

Silurian to Early Devonian organic-walled phytoplankton and miospores from Argentina: biostratigraphy and diversity trends

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The distribution and diversity of marine palynomorphs, such as acritarchs and chlorophytes, and terrestrial palynomorphs, such as miospores, are controlled mainly by palaeoenvironmental and palaeogeographical conditions. Recently, global patterns of organic-walled phytoplankton were illustrated for the Late Silurian to earliest Devonian based on data from different stratigraphic sections and palaeocontinents. Here, we analyze the Silurian and the Early Devonian diversity in the Argentinean Precordillera, Central Andean, and Chacoparanense basins. The evolution of the diversity is evaluated in a well-constrained biostratigraphic framework, bearing in mind local palaeoenvironmental conditions and changes within each basin. Taking into account recently published and unpublished data from well-dated sections, the biodiversity of Silurian phytoplankton seemingly increases upwards, reaching its maximum peak during the Ludlovian. However, palynomorphs are rarely recorded in Wenlockian strata, and the supposed Pridolian layers are not confidently well constrained. The first record of trilete spores in Argentina is Ludlovian, approximately 30 million years after their first appearance in the Late Ordovician. Palynomorph diversity increases in the Early Devonian, with a higher diversity of miospores than that of the marine phytoplankton. We interpret possible discrepancies in biodiversity trends of organic-walled phytoplankton between Argentina and other regions, as related to the quantitatively and qualitatively disparity of data, as well as the lack of rigorous biostratigraphic and palaeoenvironmental assessments of the Argentinean basins. Copyright © 2011 John Wiley & Sons, Ltd.

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1. INTRODUCTION

Palynological studies on Silurian and Lower Devonian rocks from Argentina began in the 1970s with the contributions of Pöthe de Baldi (1971, 1974), who recognized an acritarch assemblage in the subsurface Copo Formation of the Chacoparanense Basin, Santiago del Estero Province (Figure 1A). This assemblage, firstly considered as Ludlovian in age, was reinterpreted as probable Wenlockian by Rubinstein (1995). However, no independent biostratigraphic control is available for this unit.

In addition, Pöthe de Baldi recorded the first palynological assemblages from the Silurian of the Precordillera Basin (Figure 1B), coming from the Los Espejos Formation of Wenlockian?–Pridolian age and Lochkovian locally at its northernmost outcrops. The results of Pöthe de Baldi (1975a, b) were followed by palynological findings in the underlying La Chilca Formation (Hirnantian-late

Llandovery-early Wenlock?) by Melendi and Volkheimer (1982, 1983) and Pöthe de Baldi (1987, 1997a). Most of this data lacked independent biostratigraphic control due to the scarcity of fossils of recognized stratigraphic value such as graptolites or conodonts. Later, Rubinstein increased the number of studied sections and the record of marine and terrestrial taxa. She also integrated all known palynological information of the Los Espejos Formation, reappraised and updated the palynological data of the Upper Silurian of Argentina (Rubinstein 1993a, 1995), as well as reviewing Silurian acritarchs of South America (Rubinstein, 1997a). Subsequently, Pöthe de Baldi (1997b) increased the knowledge of the Argentinean Silurian palynology, adding new data from the Don Braulio Formation of the Sierra de Villicum, in the eastern Precordillera Basin (Figure 1B). Acritarchs of the upper section of this unit were considered as early-middle Llandovery, corroborating the graptolite findings which corresponds to the *Atavograptus atavus* Zone (Peralta, 1985). Pöthe de Baldi (in Peralta *et al.*, 1997) also described a marine microphytoplankton assemblage of the Tambolar Formation, at the southernmost part of the San Juan Central Precordillera, the age of which is still under discussion

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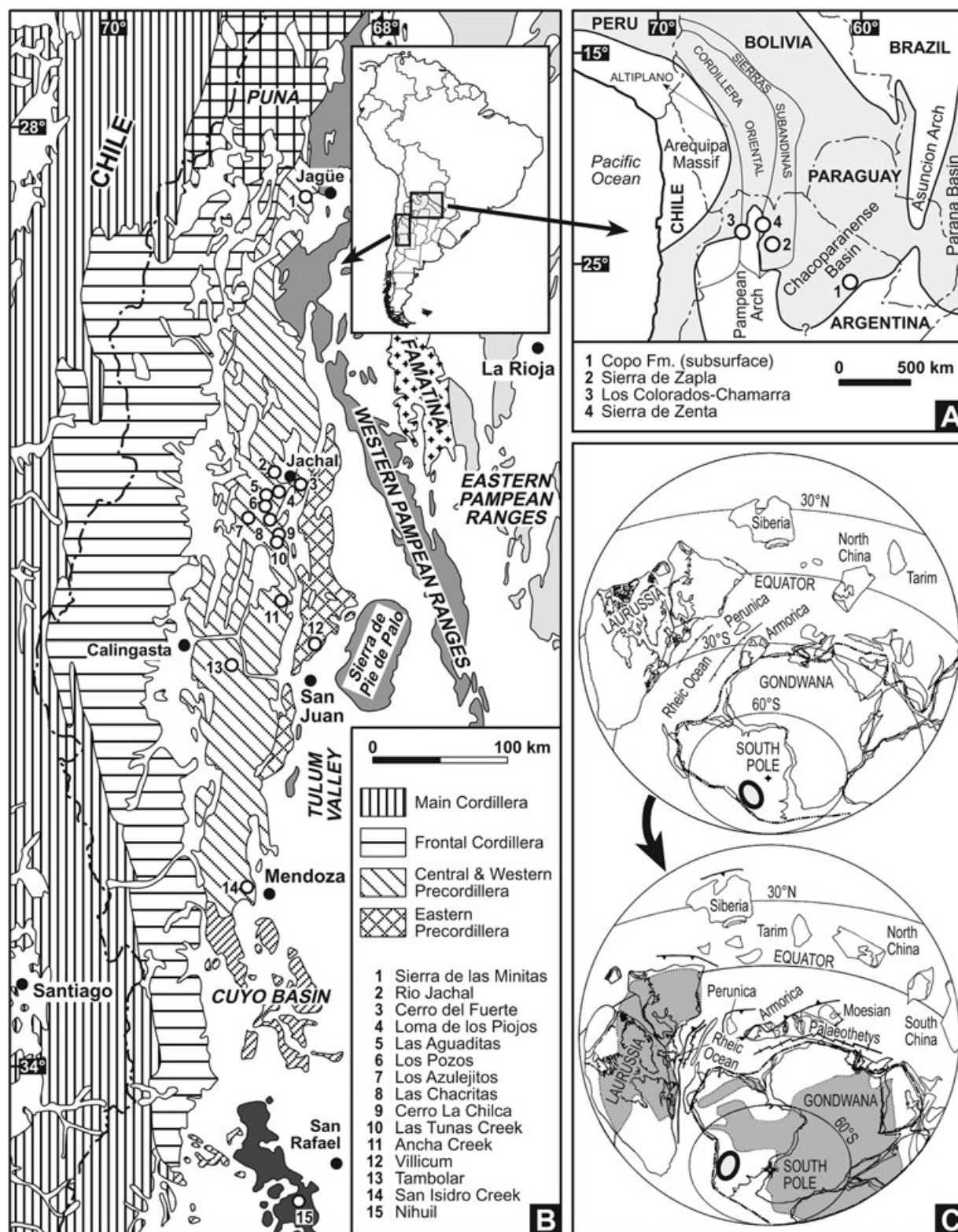


Figure 1. **A:** Location map of the Precordillera Basin showing the localities studied herein. Modified from Keller (1999) and Edwards *et al.* (2009). **B:** Silurian basins of northwestern Argentina showing the localities studied herein. Modified from Benedetto (2010). **C:** Palaeogeographic maps of the Late Silurian and Early Devonian (upper map) and of the Early Middle-Devonian (lower map), showing the location of studied basins. Continental land areas are indicated in grey. Modified from Cocks and Torsvik (2002) and Benedetto (2010).

