foreland exposed in the Subandean Ranges is characterized by the alternation of shallow-marine deltaic systems and estuarine environments, which indicates frequent coastal plain conversions (Dalrymple et al., 1992; Ardies

et al., 2002), brackish water influence (cf., Pemberton and Wightman, 1992) and repeated coastal incision induced by relative sea-level fluctuations (Astini and Marengo, 2006).

3. Material and methods

Three samples of the Labrado Formation, one from the lower Laja Morada Mb (7584), and two from the upper Lagunilla Mb. (7595 and 7596), and two samples from the basal part of the Capillas Formation (7588 and 7589) were processed using the standard palynological procedure, involving HCl–HF–HCl acid maceration of the rock samples. The obtained organic residue was then sieved using a 10 µm sieve, and oxidized up to 4 min using concentrated nitric acid. Slides were examined using light microscopy with interference phase contrast.

The palynological slides are housed in the paleopalynological slide collection of the Unit of Paleopalynology, IANIGLA, CCT-CONICET Mendoza, labelled MPLP (Mendoza-Paleopalynoteca-Laboratorio de Paleopalynología).

All the recognized taxa are listed hereafter (Appendix 1). Because of the low abundance in almost all the assemblages, with a single specimen per taxon in most of them, a taxonomical overview and some remarks are given for uncertain forms, questionable assignments or reassignments of taxa.

4. Results: palynomorph assemblages

All samples from the Labrado Formation and the sample 7588 of the Capillas Formation yielded moderately to badly preserved palynological assemblages, characterized by low diversity and abundance (Figs. 5 and 6). These assemblages mainly consist of sphaeromorphs (including *Leiosphaeridia*), and specimens of

Cymatiosphaera and *Dictyotidium?*, most of them not determinable at species level, accompanied by *Aremoricanium* and *Veryhachium trispinosum* group, while *Acanthodiacrodium costatum*, *Ferromia?* and representatives of the genus *Polygonium* first appear in sample 7588 of the Capillas Formation. Sample 7595 is characterized by the presence of undeterminable sphaeromorph acritarchs (Fig. 7D). Also present are more enigmatic palynomorphs, indicated here as spore-like microfossils, such as the specimen attributed to “*Incertae sedis* 1” (Fig. 7B, C, R, S).

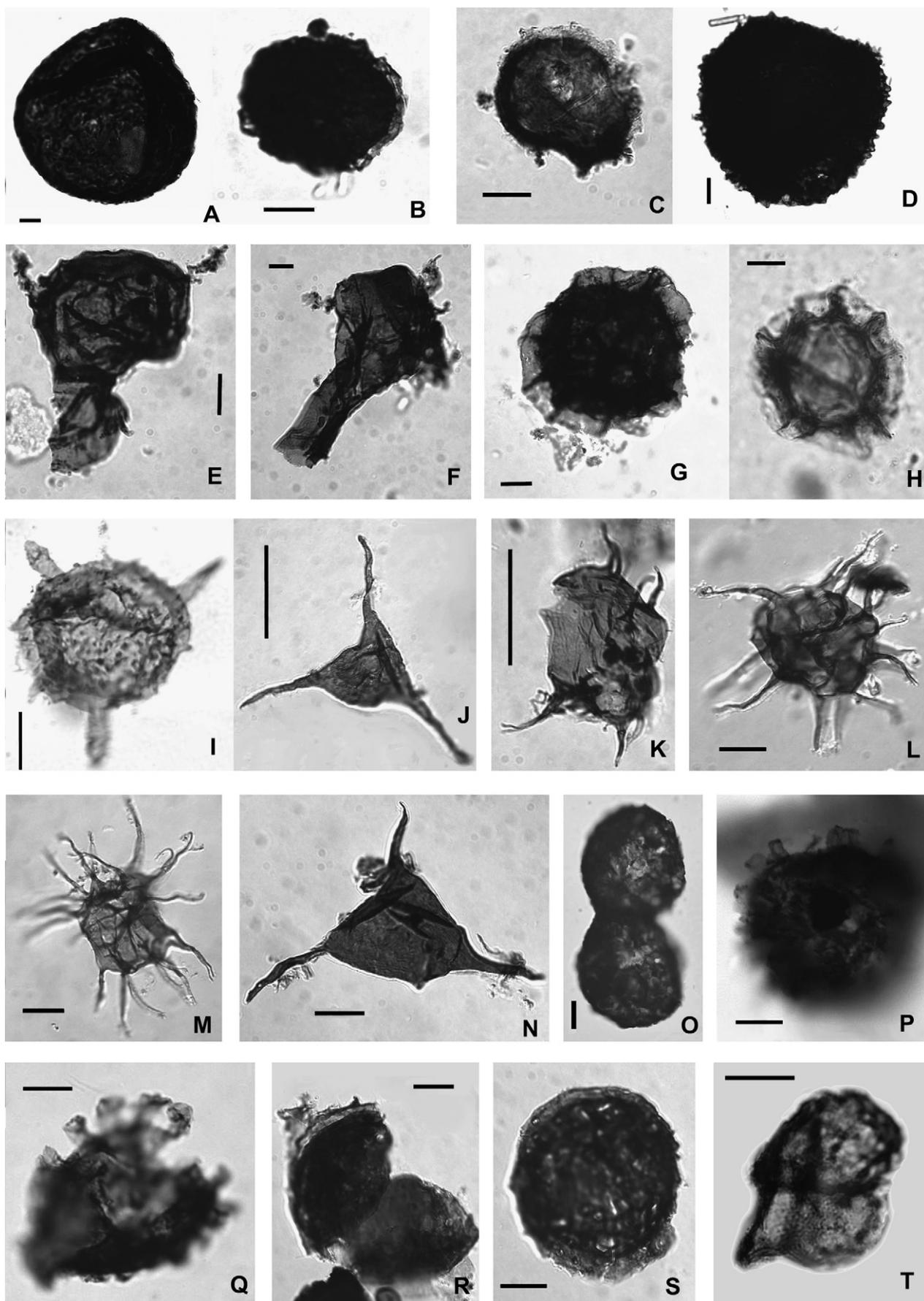
Yield of sample 7589 from the Capillas Formation was better preserved, as well as more abundant and taxonomically diverse (Fig. 5). *A. costatum* is a commonly occurring taxon. Several well preserved specimens of *Arkonina tenuata* were also observed in this sample. Other acritarch species present in sample 7589 from the Capillas Formation are: *Arbusculidium* sp. cf. *A. sp. 1* in Brocke et al. (2000); *Barakella* cf. *B. rara*; *Cymatiogalea* cf. *C. granulata*; *Ericanthea pollicipes*; *Eupoikilofusa* sp.; *Liliosphaeridium intermedium*; *Polygonium* sp.; *Pterospermella* sp.; *Rhopaliophora palmata*; *Rhopaliophora* cf. *R. membrana*; *Striatotheca microrugulata*; *Striatotheca* cf. *S. rugosa*; *Tectitheca additionalis-valida* sensu Cramer and Diez, 1977; *V. trispinosum* group sensu Servais et al., 2007 and one specimen doubtfully assigned to *Ampullula*.