(Rubinstein, 2001a). We included the data corresponding to the Tambolar Formation in the Late Silurian, based on Astini and Maretto (1996), who considered the previously mentioned formation as an equivalent of the Los Espejos Formation, as well as on the correlation of the marine phytoplankton from both units.

A sparse, low diversity, and poorly preserved acritarch assemblage was recorded from low-grade metamorphic rocks (phyllites) of the La Horqueta Formation (nowadays referred to as the Río Seco de los Castaños Formation) of the San Rafael Block, in the Nihuil locality (Figure 1B), in the southern sector of the Precordillera-Cuyania Terrane (Rubinstein, 1997b). The assemblage pointed toward a Silurian age (here considered as Late Silurian), which was later supported by isotopic evidence among other interdisciplinary analysis (Manassero *et al.*, 2009).

Rubinstein and Brussa (1999) provided for the first time an integrated palynomorph-graptolite study of the Silurian Central Precordillera Basin (La Chilca and Los Espejos formations), recognizing five palynological assemblages. Two of them, from the La Chica Formation, correspond to the *Normalograptus persculptus* (Hirnantian) and the *Stimulograptus sedgwickii*-*Spirograptus turriculatus* (upper Aeronian-lower Telychian) graptolite zones. Of the three assemblages from the Los Espejos Formation, only one corresponds to graptolite zones, which are the *Neodiversograptus nilssoni*-*Lobograptus scanicus* zones (Gorstian).

Despite previous works based on other fossil groups, as well as on organic-walled phytoplankton and miospores that indicates the Pridolian as the younger possible age for the Los Espejos Formation, new palynological studies restrict the age of the Los Espejos Formation to the Gorstian, and display no changes in palynological assemblages from base to top in many sections (Rubinstein, 2001b).

More recently, the incorporation of palynological data from new sections throughout the Central Precordillera, embracing the La Chilca and Los Espejos formations, allowed us to extend significantly the records and diversity of marine and terrestrial palynomorphs (Rubinstein *et al.*, 2006a, b; García Muro and Rubinstein, 2009; Rubinstein *et al.*, 2010a and unpublished data). These new results confirm a Ludlovian age for the Los Espejos Formation, based on acritarchs and chlorophytes. Nevertheless, the miospores of the same unit indicate a late Ludlovian-early Pridolian age. This diachronism between marine and terrestrial palynomorphs could reflect local miospore assemblage peculiarities and are still under investigation (Rubinstein *et al.*, 2010a).

The scarce palynological data from the Lower Devonian comes from the Precordillera Basin (Figure 1B). Predominant miospore assemblages, with subordinate acritarchs, documented in the Villavicencio Formation of the Mendoza Precordillera (San Isidro Creek), suggest a late Pragian to

early Emsian age. The age of the miospore assemblage can be constrained by correlation with the upper part of the Ems Biozone, in terms of the Devonian miospore zonation, of the Brazilian Amazon Basin (Rubinstein 1993b; Rubinstein and Steemans, 2007). The only Lower Devonian palynological assemblage of the San Juan Precordillera, comprising acritarchs, chitinozoans and miospores, was recorded from the lower part of the Talacasto Formation in Cerro del Fuerte. The presence of the three marine and terrestrial palynomorph groups (acritarchs, chitinozoans and miospores) permits a fairly good age control, indicating a late Lochkovian to Emsian age (Rubinstein *et al.*, 1996; Le Hérissé *et al.*, 1997).

Recently, palynological assemblages from the Sierra de las Minitas in the northernmost extent of the Precordillera Basin, in the north-west of La Rioja Province, have been recognized. The structure of the area is complex and the folded strata has been later faulted and intruded by igneous bodies. The fossiliferous strata have been dated as Early Devonian and correlated with the Talacasto Formation (Vaccari *et al.*, 2008) based on lithologic and faunal evidence. At this locality, two palynological assemblages, mainly composed of terrestrial taxa, were recorded above levels with trilobites. The lower palynological assemblage suggests a late Lochkovian age, whereas the upper one may be restricted to the late Pragian-middle Emsian (Rubinstein *et al.*, 2010b).

In the Central Andean Basin, Silurian palynomorph assemblages come mostly from the Lower Silurian of the Sierras Subandinas and the Cordillera Oriental. The first palynological results are from the lower part of the Lipeón Formation, of the Sierra de Zapla, in the Sierras Subandinas. The recorded acritarch assemblages were assigned to the late Llandovery-early Wenlock (Bultynck and Martin, 1982). Later, the lowermost levels of the Lipeón Formation in the Río Capillas (Sierra de Zapla), Sierras Subandinas, yielded diverse and well-preserved palynomorph assemblages dominated by acritarchs and prasinophyte algae, accompanied by cryptospores (Rubinstein, 2005). Dating based on graptolites and chitinozoans suggested ages ranging from the early Llandovery to the late Telychian for the lower part of this unit. However, the acritarch assemblage indicated an age around the Aeronian/Telychian boundary, and no older than late Aeronian (Rubinstein and Toro, 2006). The lower levels of the Lipeón Formation, in the Eastern Cordillera (Los Colorados-Chamarra area), yielded a marine-dominated palynomorph assemblage with subordinate terrestrial cryptospores, together with graptolites of the *Demirastrites convolutus* and probably *Stimulograptus sedgwickii* zones. Both fossil groups point to a late Aeronian age (Rubinstein and Toro, 2006). Acritarch and chitinozoan studies of the lower part of the Lipeón Formation in the Sierra de Zenta, Cordillera Oriental, suggested an age no older than Telychian (Rubinstein *et al.*, 2008a).

Recently, Le Hérissé *et al.* (2009) illustrated global patterns of organic-walled phytoplankton biodiversity during the Late Silurian (Gorstian and Ludfordian) to earliest Devonian (Lochkovian). As highlighted by these authors, and based on analogues with modern phytoplankton, it is fairly well accepted that the distribution of palaeophytoplankton was influenced by palaeogeographical and palaeoenvironmental conditions. These include temperature, salinity, light and nutrient availability in water masses, as well as global climatic changes, eustatic variations, oceanic palaeocurrents, water depth, and distance from shoreline. They also discuss the fact that the fossil phytoplankton cyst diversity does not represent a quantitative indication of primary productivity, because the fossil record depends on different factors such as taxa capable of developing a cyst, reproductive strategies of individual cyst-forming taxa, rate of sedimentation, and taphonomic processes.

Le Hérissé *et al.* (2009) suggested that relatively high phytoplankton diversity peaks occurred during the Early and Late Gorstian in the warm low latitude areas, followed by varying fluctuations during the Ludfordian and Pridolian for both the warm low-latitude and cool high-latitude areas, with a radiation of new phytoplankton taxa together with the appearance of more cosmopolitan assemblages at the beginning of the Lochkovian.

These global patterns were interpreted based on a variety of data, coming from a variety of independent age-constrained sections, in different palaeocontinents, and at different palaeolatitudes, including data from Argentina published up to 1995.

The aim of this contribution is: (1) to extend the study of biodiversity trends for Argentina, including the whole of the Silurian and the Early Devonian palynological record; (2) to consider also the biodiversity of terrestrial palynomorphs (miospores); (3) to update and constrain biostratigraphically the palynological information concerning this period; (4) to compare the Argentinean biodiversity trends with the global patterns proposed by Le Hérissé *et al.* (2009); and (5) to discuss similarities or differences in a complex geological and tectonical framework.

2. GEOLOGIC AND TECTONIC SETTING

The oceanic southern margin of Gondwana, from southern South America through Australia, is one of the longest and longest-lived known active continental margins. During the Early Palaeozoic, much of the margin was dominated by successive episodes of subduction-accretion (Pankhurst and Vaughan, 2009). This situation imprinted particular characteristics on Argentinean Palaeozoic basins related to this margin. Furthermore, the palaeogeographical reconstructions show a high latitudinal position, not far from the South Pole for these basins, particularly during the Late Silurian and the Early Middle Devonian (Figure 1C).

The Precordillera outcrops extend for almost 1000 km encompassing, from north to south, the La Rioja, San Juan, Mendoza, and La Pampa provinces. From a morphographic point of view, it has been separated into three belts: western, central and eastern (Ortiz and Zambrano, 1981). However, Astini (1992) proposed a major two-fold separation of this basin into western and eastern tectofacies that seems to be more appropriate for understanding the Early Palaeozoic rock distribution and its stratigraphic evolution. The eastern tectofacies comprise the usually named eastern and central Precordillera, whereas the western tectofacies corresponds to the western Precordillera (Astini, 2003).

The evolution of the Siluro-Devonian Precordillera Basin (Figure 2) of Argentina differs from other South American basins because it was affected by the accretion of the Cuyania Terrane to the Gondwana margin during the Middle-Late Ordovician. The collision destroyed the Cambrian-Ordovician passive margin, generating a dramatic change in the configuration of the sedimentary basins (Benedetto, 2010). Astini (1992) inferred a peripheral bulge related to the early stages of a foreland basin developed along a colliding irregular continental margin. One of the main consequences of the collision was the development of a flexural bending in the Central Precordillera, named the Talacasto-Tambolar arch by Astini *et al.* (1995), which endured

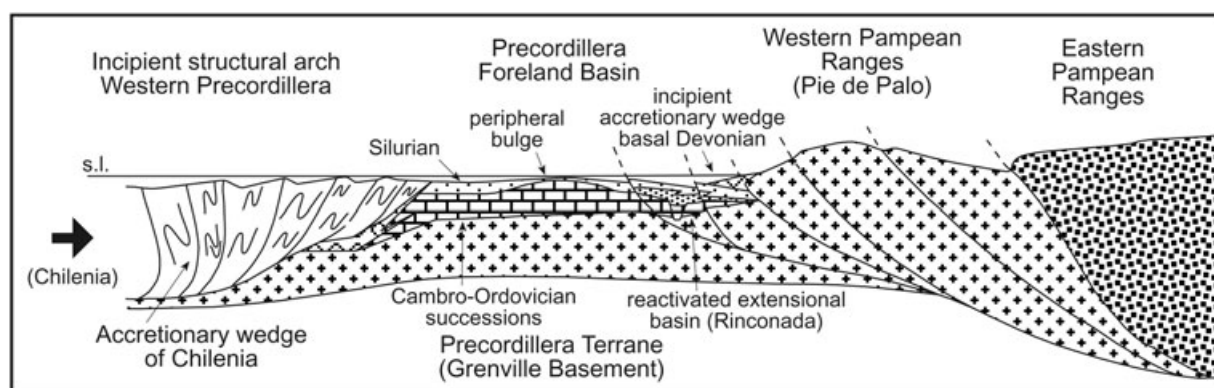


Figure 2. Evolution of the Precordillera Basin during the Silurian and the Devonian. Modified from Astini (1996).

recurring relaxation and contraction events. Towards this arch, there is an evident wedging of the stratigraphic units in addition to important interruptions of sedimentation. The Siluro-Devonian succession of the Precordillera constitutes a typical foreland deposit, reaching a thickness of around 1500 m. It was deposited between the Tambolar arch and the orogenic belt. These deposits and the sequence arrangement have been interpreted as a consequence of lithosphere rheology and eustasy (Astini *et al.*, 1995).

Silurian and Devonian siliciclastic sequences are mainly characterized by fine-grained shelf deposits and they are mostly confined to the eastern tectofacies.

A transgressive to high sea-level stand history has been interpreted for both the La Chilca and the Los Espejos formations, based on the presence of a thin iron veneer and phosphate-rich chert conglomerates at their base, succeeded by shaly intervals with a gradual upward thickening and coarsening. The internal cyclic stacking patterns, most evident in the Los Espejos Formation, are considered to be generated by forced regressions. The upper third of the Los Espejos Formation shows evidence of subaerial exposures at the top of the regression cycles. Major exposure and erosional unconformities developed at the top of both units, together with the north-south diachronic boundary at the base of the Silurian succession, have been interpreted as a forebulging in a partitioned foreland basin located between the Gondwana continent and the Precordillera Terrane (Astini and Maretto, 1996). These authors also consider the Tambolar Formation as a condensed equivalent of the Los Espejos Formation to the south.

During the Early Devonian, a significant diastrophism, probably related to the collision of another continental terrane (Chilenia), drastically changed the basin configuration, modifying the dominantly accommodational regime that characterized the Silurian to a supply-dominated regime that started in the Devonian (Figure 2). Thus, cyclic patterns of shallow-marine sequences continued developing, with progressive increments of the sedimentation rate (Astini and Maretto, 1996).

In the eastern-most margin of the Precordillera Basin, the Silurian begins within the uppermost part of the Don Braulio Formation (Villicum locality), represented by a transgressive muddy shelf succession considered to be related to a glacio-eustatic sea-level rise after the Hirnantian glaciation (Astini and Buggisch, 1993). No palynological data corresponding to the Llandovery and Wenlock wildflysch deposits of the Mogotes Negros-Rinconada Formation are available. These Silurian deposits have been considered as possible stages of collisional relaxation, as a consequence of a north-south shear zone that displaced the Precordillera, among other origins (Astini *et al.*, 1995; Benedetto, 2010).

The most abundant Silurian palynological data comes from the La Chilca and the Los Espejos formations, in the Central Precordillera of San Juan. Astini and Piovano (1992)

identified five facies in the La Chilca Formation corresponding to inner shelf and shoreface to offshore transition associations, whereas in the Los Espejos Formation they recognized five associations that represent muddy shelf with no influence of wave action, inner shelf exposed to storm activity, and storm-dominated shoreface to offshore-transition environments. The La Chilca Formation is sand-dominated, whereas the Los Espejos Formation is mud-dominated with mixed sand and mud towards the top. The lower part of the La Chilca Formation was assigned to the Hirnantian (latest Ordovician), followed by the Rhuddanian (Early Silurian), based on the graptolite zones *Normalograptus persculptus* and probable *Parakidograptus acuminatus* and *Atavograptus atavus* (Brussa, 1987; Cuerda *et al.*, 1988; Rickards *et al.*, 1996). Kerleñevich and Cuerda (1986) dated as late Llandovery-Wenlock the upper part of the La Chilca Formation, by means of graptolites. However, Benedetto (1995) stated that the brachiopod fauna indicates an unquestionable Llandovery age for the middle and upper part of this formation.

The age of the Los Espejos Formation is mainly based on the distribution of brachiopod faunas (Benedetto *et al.*, 1992). These authors distinguished four faunas, assigning the older one to a probable Wenlock, and the subsequent faunas to the Ludlow, Pridoli, and Early Lochkovian at the top of the unit in Cerro del Fuerte. Unfortunately, graptolites and conodonts are scarce and they do not help to constrain the overall age of the formation. Graptolites such as *Monograptus uncinatus notouncinatus* Cuerda, *Monograptus leintwardinensis* var. *incipiens* Elles and Wood and *Monograptus argentinus* Cuerda have been identified near the middle of the unit, allowing Cuerda (1969) to assign an age ranging from late Llandovery-early Wenlock to early-middle Ludlow for the Los Espejos Formation. Rickards *et al.* (1996) recorded graptolites corresponding to the *Neodiversograptus nilssoni* - *Lobograptus scanicus* zones. This finding in the upper third of the Los Espejos Formation in Cerro del Fuerte indicates an early Ludlovian age. After the pioneer conodont studies carried out by Hünicken (1975) and Hünicken and Sarmiento (1988), Albanesi *et al.* (2006) documented the *Kockelella variabilis variabilis* conodont Zone of early Ludlovian (Gorstian) age in shell beds of the middle-upper part of the Los Espejos Formation.