5. Discussion on spore-like microfossils

Sporomorphs or “spore-like palynomorphs” such as monads (Fig. 7A–C, R, S), dyads (?*Dyadospora murusattenuata* Strother and Traverse, 1979 sensu Steemans et al., 1996; Fig. 7O), and tetrads (although in planar configuration: Fig. 7T) are common components of the palynomorph assemblages recovered from all the sampling levels. Although these forms (of uncertain origin and

Genus/samples	7584	7596	7595	7588	7589
<i>Cymatiosphaera</i>	12.5	1.4	2.3	–	–
<i>Leiosphaeridia</i>	87.5	35.1	40.8	50.7	17.5
cf. <i>Aremoricanium</i>	–	1.4	–	–	–
<i>Dictyotidium?</i>	–	5.4	4.6	–	–
<i>Aremoricanium</i>	–	–	2.3	–	–
Acritarch gen. et sp. indet.	–	–	17.7	7.2	–
<i>Veryhachium</i>	–	–	2.3	1.4	6.0
<i>Ferromia?</i>	–	–	–	2.9	–
<i>Polygonium</i>	–	–	–	27.5	39.8
<i>Acanthodiacrodium</i>	–	–	–	1.4	2.4
<i>Ampullula?</i>	–	–	–	–	–
<i>Arbusculidium</i>	–	–	–	–	0.6
<i>Arkonina</i>	–	–	–	–	3.6
<i>Barakella</i>	–	–	–	–	1.2
<i>Cymatiogalea</i>	–	–	–	–	0.6
<i>Ericanthea</i>	–	–	–	–	0.6
<i>Eupoikilofusa</i>	–	–	–	–	0.6
<i>Liliosphaeridium</i>	–	–	–	–	1.2
<i>Michrystidium</i>	–	–	–	1.4	6.6
<i>Pterospermella</i>	–	–	–	–	1.2
<i>Rhopaliophora</i>	–	–	–	–	1.2
<i>Striatotheca</i>	–	–	–	–	1.2
<i>Tectitheca</i>	–	–	–	–	1.2
<i>Incertae sedis</i>	–	56.8	30.0	7.2	13.9
?Morphon <i>D. murusattenuata</i>	–	–	–	–	0.6
Total N° specimens	8	74	130	69	166
Total N° species/diversity	2	5	8	9	21

Fig. 6. Relative abundances (percentages) of the recorded genera per sample, total number of counted specimens and total number of species (diversity). Organic-walled microfossils were encountered in one palynological slide, when they were at least 100 individuals (7595 and 7589) and in three palynological slides in the other levels (7584, 7596 and 7588).



biological affiliation) could be included within the “acritarchs”, we prefer to discuss them separately because:

- 1) Their morphology is conspicuously different from microphytoplankton cysts which represent the large majority of palynomorphs currently grouped in the informal category “acritarchs” (e.g., Vecoli and Le Hérissé, 2004), and is more similar to cryptospore morphology;
- 2) They occur more abundantly in proximal, marginal marine sediments where influence of terrestrially-derived deposition is more likely, as indicated by the sedimentological and sequence stratigraphic analyses;
- 3) Their age is consistent with the existence of primitive embryophyte land plants since Darriwilian times on the continents (Strother et al., 1996).

There is currently a debate on the meaning of the term “cryptospores”. According to Steemans (1999), Wellman and Gray (2000) and Steemans et al. (2009) cryptospores are considered to represent dispersed spores derived from the most ancient terrestrial flora (primitive embryophytes). However, enigmatic palynomorphs supposed to be of non-marine origin, based on their morphology, wall ultrastructure, as well as their depositional palaeoenvironment (i.e., proximal marine deposits), have been described from sediments as old as the Middle Cambrian (Strother and Beck, 2000; Taylor and Strother, 2008, 2009). Other spore-like microfossils are known since a long time to abundantly occur in Lower Ordovician sediments especially in Gondwanan localities, such as *Virgatasporites* and *Attritasporites* (Combaz, 1967; Vavrdová, 1990; Richardson, 1996; Vecoli, 2004). Richardson (1996), considered that grouped sporomorphs, monads, and coenobial masses present in Tremadocian-Arenig sediments, showing differences with distribution patterns of prasinophyte phycomata in palynofacies and having robust walls, may indicate a terrestrial origin, probably with algal affinities. He named “pre-cryptospores” these probably land-derived palynomorphs. As pointed out by the same author, some monad cryptospores may be difficult to distinguish from sphaeromorph acritarchs and only an accurate analysis of preservation, abundance and distribution of palynomorphs would permit to decide either a marine or a terrestrial origin for them. Strother and Beck (2000), considered that cryptospores do not represent exclusively the products of embryophytes and proposed to extend the definition to include non-embryophytic terrestrial remains such as chlorophyte spores. According to Strother and Beck (2000), any organic-walled microfossils of non-marine origin derived from cryptogams, capable to produce a resistant spore-wall of sporopollenin or other organic polymers, should be considered as cryptospores. Therefore, all problematic non-marine forms would be included within cryptospores as well as marine problematic forms are included in the term acritarch, considering that acritarchs are generally interpreted as marine organisms (Servais et al., 2004). Later, Strother (2006) went further with his interpretations considering that even the Cambrian cryptospores are compatible with a possible embryophytic derivation, then

concluding that embryophytes could occupy terrestrial habitats throughout the whole Paleozoic.