The muddy shelf deposits of the lower part of the Talacasto Formation contain a rich and diverse invertebrate fauna, although neither graptolites nor conodonts were found. Consequently, on the basis of brachiopod faunas, the stratigraphic unit was assigned to the Lochkovian-Emsian (Herrera, 1993).

In the Sierra de Las Minitas, Early Devonian palynomorph assemblages (Rubinstein *et al.*, 2010b) come from the northernmost outcrops of the Talacasto Formation (Vaccari *et al.*, 2008), particularly from the facies association 'a' (Astini and Ezpeleta, 2008). This facies is composed of profusely bioturbated, mainly shaly to silty beds, with frequent thin beds of

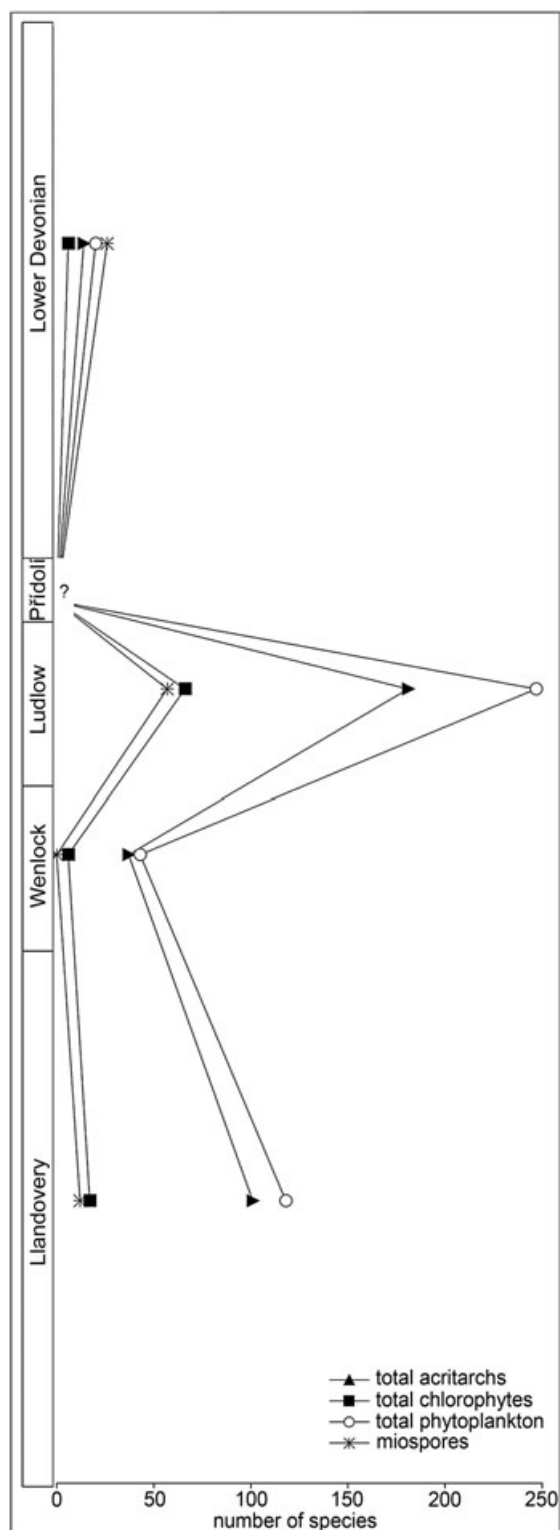


Figure 3. Diversity trends of acritarchs, chlorophytes, total phytoplankton, and miospores. Composite species diversity values are plotted by series. The dataset includes all localities listed in Figure 6.

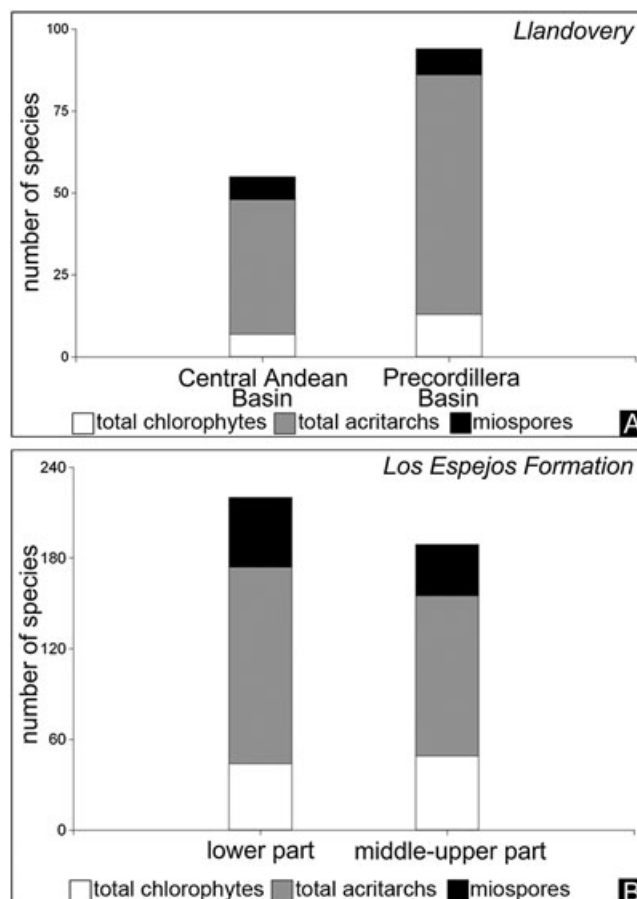


Figure 4. A: Llandovery diversity trends of chlorophytes, acritarchs and miospores within the Central Andean Basin (Lipeón Formation) and the Precordillera Basin (La Chilca Formation). It includes localities 1 to 16 of Figure 6. B: Ludlovian diversity trends of chlorophytes, acritarchs, and miospores within the Los Espejos Formation, separating the lower part from the middle to upper part of the stratigraphic unit. They include localities 20 to 25 and 28 to 36 of Figure 6.

fine-grained sandstones with lenticular and wavy bedding. It includes carbonate-rich bioturbated nodules with an associated fauna consisting of trilobites, corals, sponges, bivalves, nautiloids, conulariids, and brachiopods (Rustán *et al.* in press).

The Lower Devonian deposits of the Villavicencio Formation, in the Mendoza Precordillera, are interpreted as typical facies of storm-dominated, shallow-marine shelf sands, and are scarce in fossils (Rubinstein and Steemans, 2007). At the same locality, the San Isidro Creek, Edwards *et al.* (2001, 2009) described a plant assemblage, but the dating of these plants was mainly based on the previous palynological results (Rubinstein, 1993b).

The Central Andean Basin, located in northwest Argentina and extending into Chile, Bolivia, and Peru, includes the palynologically-productive Silurian outcrops of the Cordillera Oriental and Sierras Subandinas. Towards the south of this basin, Silurian and Devonian rocks extend farther east into the subsurface of the Chaco Plain, where they constitute

the Chacoparanense Basin. The Central Andean Basin has a complex evolutionary history during the Early-Middle Palaeozoic. It develops as a foreland basin behind the Arequipa-Antofalla Massif, with an active subduction zone to the west, and is dominated by large-scale transtensional or transpressional conditions from the Late Ordovician to the Triassic (Sempere, 1995). The origin of these deposits is still being debated, and includes such theories as transpressional forces producing intermittent subsidence at the margin of the craton, where the depocentre was defined; a simple subduction model with a magmatic arc and a foreland basin without compression from the orogen; or even an extensional model (Benedetto, 2010).