Taylor and Strother (2008, 2009) introduced the term synoecospore packets for spore units including a common enclosing structure, named as synoecospore wall, and commonly occurring in Cambrian sediments of North America. Based on TEM analysis, they provided new information about the wall ultrastructure of these sporomorphs, discussing the possible evolutionary pathway from algae to land plants. Our material does not permit to recognize synoecospore morphotypes because of poor preservation, therefore further comparison with the Cambrian sporomorphs cannot be provided.

The spore-like palynomorphs (or “sporomorphs”) recovered from the Labrado and Capillas formations (e.g., Fig. 7B, C, R–T), occur as single individuals or as clusters, in planar tetrads, probably dyads and most of them enclosed within envelopes or with marginal thickening and thus approach to the morphological definition of cryptospores. Accordingly, all palynomorphs grouped here under the term “spore-like microfossils” can be accommodated in the cryptospore definition of Strother (2006). On the other hand, following the cryptospore definition of Steemans (1999), only *D. murusattenuata* (Fig. 7O) would be possibly included within the cryptospores, and all other forms would be identified as “acritarchs”. However, this latter solution is not satisfactory because it does not permit to differentiate a group of palynomorphs which are morphologically distinct from marine microphytoplankton cysts (i.e., the acritarchs).

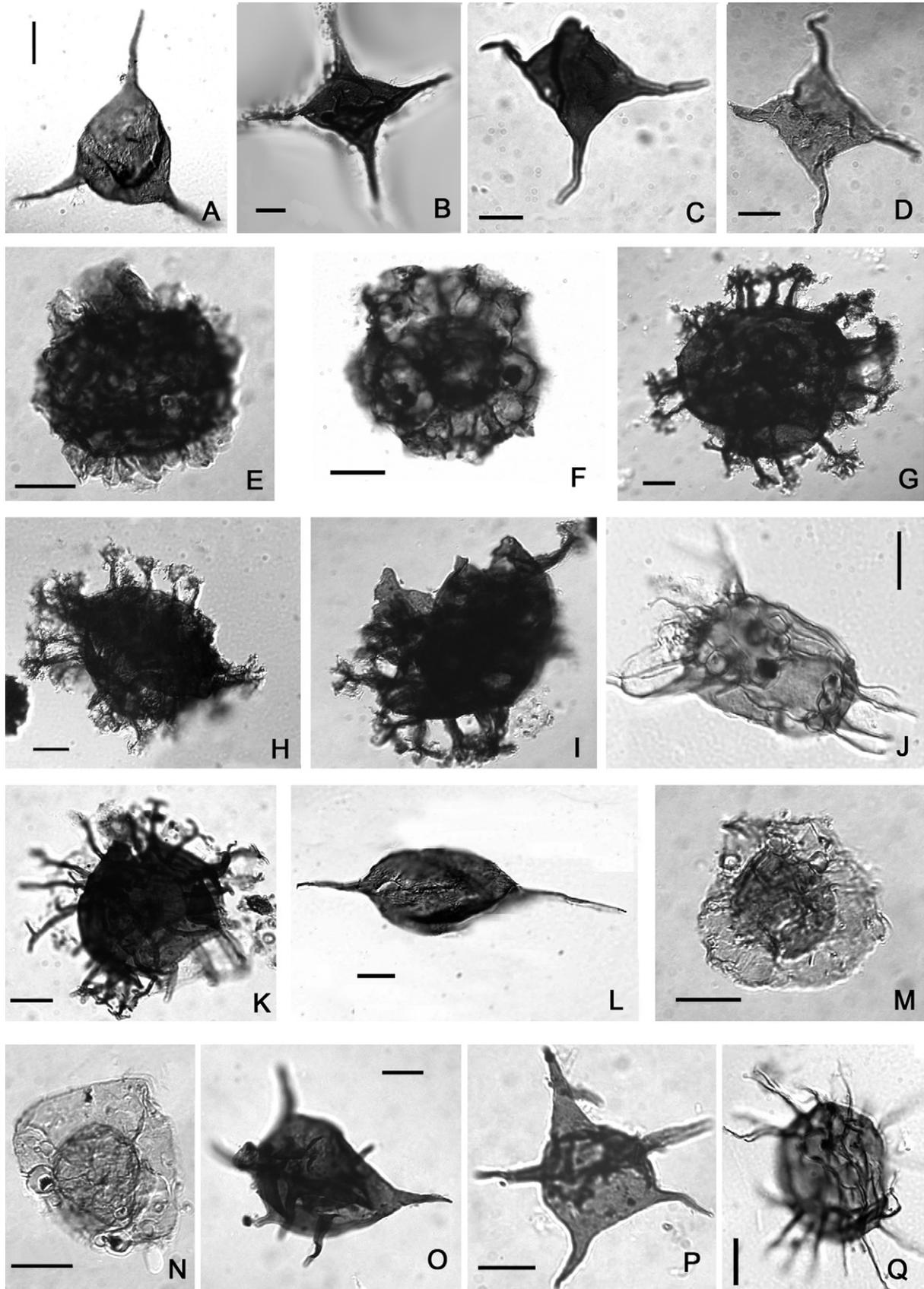
Accordingly, without further venturing into the discussion on the land-plant vs. algal origin of the “spore-like palynomorphs”, we propose here that these enigmatic palynomorphs have a non-marine origin and thus should be clearly kept separately from the acritarchs (marine microphytoplankton cysts).