The Lipeón Formation initiates a new supercycle (Cinco Picachos) with the deposition of oolitic ironstones during the transgression that followed the Hirnantian glaciation. These Silurian deposits from the lower part of the unit correspond to a series of high-frequency sea-level fluctuations, interpreted as related to transgressive-ravinement surfaces that truncated Fe^{2+} -saturated estuaries after glacial waning and isostatic rebound (Astini, 2003). Even if the whole formation ranges from the Llandovery to the Pridoli, mainly based on graptolites, trilobites and brachiopods (Benedetto, 1991; Waisfeld and Sanchez, 1993; Toro, 1995), its lower part was restricted to the Llandovery.

3. METHODOLOGY

Le Hérisse *et al.* (2009) divide the organic-walled phytoplankton in three major groups: (1) marine chlorophytes (prasinophytes and possible prasinophytes); (2) marine acritarchs; (3) nonmarine palynomorphs (coenobia, including Hydrodictaceae, Zygnemataceae, and acritarchs).

In agreement with these authors, we make use of this classification for the biodiversity analysis of the Argentinean phytoplankton, in order to compare our results with the global patterns proposed by them. Furthermore, the term miospore (cryptospores and trilete spores) is used for the land-derived palynomorphs.

Both published and unpublished data embracing the Silurian and the Early Devonian of Argentina are included in our dataset. With the purpose of avoiding, as much as possible, inflating the number of taxa, we have submitted the data to a critical analysis, especially if the information is exclusively available in the literature.

We consider that the accuracy of the palynological data for the time interval investigated herein, particularly the differences in availability of independent stratigraphic control, allows us to interpret the biodiversity at the series level (Llandovery, Wenlock, Ludlow, Pridoli and Lower Devonian), according to the International Stratigraphic Chart of the International Commission on Stratigraphy (2009).

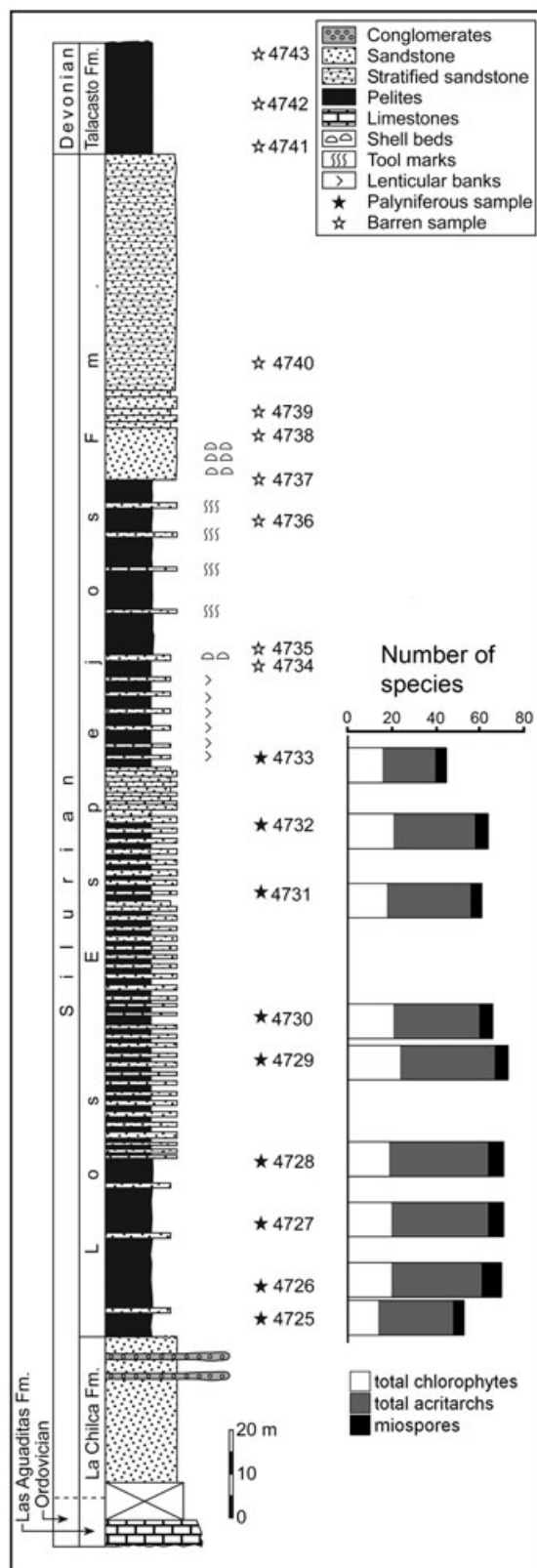


Figure 5. Diversity trends of chlorophytes, acritarchs and miospores based on individual samples of the Los Espejos Formation in Las Chacritas section (García Muro and Rubinstein, unpublished).

Because of the disparity in the detail with which each of the sections and areas were studied (e.g. frequency of sampling, productive levels, and systematic classification) we have considered the composite species diversity values. These were based on the total samples for each chronostratigraphic series, instead of on the individual samples (Figure 3).

Due to the presence of organic-walled phytoplankton and miospores in the Llandovery of the Central Andean Basin and the Precordillera Basin, we also compared the diversity trends between both basins (Figure 4A).

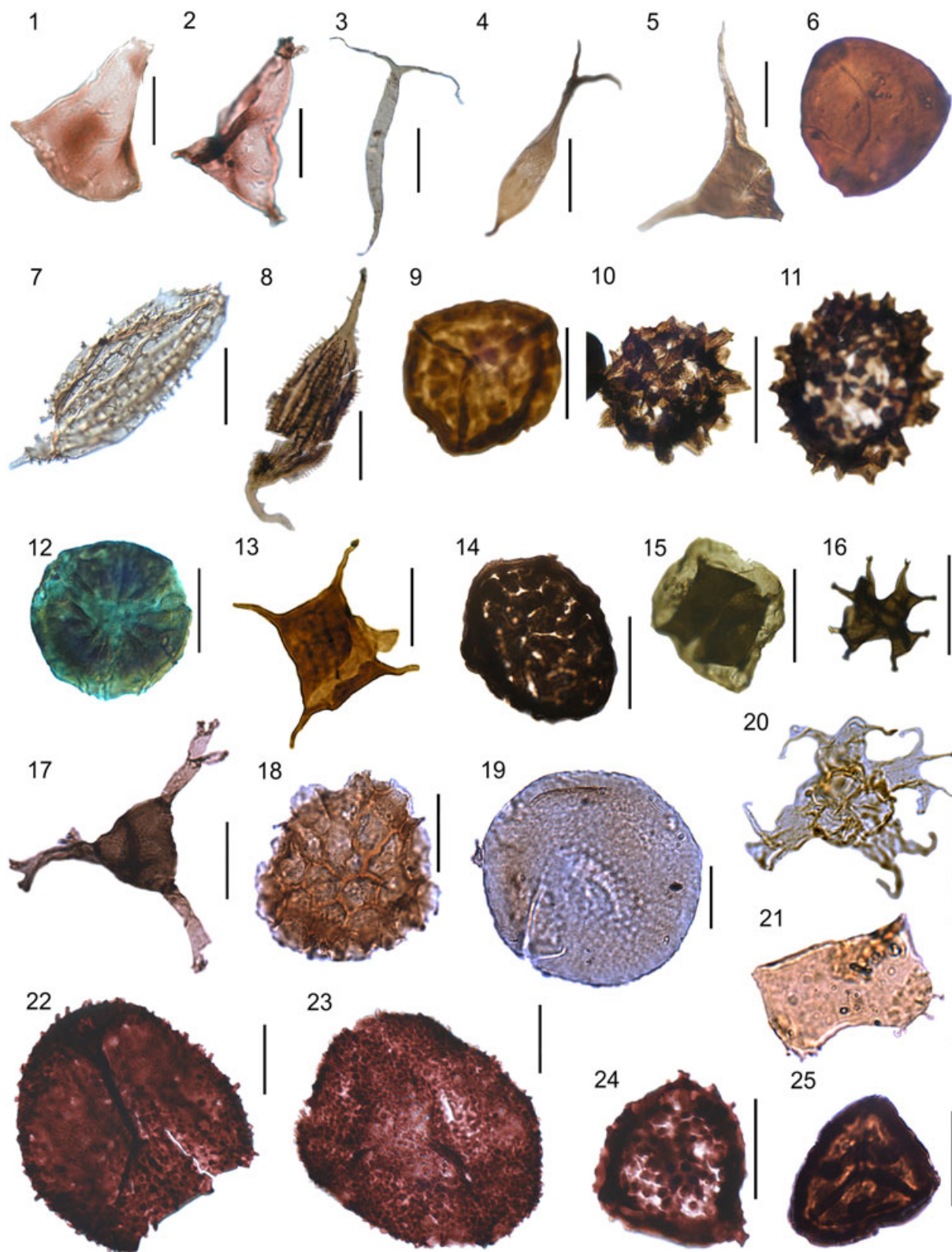
The majority of data comes from the Late Silurian of the Precordillera Basin, mainly from the Los Espejos Formation. For this reason, and taking into account the distribution of data throughout this unit, we compare the diversity trends between the lower part, and the middle to upper part of the formation (Figure 4B). In addition, plotting of diversity per sample is displayed for the Las Chacritas section, where the sampling has included the whole stratigraphic unit, and

also the lower part of the overlying Talacasto Formation (Figure 5).

The major discrepancy in species diversity of the Los Espejos Formation between the contribution of Le Hérisse *et al.* (2009) and the present work, is due to the amount of new data available, coming from studies carried out after the paper of Rubinstein (1995), which was used by Le Hérisse *et al.* (2009) for analysing the diversity trends of Argentina. New data comes from several sections throughout the basin (see Figures 1 and 6). These sections provide productive samples that encompass the whole Los Espejos Formation in its different lithofacies, and especially more samples from the lower section of the unit, which is rich and diverse in organic-walled phytoplankton. Even though part of this information remains unpublished, a detailed palynological study of the Los Espejos Formation, in the Las Chacritas section, has been recently concluded (Rubinstein and García Muro, 2011). In addition to this, the relative

		Central Andean Basin	Chacoparanense Basin	Precordillera Basin	Localities	Fms.
Silurian	Llandovery			Melendi, Volkheimer, 1982 Melendi, Volkheimer, 1983 Pöthe de Baldis, 1987 Pöthe de Baldis, 1997a Pöthe de Baldis, 1997b Rubinstein, 1997a Rubinstein, Brussa, 1999 Rubinstein, 2001a Rubinstein, 2001b Rubinstein <i>et al.</i> , 2006a Rubinstein <i>et al.</i> , 2006b Rubinstein, unpubl.	1 Ancha Creek/Talacasto 2 Ancha Creek/Talacasto 3 Los Azulejitos 4 Ancha Creek/Talacasto 5 Villicúm 6 REVISION (all localities until 1999) 7 Ancha Creek/Talacasto-Las Tunas Creek 8 REVISION (all localities until 2001) 9 REVISION (all localities of the Precordillera until 2001) 10 Ancha Creek/Talacasto-Cerro La Chilca-Río Jáchal 11 Ancha Creek/Talacasto 12 Ancha Creek/Talacasto-Cerro La Chilca-Río Jáchal	L Ch L Ch L Ch L Ch M N-R L Ch-Li L Ch L Ch-Li L Ch L Ch L Ch L Ch
	Wenlock	Rubinstein, 2005 Rubinstein, Toro, 2006 Rubinstein <i>et al.</i> , 2008 Rubinstein, Delabroye unpubl.			13 Sierra de Zapla 14 Los Colorados-Chamarra 15 Sierra de Zenta 16 Sierra de Zenta	Li Li Li Li
Devonian	Ludlow		Pöthe de Baldis, 1971 Pöthe de Baldis, 1971	Pöthe de Baldis, 1975a Pöthe de Baldis, 1975b Pöthe de Baldis, 1981 Rubinstein, 1993 Rubinstein, 1995 Rubinstein, 1997a Rubinstein, 1997b Peralta <i>et al.</i> , 1997 Pöthe de Baldis, 1998 Rubinstein, Brussa, 1999 Rubinstein, 2001a Rubinstein, 2001b Rubinstein <i>et al.</i> , 2006a Rubinstein <i>et al.</i> , 2006b García Muro, Rubinstein, 2009 Rubinstein <i>et al.</i> , 2010 Rubinstein, García Muro unpubl.	17 Sierra de Zapla 18 Santiago del Estero Prov. (subsurface) 19 Santiago del Estero Prov. (subsurface) 20 Los Pozos 21 Los Pozos 22 Los Azulejitos 23 Río Jáchal-Loma de los Piojos-Las Aguaditas 24 REVISION (18 + 19 + 20 + 21 + 22 + 23) 25 REVISION (all Silurian localities until 1996) 26 Nihuil 27 Talacasto 28 Los Azulejitos 29 Ancha Creek/Talacasto-Cerro del Fuerte 30 REVISION (all localities until 2001) 31 REVISION (all localities of the Precordillera until 2001) 32 Ancha Creek/Talacasto-Cerro La Chilca-Río Jáchal 33 Ancha Creek/Talacasto 34 Las Chacritas 35 Ancha Creek/Tal.-C. La Chilca-R. Jáchal-Las Chacritas 36 Ancha Creek/Tal.-C. La Chilca-R. Jáchal-Las Chacritas	Li Co Co L E L E L E L E (Co) L E R S C Tm L E L E-Tm L E L E L E L E L E L E
	Lower Dev.			Le Hérisse <i>et al.</i> , 1996 Rubinstein 1993 Rubinstein, Steemas, 2007 Rubinstein <i>et al.</i> , 2010	37 Cerro del Fuerte 38 San Isidro Creek 39 San Isidro Creek 40 Sierra de las Minitas	TI Vi Vi TI

Figure 6. List of the studied basins, localities and formations, according to authors and date of publication. Abbreviations of the formations (Fms.): La Chilca (L Ch); Lipeón (Li); Copo (Co); Los Espejos (L E); Río Seco de los Castaños (R S C); Mogotes Negros-Rinconada (M N-R); Tambolar (Tm); Talacasto (TI); Villavicencio (Vi).



stratigraphic position and ages of the sections considered by Le Hérisse *et al.* (2009) for their diversity analysis of the Los Espejos Formation (Los Pozos, Los Azulejitos, La Chacritas, Río Jáchal, Las Aguaditas, Loma de los Piojos), have been later dismissed (Rubinstein, 2001b). Taking into account the difficulties that still persist when correlating the sections, and their biostratigraphic constrain, we prefer to infer the diversity trends at the series level (i.e. Ludlow) instead of the diversity by sections, as in Le Hérisse *et al.* (2009). Consequently, the difference in the number of acritarch and chlorophyte species between this paper and the results presented by other authors, is also due to the different methodologies in use.

The studied basins, localities, and formations are listed, according to authors and date of publication, in Figure 6.