6. Biostratigraphy

Molyneux (1990, 1999) highlights major changes in the composition of acritarch assemblages around the Arenig/Llanvirn boundary in England, where *Arkonía* and *Frankea* representatives first appear (*Frankea hamata*-*Striatotheca rarirrugulata* acritarch Zone). Other proposals of biozones for this age correspond to the Algerian Sahara with the Zone E, supposed to be late Arenig-Llanvirn (Jardiné et al., 1974), or more probably Llanvirn according to Molyneux et al. (1996), Vecoli (1999) and to Jordan, with the JO-3 Palynozone, considered as Llanvirn and containing *Frankea* (Keegan et al., 1990). However, acritarch data from precisely dated Llanvirn strata, in terms of British nomenclature, are scarce.

A group of species present in the Capillas assemblages first appears in the Lower Ordovician, in the Floian or even in the Tremadocian Stage. *R. palmata* has been recorded from the Tremadocian (*Araneograptus murrayi* Zone) of the Cordillera Oriental (Eastern Cordillera), Central Andean Basin (Rubinstein et al., 2007; de la Puente and Rubinstein, 2009), while *A. costatum*, *C. granulata*, and *Tectitheca additionalis*-*Tectitheca valida*, have been recovered from levels corresponding to the *Tetragraptus akzharensis* Zone and *S. microrugulata* from levels corresponding to the “*Baltograptus*

Fig. 7. A. Incertae sedis 3. Lagunilla Member, Labrado Formation. 7595f, S36/0. B. Incertae sedis 1. Lagunilla Member, Labrado Formation: B, 7595a, H43/1. C. Incertae sedis 1. Lagunilla Member, Labrado Formation 7595a, F32/2. D. “Acritarch gen. et sp. indet. 1” Lagunilla Member, Labrado Formation. 7595f, U38/2. E. *Aremoricanium* sp. Lagunilla Member, Labrado Formation. 7595a, O37/3. F. *Aremoricanium* sp. Lagunilla Member, Labrado Formation. 7595a, M26/1. G. *Cymatiosphaera* sp. 2. Lagunilla Member, Labrado Formation. 7595f, F25/1. H. *Cymatiosphaera* sp. 1. Laja Morada Member, Labrado Formation. 7584b, C32/0. I. *Ferromia?* sp. Capillas Formation. 7588c, B22/1. J. *Arkonía tenuata* (Burmman, 1970). Capillas Formation. 7589g, C25/0. K. *Arbusculidium* cf. A. sp. 1 in Brocke et al. (2000). Capillas Formation. 7589h, E31/4. L. *Polygonium* sp. Capillas Formation. 7589c, E39/4. M. *Acanthodiacrodium costatum* (Burmman, 1968) Capillas Formation. 7589f, E28/2. N. *Arkonía tenuata* (Burmman, 1970). Capillas Formation. 7589e, M33/2. O. ?Morphon *Dyadospora murusattenuata* (Strother and Traverse 1979) sensu (Steemans et al., 1996). Capillas Formation, 7589h, F23/0. P. *Rhopaliophora palmata* (Combaz and Peniguel, 1972; Playford and Martin, 1984). Fm. Capillas, 7589h, E31/3. Q. *Ampullula?* sp. Capillas Formation. 7589f, J27/0. R. Incertae sedis 1. Capillas Formation, 7589h, D39/0. S. Incertae sedis 1. Capillas Formation, 7589h, P36/1. T. Incertae sedis 2. Tetrad. Lagunilla Member, Labrado Formation, 7595a, N25/1. Each figured palynomorph is located by sample, slide number and England Finder coordinates. The scale bars represent 10 μ m.



deflexus” Zone, both of them of the Floian of the same region (Rubinstein et al., 2007 and Rubinstein unpublished data). In the upper Suri Formation of the Famatina System, northwestern Argentina, *R. membrana* together with chitinozoans of the *Eremochitina brevis* Zone are present in levels containing *Oepikodus evae*, assigned probably to the latest Early Ordovician (SS. F13) (Achab et al., 2006). The Stage Slices (SS) are used herein according to the new subdivision of the Ordovician proposed by Bergström et al. (2008).

Possibly, the most relevant acritarch to constrain the age of the basal part of the Capillas Formation is the genus *Arkonía*. Even if *Arkonía* was considered a stratigraphic marker for the Llanvirnian, specimens belonging to this genus have been recorded below the Arenig/Llanvirn boundary (Servais, 1997), likewise the specimens of the Tadla Basin, Morocco, assigned to the late Arenig-early Llanvirn by Cramer et al. (1974b) and redated as late Arenig by means of chitinozoans (Soufiane and Achab, 1993). The first occurrence of *Arkonía* approximately corresponds to the British *Didymograptus hirundo* graptolite Zone (Brocke et al., 1995) which is confirmed in the Tadla Basin by the co-occurrence with chitinozoans of the *Desmochitina bulla* Zone (Soufiane and Achab, 1993), corresponding to the uppermost Arenig, that is the lower part of the Darriwilian (middle part of TS. Da1). Additionally, the upper part of the Klavaba Formation, in Bohemia, yields *Arkonía* from levels corresponding to the *D. bulla* chitinozoan Zone (Fatka et al., 1994), thus confirming the early Darriwilian age. In South China, *Arkonía* also occurs at the base of the Darriwilian (Li et al., 2000). Burmann (1970) first described *A. tenuata* for the late Llanvirn of an unidentified locality of Eastern Germany, subsequently recognized as the Island of Rügen (Servais, 1997). It has also been recovered from the Rheinisches Schiefergebirge, Germany (Maletz and Servais, 1993) and the “Band de Sambre-et-Meuse”, Belgium (Servais and Maletz, 1992), in levels assigned to the early Llanvirn based on graptolites. In fact, Servais (1997) in his review of the genus *Arkonía* indicates that specimens of this genus constitute a plexus of forms in Llanvirn assemblages of Belgium and Germany. The presence of *A. tenuata* in Pakistan, in assemblages VK2 and VK3 assigned to the early late Arenig and the Arenig/Llanvirn boundary respectively, lack independent biostratigraphic control (Quintavalle et al., 2000). In North Africa *A. tenuata* has been recorded in the *Frankea santbernardensis-Vogtandia ramificata* Assemblage Zone assigned to the Llanvirn (Vecoli, 1999).

Together with *Arkonía*, taxa such as *A. costatum*, *T. additionalis-valida* and *E. pollicipes*, have been recovered from the Tadla Basin, Morocco (Cramer et al., 1974b), and *C. granulata* and *E. pollicipes* from the Prague Basin (Vavrdová, 1990). The Assemblage D of South China, assigned probably to the Arenig/Llanvirn boundary or early Llanvirn, contain *L. intermedium*, *C. granulata* and *Arbusculidium* sp. 1 (Brocke et al., 2000).

L. intermedium is a widespread species recorded from the Arenig/Llanvirn transition in several localities of Baltica and Gondwana (Tongiorgi et al., 2003 and references herein). Bagnoli and Ribecai (2001) pointed out the importance of the genus *Liliosphaeridium* which first appears in Öland, apparently at the base of the Darriwilian, and has a relatively short stratigraphic distribution. This

species ranges from the late Volkhov to the Kunda, in terms of Baltic stratigraphy (late Arenig-early Llanvirn), independently dated by conodonts and trilobites (Tongiorgi et al., 2003).

Another useful genera for dating is *Aremoricanium*, which is positively recognized in the Lagunilla Member of the Labrado Formation. Some species of this genus, which was firstly recovered from the Llanvirn-Llandeilo Series of North America (Loeblich and MacAdam, 1971), have been found later in the Tadla Basin (Cramer et al., 1974b) in the uppermost Arenig (Ts. 4a). Brocke et al. (2000) indicate the presence of *Aremoricanium* aff. *simplex* Loeblich and MacAdam, 1971 in their “Assemblage A”, corresponding to the upper lower Arenig (*Azigograptus suecicus* and lower *Undulograptus sinodontatus* Zones), or Dapingian (early Middle Ordovician).

The FADs of *B. rara* and *S. rugosa* correspond to the *A. suecicus* local zone in south China, while the FAD of the genus *Ampullula* is in underlying *Corymbograptus deflexus* Zone (Yan, 2004). The *A. suecicus* Zone involves the Lower-Middle Ordovician boundary in this region (Zhang and Chen, 2003).

Curiously, the genus *Frankea*, a marker of the Middle Ordovician for Gondwanan and peri-Gondwanan assemblages is absent in northwestern Argentina, as well as in China (Brocke et al., 2000; Li et al., 2003). The absence of *Frankea* could be related either to the paleogeographic position at middle paleolatitudes of northwestern Argentina, similar to the paleolatitude of south China, as to paleoenvironmental conditions due to the relatively shallow-marine setting, with scarce and low-diverse palynomorph assemblages. Further investigations in the section might shed light on the controversy: paleogeography vs. ecological requirements.

Considering Argentinian data, palynomorph assemblages of the Cordillera Oriental younger than Floian are unknown up to now. The only acritarch assemblage attributed to the Llanvirn comes from the Los Azules Formation, Precordillera Basin. Nevertheless, it is composed mainly by Leiospheres, lacking any stratigraphic value (Ottone et al., 1999).

As it is observed in coeval acritarch assemblages of other regions (i.e., North Africa, South China), it is difficult to recognize the Arenig-Llanvirn boundary by means of acritarchs, because there are no marked changes in the acritarch assemblages in correspondence to this boundary. Nevertheless, the palynological assemblages recovered from the Capillas Formation seem to point out to an age not older than Darriwilian. Then, it can be concluded that despite difficulties in recognizing the Arenig-Llanvirn boundary, acritarchs are in general very useful for identifying the Global Stages defined by the International Subcommittee on Ordovician Stratigraphy, such as the Darriwilian.

The Labrado Formation, particularly its upper Lagunilla Member could indicate the base of the Middle Ordovician (Dapingian?), based on the occurrence of *Aremoricanium*.

7. Paleobiogeography

Two different acritarch assemblages, which appear to correspond to distinct biogeographic provinces, have been differentiated in the Lower-Middle Ordovician. One is characteristic of low intermediate paleolatitudes, being mainly recorded from Baltic

Fig. 8. A. *Arkonía tenuata* (Burmann, 1970). Capillas Formation, 7589g, N38/0. B. *Striatotheca* cf. *S. rugosa* (Tongiorgi et al., 1995). Capillas Formation, 7589a, S25/2. C. *Striatotheca microrugulata* (Vavrdová) (Martin, 1977). Capillas Formation, 7589h, P25/4. D. *Striatotheca microrugulata* (Vavrdová) (Martin, 1977). Capillas Formation, 7589h, U41/4. E. *Rhopaliophora* cf. *R. membrana* (Li, 1987). Capillas Formation, 7589h, W37/1. F. *Ericanthea pollicipes* (Cramer and Díez, 1977). Capillas Formation, 7589h, V40/2. G. *Liliosphaeridium intermedium* (Eisenack) (Playford et al., 1995). Capillas Formation, 7589c, W45/4. H. *Liliosphaeridium intermedium* (Eisenack) (Playford et al., 1995). Capillas Formation, 7589h, X41/0. I. *Liliosphaeridium intermedium* (Eisenack) (Playford et al., 1995). Capillas Formation, 7589h, J42/1. J. *Barakella* cf. *B. rara* (Tongiorgi et al., 1995). Capillas Formation, 7589h, N42/0. K. *Cymatiogalea* cf. *C. granulata* Vavrdová, 1966. Capillas Formation, 7589f, L25/4. L. *Eupoikilofusa* sp. Capillas Formation, 7589h, T37/0. M. *Pterosperrmella* sp. Capillas Formation, 7589e, Q38/0. N. *Pterosperrmella* sp. Capillas Formation, 7589h, G32/1. O. *Tectitheca additionalis-valida sensu* (Cramer et al., 1974a). Capillas Formation, 7589h, M42/3. P. *Tectitheca additionalis-valida sensu* (Cramer et al., 1974a). Capillas Formation, 7589h, S31/2. Q. *Acanthodiacrodiium costatum* (Burmann, 1968) Rubinstein et al. Capillas Formation, 7589h, M42/0. Each figured palynomorph is located by sample, slide number and England Finder coordinates. The scale bars represent 10 µm.