A selection of Silurian and Devonian palynomorphs of the studied localities is shown in Figure 7.

4. PALYNOLOGICAL RESULTS

4.1. Llandovery

The relatively high diversity of phytoplankton that reaches 116 species (17 chlorophytes and 99 acritarchs) is illustrated in Figure 3.

The composite data from the Lipeón Formation, where productive samples come from the lower part of the unit, shows a relatively high diversity with 48 phytoplankton species (seven chlorophytes and 41 acritarchs). Miospores diversity, only represented by cryptospores, reaches 13% of the palynological assemblage (seven species), indicating a low terrestrial input (Figure 4A).

The Llandovery diversity of the Precordillera Basin, mainly represented by data from the La Chilca Formation, displays a higher level by reaching 86 phytoplankton species (13 chlorophytes and 73 acritarchs), whereas subordinate cryptospores are represented by eight species (Figure 4B). This proportion evidences a lower participation of land-derived palynomorphs in relation to the Central Andean Basin. Surprisingly, data coming from the uppermost part of the Don Braulio Formation (Villicum locality), from levels related to the *Atavograptus atavus* graptolite Zone (Early Rhuddanian), is more than twice that recorded in the La Chilca Formation (five chlorophytes and 42 acritarchs). In addition, the lowest Silurian levels of the La Chilca Formation were barren, or with low diversity palynological assemblages.

4.2. Wenlock

Even if the basal part of the Los Espejos Formation was considered as probably Wenlockian in age, the stratigraphic range of the phytoplankton recovered from the basal levels in different localities of the Precordillera does not indicate an age older than Ludlovian, which is also supported by trilete spores. Therefore, palynomorph assemblages assigned to the Wenlock are sparse, and are only registered in the Central Basin and the Chacoparanense Basin (Lipeón Formation and Copo Formation, respectively). The maximum diversity corresponds to the Copo Formation, with 35 phytoplankton species (six chlorophytes and 29 acritarchs; Figure 3). No miospores were recorded from the Wenlock, a fact that would suggest a deeper water marine environment compared with Llandovery deposits.

Figure 7. Selected Silurian and Devonian palynomorphs of the studied localities. The scale bars represent 20 µm. 1: *Onondagaella asymmetrica* (Deunff) Playford, 1977. Lipeón Formation (Sierra de Zenta, Cordillera Oriental). MPLP 7395 G (E35.3). 2: *Crassiangulina variacornuta* Wauthoz *et al.*, 2003. Lipeón Formation (Los Colorados-Chamarra, Central Andean Basin). MPLP 7395 G (F41.3). 3: *Domasia elongata* Downie, 1960. Lipeón Formation (Sierra de Zapla, Central Andean Basin). MPLP 7582E (L33.2). 4: *Domasia amphora* Martin, 1966. Lipeón Formation (Sierra de Zenta, Central Andean Basin). MPLP 8822A (M24). 5: *Beromia rexroadii* Word, 1996. Lipeón Formation (Sierra de Zapla, Central Andean Basin). MPLP 7582E (M27). 6: *Imperfectotrilites vavrdovae* (Richardson) Steemans *et al.*, 2000. Lipeón Formation (Sierra de Zapla, Central Andean Basin). MPLP 7582E (F25.2). 7: *Dactylofusa maranhensis* Brito and Santos, 1965. Lipeón Formation (Sierra de Zapla, Central Andean Basin). MPLP 7582E (Y34.2). 8: *Dactylofusa estillis* Cramer and Díez, 1972. Lipeón Formation (Sierra de Zenta, Central Andean Basin). MPLP 8822A (D28.3). 9: *Synorisporites verrucatus* Richardson and Lister, 1969. Los Espejos Formation (Ancha Creek, Precordillera Basin). 60986 (U30.3). 10: *Tylotopalla digitifera* Loeblich, 1970. La Chilca Formation (Ancha Creek, Precordillera Basin). 60972 (W29/1). 11: *Tylotopalla caelamenicutis* Loeblich, 1970. La Chilca Formation (Ancha Creek, Precordillera Basin). 90972 (H41). 12: *Artemopyra urubuense* Steemans *et al.*, 2008. Los Espejos Formation (Ancha Creek, Precordillera Basin). 60704 (K35.3). 13: *Neoverghachium carminae* (Cramer) Cramer, 1970. Los Espejos Formation (Ancha Creek, Precordillera Basin). 60667 (O46.4). 14: *Chelinospora poecilomorpha* (Richardson and Ioannides) Richardson, Rodríguez and Sutherland, 2001. Los Espejos Formation (Las Chacritas, Precordillera Basin). MPLP 4725D (X35.4). 15: *Quadratum fantasticum* Cramer, 1964. Los Espejos Formation (Las Chacritas, Precordillera Basin). MPLP 4728B (Y25.2). 16: *Polyplanifer simplex* Pöthé de Baldi, 1981. Los Espejos Formation (Las Chacritas, Precordillera Basin). MPLP 4733B (S29.2). 17: *Ozotobranchion dactylos* (Cramer) Playford, 1977. Los Espejos Formation (Las Chacritas, Precordillera Basin). MPLP 4727B (Y42.1). 18: *Dictyotrilites emsiensis* (Allen) McGregor, 1973. Talacasto Formation (Cerro del Fuerte, Precordillera Basin). MPLP 5281B (E25). 19: *Orygmahapsis fistulosa* (Colbath) Colbath, 1987. Talacasto Formation (Cerro del Fuerte, Precordillera Basin). 35601 (D41.1). 20: *Demorhethium lappaceum* Loeblich and Wicander, 1974. Talacasto Formation (Cerro del Fuerte, Precordillera Basin). 35609 (J45.1). 21: *Schizocystia pilosa* Jardín *et al.*, 1972. Talacasto Formation (Cerro del Fuerte, Precordillera Basin). 35601 (E55). 22: *Dibolisporites echinaceus* (Eisenack) Richardson, 1965 emend. McGregor, 1973. Villavicencio Formation (San Isidro Creek, Precordillera Basin). 4149Cg (F28.4). 23: *Acinosporites* sp. Villavicencio Formation (San Isidro Creek, Precordillera Basin). MPLP 4149C (N33). 24: *Raistrickia* cf. *R.* sp. A in Le Hérisse, 1983. Villavicencio Formation (San Isidro Creek, Precordillera Basin). MPLP 4149Ce (P25.2). 25: *Knoxisporites riondae* Cramer and Díez, 1975. Talacasto Formation (Sierra de Las Minitas, Precordillera Basin). MPLP 9771B (R38.3). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

4.3. Ludlow

Ludlovian marine and terrestrial palynomorphs have been described and discussed in numerous papers as mentioned above. Ludlovian palynomorphs mainly come from the Los Espejos Formation. However, palynomorphs from the Tambolar and the Río Seco de los Castaños formations are assigned herein to this age, as explained above.

Noticeably, the highest peaks of diversity of both marine phytoplankton and miospores correspond to this epoch, with a total number of 246 phytoplankton species (66 chlorophytes and 180 acritarchs) and 57 miospores (Figure 3).

It is evident that this large number of taxa for the Ludlow could be easily reduced with an integrated systematic and biostratigraphic revision of the whole database, and if Gorstian and Ludfordian stages could be differentiated.

The hiatus at the base and top of the Los Espejos Formation and the scarcity of biostratigraphic markers make it difficult to define an accurate stratigraphic range for the unit throughout the basin. In addition, the distribution of phytoplankton and miospores is similar from the base to the middle-upper part of the formation, with a decreasing tendency until their complete disappearance near the formation top, which occurs in almost all the studied sections (the upper 25 m to 150 m are usually barren). The only exception is in the Río Jáchal locality, where miospore assemblages dominate (more than 50%) until less than 1 m below the boundary with the overlying Talacasto Formation (Rubinstein, unpublished). These uppermost assemblages are evidence of the increase of terrestrial palynomorphs towards the boundary with the Devonian wherever palynological data is available.