localities (Vavrdová, 1974; Volkova, 1997; Tongiorgi and Di Milia, 1999) and the other, formerly named “Mediterranean Province” (Vavrdová, 1974; Li, 1987, 1989; Martin, 1982) and successively renamed “peri-Gondwanan province” (Albani, 1989; see exhaustive review in Playford et al., 1995), is distributed along the periphery of Gondwana from Argentina to north Africa including Iran, Pakistan and southern China. This “province” occurs close to the south pole but also reaches intermediate latitudes (i.e., the Yangtze Platform in South China: Li, 1987; Tongiorgi et al., 1995), therefore its distribution was probably not entirely controlled by climatic zones, but also by oceanic currents (Tongiorgi et al., 1998) as well as by continental configuration (Li and Servais, 2002).

In the acritarch assemblage from the lower part of the Capillas Formation, the presence of characteristic genera of the “peri-Gondwanan province”, such as *Arbusculidium*, *Striatotheca* and *Arkonina* clearly indicates affinities with peri-Gondwana assemblages. These peri-Gondwanan affinities have been already indicated for Lower Ordovician acritarch assemblages from the Saladillo, Parcha and Acoite formations in the Cordillera Oriental (Rubinstein et al., 1999; Rubinstein and Toro, 2001), the Zanjón Formation in the Sierras Subandinas (Rubinstein, 2005; Rubinstein and de la Puente, 2008) and the Suri Formation in the Famatina Basin (Achab et al., 2006).

The acritarch genus *Frankea* is also considered to be a biostratigraphical and paleobiogeographical marker for the peri-Gondwana Province and it has never been found in other regions (Servais, 1993; Fatka et al., 1997; Vecoli et al., 1999). *Frankea* appears for the first time in the *Isograptus gibberulus* graptolite Biozone in the British Isles, corresponding to the first stage of the Middle Ordovician or Dapingian (Cooper et al., 1995; Li et al., 2003). The absence of the genus *Frankea* in Argentina, in the uppermost Zanjón Formation (unpublished data), the Labrado Formation and the lower part of the Capillas Formation (Dapingian-Darriwilian), as well as in south China (Brocke et al., 2000) should be highlighted. It might be related to the intermediate latitudinal position of both regions in the Middle Ordovician thus indicating a probable latitudinal or temperature control for the distribution of this taxon, or due to local environmental conditions in shallow-marine marginal facies.

8. Paleoenvironmental interpretation

Alternations of shallow-marine deltaic systems and estuarine environments, with frequent coastal plain changes, brackish water influence and repeated coastal incision induced by relative sea-level fluctuations, characterize the Sierras Subandinas' Ordovician deposits. These paleoenvironmental changes are defined according to sedimentological and sequence stratigraphic analyses (Fig. 4), and clearly demonstrate an influence of terrestrially-derived sedimentation in the overall shallow-marine setting of the study succession. The composition of the palynological assemblages recovered from the five study samples (specially the variation in relative abundance of taxa and the occurrence of specific palynomorphs of problematic origin and interpretation) can be analyzed in the background of the different paleoenvironmental settings corresponding to each sampling level, and compared with predictions of published models of acritarch distribution in relation to paleoenvironmental conditions. Many previous studies have proposed various models linking the characteristics of acritarch assemblages to changing paleoenvironmental conditions, and these models have been variously used as tools for paleoenvironmental interpretations (e.g., Staplin, 1961; Smith and Saunders, 1970; Jacobson, 1979; Dorning, 1981; Al-Ameri, 1983; Wicander and Wood, 1997; Vecoli, 2000, 2004; Tongiorgi et al., 2003; Molyneux, 2009). The principal difficulty in establishing models of

palynomorph distributional patterns as a function of varying paleoenvironmental parameters in Early Paleozoic times, is the generally unknown biological affinity of the acritarchs as well as of other palynomorphs such as the chitinozoans. Nonetheless, a reasonable assumption can be made that for acritarchs, as with modern phytoplankton (e.g., Dale, 1996), a direct correlation between algal diversity and cyst morphology, and environment, exists (Vecoli, 2000; Tongiorgi et al., 2003). Moreover, many of the previous studies on acritarch distributional patterns in ancient sediments, provide empirical support for such an assumption (e.g., Staplin, 1961; Jacobson, 1979; Dorning, 1981; Al-Ameri, 1983; Wicander and Wood, 1997; Molyneux, 2009). Detailed reviews of previous acritarch-based paleoenvironmental models can be found in Vecoli (2000) and Tongiorgi et al. (2003), and will not be rediscussed herein. In general, the majority of these models assume that along an onshore–offshore transect, highest acritarch diversity is located in offshore shelf environments, whereas fossil microphytoplankton assemblages from nearshore shelf and deep-water basin environments are characterized by reduced diversity and dominance of morphologically simple (sphaeromorphs) forms (e.g., Jacobson, 1979; Dorning, 1981; Vecoli, 2000, 2004; Li et al., 2004). Moreover, Vecoli (2000, 2004) and Tongiorgi et al. (2003) proposed that certain species show limitation of their occurrence to specific paleoenvironments. In general, such studies have been conducted in continental platform successions, and have consistently shown a pattern in which high acritarch diversity correlated to periods of transgression and highstand, and low diversity correlated to periods of regressions and sea-level lowstands. Recently, a study of acritarch assemblages from an outer shelf to slope facies in northern England (Skiddaw Group), showed that changes in diversity followed an apparently reverse pattern from those observed in continental platform setting, i.e., correlation of high acritarch diversity with lowstands, and low diversity with highstands (Molyneux, 2009). This apparent contradiction could be explained by postulating a shift in the location of high-diversity phytoplankton assemblages further onto continental platforms during transgressions and highstands, and basinwards during regressions and lowstands (Molyneux, 2009). In practice, this study demonstrated the necessity of independent paleoenvironmental evidence in order to constrain, at least in a part of the studied succession, the polarity of the shift in location of high-diversity acritarch assemblages during sea-level changes before any meaningful paleoenvironmental interpretation of palynological data can be made.

According to the discussion above, and taking account all the limitations of the various proposed models of fossil microphytoplankton distribution, it is to be expected that, in one given location, a change in sea level (transgression or regression) will result in a change in composition and diversity of acritarch assemblages. This observation can then be used to tentatively track paleoenvironmental (sea level) changes, better if in complement with other independent lines of evidence.

In this section, we will examine what are the relationships between the lithofacies changes occurring in the Río Capillas (Sierras Subandinas) section and changes in the composition of palynological assemblages.

Rich and diverse acritarch and chitinozoan assemblages characterize the Zanjón Formation which is interpreted as deposited in a tidal flat (Rubinstein, 2005). Just above the Zanjón Formation, the Laja Morada Member of the Labrado Formation shows sedimentological characters evidencing a fluctuating subaerial exposure, characteristic of interfluvial, attributed to a relative sea-level drop. The acritarch assemblages from the upper part of the Laja Morada Member (sample 7584) are poorly preserved and undiversified (Figs. 5 and 6), containing only sphaeromorph acritarchs and few taxa attributable to the prasinophyte algae; they are interpreted

herein as indicating proximal, marginal marine settings. The Lagunilla Member of the Labrado Formation represents the transition from predominantly sandy fluvial facies to a tide-dominated estuarine environment. The corresponding palynological assemblages (samples 7595 and 7596) show a marked increase in abundance and diversity of the acritarchs, especially in the upper part of the unit (sample 7595; Figs. 5 and 6), even though sphaeromorph acritarchs are still the predominant component. These assemblages are also characterized by the common occurrence of spore-like microfossils (e.g., Fig. 7A–C, T). Taking into account the information derived from the sedimentological and sequence stratigraphic analyses, the characteristics of the palynological assemblages from the three samples taken from the Labrado Formation can be associated with a scenario of gradually deepening marine conditions, in an estuarine complex, in the context of a transgressive system tract.

The Capillas Formation begins with a maximum flooding surface and represents the only open marine deposits of the study section; the sedimentological analysis of these sediments shows a shallowing upwards sequence linked to the progradation of a deltaic complex during a highstand system tract. The stratigraphically lowest sample collected from the basal part of the Capillas Fm. (sample 7588) yielded a markedly more abundant and more diversified palynological assemblage compared to those from the Labrado Fm. (Figs. 5 and 6). This assemblage is dominated by acritarchs, although it contains spore-like palynomorphs. Among the acritarchs, *Leiosphaeridia* and *Polygonium* are the dominant taxa, but a range of morphologically complex acritarchs also occurs even if in low abundance, such as *Ferromia?* and *Acanthodiacrodium*. Diversity and abundance of acritarchs further increase in sample 7589 (Capillas Formation, ca. 20 m above sample 7588); furthermore, palynomorphs and amorphous organic matter is much more better preserved than in the previous investigated levels from the Capillas and Labrado formations. The acritarch assemblage of sample 7589 is characterized by dominance of the genera *Polygonium* and *Leiosphaeridia*, accompanied by a less common occurrence of morphologically complex taxa, such as *Liliosphaeridium* and *Cymatiogalea*. Spore-like palynomorphs are also common in the palynological assemblage. The depositional palaeoenvironment of sample 7589 is interpreted as transitional between aggrading and prograding stages of a highstand system tract.

In summary, even in the present context of a very limited set of samples, the diversity, abundance, and state of preservation of palynomorphs and organic matter seem to show consistent variations according to changes in palaeoenvironment as tracked by the sedimentological and sequence stratigraphic analyses. The present data appear consistent with previous observations and proposed models linking acritarch diversity and abundance to sea-level changes, in which diversity of acritarch assemblages and quality of preservation of organic matter increase from very proximal (Laja Morada Member of the Labrado Formation) to more distal, open marine strata deposited in the context of a highstand system tract. The presence of palynomorphs of uncertain origin but for which it can be reasonably assumed a non-marine derivation, based on morphological grounds as well as from their highest abundances in sediments for which a high input of terrestrially-derived deposition can be demonstrated, is also noteworthy in most of the studied samples.

The present results, even if based on a small dataset, thus tend to confirm that palynomorph abundance can be effectively used as a complementary tool for palaeoenvironmental interpretation, namely for tracking changes in sea level and/or for evaluating the degree of proximity-distality in a stratigraphic section. However, the integration of palaeoenvironmental data from sedimentological and/or sequence stratigraphic analyses remains fundamental for a correct interpretation of the palynological data.

9. Conclusions

The usefulness of the organic-walled microfossils from the Middle Ordovician Labrado and Capillas formations, of the Sierras Subandinas, in terms of biostratigraphy and palaeoenvironmental and paleogeographical applications, evidently comes out from the analysis and discussion of data. This is particularly significant because it involves a section with frequent subaerial exposures and largely marginal marine settings, almost devoid of fossils.

Concerning the age-dating, the palynological assemblages of the Labrado and lower Capillas Formation allow constraining the studied interval to the Dapingian?–Darriwilian.

From a paleogeographical point of view, the presence of typical peri-Gondwana taxa in the Capillas Formation enables correlation with the cold to cool-temperate water province, consistently with evidence from Lower Ordovician acritarch assemblages from the Cordillera Oriental, in the Central Andean Basin and from the Famatina Basin, in the western margin of Gondwana.

The evident match between the composition of the palynological assemblages and the palaeoenvironmental interpretation based on facies analysis, geometry and paleocurrent measurements and recognition of depositional sequences, demonstrate that palynological assemblages can be valuable as palaeoenvironmental or paleoecological indicators.