The upper one-third of the Los Espejos Formation in the Cerro del Fuerte section, yielded a palynological assemblage coming from levels dated as Gorstian by graptolites. Samples above this, which were supposed to be of Pridolian and Lochkovian age, were barren.

The stratigraphic range of miospores present throughout the Los Espejos Formation suggests an age closer to the Ludfordian-Pridoli, showing a slight divergence with phytoplankton dating.

Taking each section of the Los Espejos Formation separately, the diversity reaches values that range from around 20 phytoplankton species to more than 100, with a clear predominance of acritarchs over chlorophytes; miospores range from barren to a maximum of 38 species. This suggests that even with variations in diversity between different localities, probably due to disparities in local palaeoenvironments, the Los Espejos Formation has the most diversified marine and terrestrial palynomorphs of the entire studied interval.

In view of the division in facies of the Los Espejos Formation and the distribution of samples in all of the investigated sections, data from the lower part and for the middle-upper

part is plotted to compare the diversity (Figure 4). As observed in this figure, the diversity decreases quite similarly for both marine and terrestrial palynomorphs in the middle-upper part, thus, predicting the complete disappearance of palynomorphs towards the top.

Considering the Las Chacritas section (Figure 5), where the abundance of species has been drawn per sample, the diversity trend shows a gradual increase in the lower section turning into a gradual decrease upwards, before becoming barren in the middle and upper thirds. The miospores from this section roughly follow the trend of the phytoplankton diversity.

4.4. Pridoli

From a palynological point of view, the presence of the Pridoli is still unconfirmed. Despite the results summarized in Rubinstein (1995) indicating a late Ludlovian-Pridolian? age for the upper part of the Los Espejos Formation, the Pridolian age was later dismissed by the same author, based on a revision of stratigraphic ranges of palynomorphs and new data (Rubinstein, 2001b).

As a result, no reliable data is presently available for the Pridoli (Figure 3).

4.5. Lower Devonian

Only three localities (Mendoza, San Juan and La Rioja provinces) along the extended Devonian outcrops of the Precordillera Basin yielded Early Devonian palynological assemblages. The total composite diversity is significantly low, compared with the Silurian (Figure 3). It exhibits a clear change of previous trends, with the predominance of land-derived palynomorphs represented mainly by trilete spores (six chlorophytes, 14 acritarchs and 26 miospores). The richest marine phytoplankton diversity (six chlorophytes, nine acritarchs) accompanied by subordinate miospores (nine taxa) occurs in the Cerro del Fuerte section (late Lochkovian to Emsian), while phytoplankton dramatically decrease in the San Isidro Creek and Sierra de las Minitas localities of late Pragian to early Emsian age and late Lochkovian to middle Emsian age, respectively. This could indicate a near-shore environment for the latter two localities, located near the southern and northern margins of the basin.

5. CONCLUSIONS

Our contribution improves the knowledge of the phytoplankton and miospores diversity from the Silurian to the Lower Devonian of Argentina. It is based on a critical review and analysis of all published information, as well as new unpublished data.

We recognize the necessity of an exhaustive systematic revision of data, in order to avoid an obvious inflation in the number of taxa that might mask the real diversity values. However, we are aware that the preservation of most of the palynological assemblages prevents positive taxonomic assignment, thus raising the number of species with many of them described in open nomenclature.

For these reasons, and the disparity of data from different localities and basins, we unify the composite species diversity values into a single figure (Figure 3), where a preliminary diversity trend can be drawn.

The Llandovery is a period with relatively high diversity in the phytoplankton, while miospores are represented by low percentage and only by cryptospores, even if they come from marginal marine depositional environments. A drop in the diversity can be seen during the Wenlock, followed by a rise in diversity with a dramatic peak during the Ludlow, for both terrestrial and marine palynomorphs. The decline during the late Ludlow, Pridoli, and earliest Lochkovian may be related to environmental conditions that prevent palynomorph preservation. The diversity trend shows a progressive increase in diversity starting from the late Lochkovian to the Emsian for both phytoplankton and miospores, along with an inversion of diversity values, with miospores (mainly trilete spores) reaching higher diversity values than the marine phytoplankton. Chlorophyte overall diversity follows the acritarch trend.

Levels of morphologic innovations of the phytoplankton, as indicated by Le Hérisse *et al.* (2009), can be observed in the Ludlow with the appearance of genera such as *Ozotobrachion* and *Fimbriaglomerella*, and in the Early Devonian with the first occurrence of *Demorhethium* and *Schizocystia*. Of note is that the trilete spores, which first appear in the Ludlow, display well-diversified assemblages and complex morphologies (e.g. *Chelinospora*, *Synorisporites*, *Amicosporites*).

Le Hérisse *et al.* (2009) stated that for the warm low latitudes there is a distinct diversity peak during the early Gorstian. They compared these results with the high diversity shown by Argentinean Ludlovian assemblages, which also yield many species in common with coeval assemblages (i.e. Welsh Basin and Borderland, Spain and France). The Ludfordian, as well as the Pridoli, do not show noticeable diversity trends, which is interpreted as probably related to different depositional environments and lithofacies, but we have no supporting data.

During the Lochkovian, Le Hérisse *et al.* (2009) observed an initial radiation of new prasinophyte and acritarch taxa as indicated by key sections in the Laurussia and Gondwana palaeocontinents, with an increase of cosmopolitan species. In Argentina, the scarcity of data allows us to make a slight comparison with this worldwide radiation.

The comparison with the proposed global patterns is probably strongly biased, not only due to differences in

depositional environments and lithofacies, but also due to the geodynamic of the Argentinean basins, developed in an active margin, that imprinted particular characteristics on the deposits (e.g. facies associations, hiatus, environmental stress conditions). As a result, the observed diversity trends might reflect changing facies and conditions of preservation rather than true biodiversity patterns. In fact, the distribution of land-derived palynomorphs is strongly related to inshore-offshore trends. Thus, the predominance of miospores in the Early Devonian matches with the tendency of continentalization of the depositional systems.

In contrast, the high latitudes of these basins in the period considered do not seem to affect the diversity in any particular way. In fact, the Solimoes Basin located higher than 60°S during the Early Devonian, yielded a phytoplankton assemblage composed of 47 species of acritarchs and chlorophytes (Rubinstein *et al.*, 2008b). The presence of *Demorhethium lappaceum*, *Duvernaysphaera actinota*, *Riculusphaera fissa*, *Thysanoprobolus polykion*, *Winwaloeusia distracta*, and *?Cymatiosphaera florida* allow correlation with contemporaneous assemblages from other regions and palaeolatitudes. This assemblage, corresponding to 18 core samples, is independently dated by miospores and chitinozoans as late Lochkovian. As opposed to the Argentinean low-diversity Early Devonian palynomorphs, those of the Solimoes Basin were developed in an intracratonic basin.

Therefore, based on the data available from the Late Silurian–Early Devonian palynological assemblages from the Precordillera, Central Andean Basin, and Chacoparanense Basin; and considering issues of preservation and taxonomy, it seems that the diversity of both marine and terrestrial palynomorphs tends to increase towards the Late Silurian, with its maximum peak in the Ludlow. After a decline during the latest Silurian–earliest Devonian, the diversity progressively increases from the late Lochkovian. The marine phytoplankton clearly dominates throughout the Silurian; however, miospores dominate several palynological assemblages during the Early Devonian.

Nevertheless, in view of the present state of knowledge, the diversity trends of Argentinean palynomorphs are still preliminary, and should be cautiously regarded when used for interpretation of global tendencies.

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