Acknowledgments

This work has been supported by CONICET (PIP N° 5948), FONCYT (PICT 2006 N° 01272), and SECYT-ECOS Project A05U01 (Scientific Cooperation Programme between Argentina and France). It is a contribution to the International Geoscience Programme IGCP 503 'Ordovician Paleogeography and Palaeoclimate'. The authors are grateful to Alejandra Moschetti for her laboratory assistance and to Florencia Carotti for the help in photographic figures. We wish to express our gratitude to Stewart Molyneux (BGS, Keyworth, Nottingham, UK) and Philippe Steemans (University of Liège, Belgium) for their valuable advices about the manuscript. Thanks are also expressed to Victor Ramos and Guillermo Ottone (University of Buenos Aires, Argentina) for reviewing the manuscript and adding useful comments.

Appendix 1. : List of species

Acritarchs and prasinophytes

Acanthodiacrodium costatum Burmann, 1968 (Figs. 7M and 8Q)

Remarks: This species is here interpreted as accommodating a wide range of morphological variability, according to the remarks by Cramer and Díez (1977), Albani (1989), and Vecoli (1999), that is to include as synonymies the species *Acanthodiacrodium latizonale* (Burmann, 1968) and *Acanthodiacrodium rectinerve* (Burmann, 1968).

Ampullula? sp. (Fig. 7Q)

Remarks: Single specimen showing the typical ellipsoidal vesicle bearing a large process extending in tubular, neck-like extension, and other smaller processes which are hollow, distally widened, lobated and serrated, and probably opened. Because of bad preservation, it was not possible to exactly distinguish the morphology of the neck-like extension, or if the processes are connected or not with the vesicle's cavity: for these reasons the present attribution to *Ampullula* (Righi, 1991) emend. (Brocke, 1997) is questionable.

Arbusculidium sp. cf. A. sp. 1 in Brocke et al. (2000) (Fig. 7K)

Aremorianium sp. (Fig. 7E and F)

Remarks: Specimens previously assigned to ?*Americanium simplex* (Loeblich and MacAdam, 1971; Rubinstein, 2005, pl. 1, fig. 7) are here positively attributed to the genus *Americanium* because of their ellipsoidal vesicle and apical tubular extension. However, the specimens occurring in sample 7595 of the Labrado Formation are distinguished from other species of the genus *Americanium* by their dimensions and the lack of processes.

Arkonía tenuata Burmann (1970) (Figs. 7J, N; Fig. 8A)

Remarks: New findings of well preserved specimens permitted to reattribute the specimens assigned to *Arkonía* sp. in Rubinstein (2005; pl. 1, fig. 8) to *A. tenuata*.

Barakella cf. *B. rara* Tongiorgi et al. (1995) (Fig. 8J)

Remarks: This specimen was erroneously attributed to *Arbusculidium filamentosum* in Rubinstein (2005).

Cymatiogalea cf. *C. granulata* Vavrdová, 1966 (Fig. 8K)

Cymatiosphaera sp. 1 (Fig. 7H)

Cymatiosphaera sp. 2 (Fig. 7G) *Dictyotidium?* sp.

Ericanthea pollicipes Cramer and Díez (1977) (Fig. 8F)

Eupoikilofusa sp. (Fig. 8L)

Remarks: This form considered as *Dactylofusa* cf. *D. striatogranulata* (Jardiné et al., 1974) in Rubinstein (2005) have not the typical ornamentation of the genus, consisting in short processes often arranged in rows.

Ferromia? sp. (Fig. 7I)

Remarks: This single specimen has been described and illustrated in Rubinstein (2005, pl. 1, fig. 11) and therein attributed to *Leptotolypa evexa* (Colbath 1979). The specimen is ornamented with spines and not with the coarse wrinkles and grana typical of *L. evexa*. The form is accordingly re-assigned to *Ferromia* with doubts because it lacks the circular excystment opening with operculum characteristic of *Ferromia* (Vavrdová, 1979).

Liliosphaeridium intermedium (Eisenack) Playford et al. (1995) (Fig. 8G–I)

Polygonium sp. (Fig. 7L)

Pterospemella sp. (Fig. 8M, N)

Rhopalophora palmata (Combaz and Peniguel, 1972; Playford and Martin, 1984) (Fig. 7P)

Rhopaliophora cf. *R. membrana* (Li, 1987) (Fig. 8E)

Striatotheca microrugulata (Vavrdová) (Martin, 1977) (Fig. 8C and D)

Striatotheca cf. *S. rugosa* Tongiorgi et al. (1995) (Fig. 8B)

Tectitheca additionalis-valida sensu Cramer and Díez (1977) (Fig. 8O and P)

Remarks: Present specimens appear as intermediate forms between *T. additionalis* (Burmman, 1968), and *T. valida* (Burmman, 1968), as also observed by Cramer and Díez (1977) for their upper Arenig-Llanvirn Moroccan specimens.

Veryhachium trispinosum group sensu Servais et al., 2007

Acritarch gen. et sp. indet. 1 (Fig. 7D)

Remarks: Undeterminable acritarch because of poor preservation and scarcity of specimens. It is characterized by straight or concave sides and polymorphic processes showing rounded or bifurcate tips.

Spore-like microfossils

?Morphon *Dyadospora murusattenuata* Strother and Traverse (1979) sensu Steemans et al., 1996 (Fig. 7O)

Remarks: Specimens displaying dyad configuration. They are doubtfully assigned to the Morphon *D. murusattenuata* (Strother and Traverse 1979) sensu Steemans et al., 1996 because a definite cryptospore affinity for these dyads cannot be established.

Incertae sedis 1 (Fig. 7B, C, R, S)

Remarks: Specimens showing a spore-like appearance, with a thick-walled spherical to ellipsoidal vesicle (29–36 µm in diameter), completely enclosed within a thin, membranous envelope.

Incertae sedis 2 (Fig. 7T)

Remarks: Planar tetrads (maximum diameter 26.5 µm), within which, each individual sporomorph shows a marginal thickening

Incertae sedis 3 (Fig. 7A)

Remarks: Specimens displaying a double-walled, spherical vesicle, with a thicker inner wall, and a thinner outer wall sculptured by sinuous rugulae. Even if they look like a cryptospore, probably a new form, the few and moderately preserved specimens recovered in this study do not permit a better identification to the institution of a new taxon, so we prefer to retain these forms as Incertae Sedis.

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