



The palynological record across the Ordovician/Silurian boundary in the Cordillera Oriental, Central Andean Basin, northwestern Argentina



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ABSTRACT

The Hirnantian “glacial horizon” has been recognized across the Central Andean Basin (Puna, Cordillera Oriental, Sierras Subandinas and Sistema de Santa Bárbara) in northwestern Argentina. It is represented by glaciofluvial to glaciomarine facies which unconformably overly Lower to Middle Ordovician stratigraphic units. In the Cospalá area, in the eastern margin of the Cordillera Oriental, the glacial deposits are assigned to the Cospalá Formation. The Lower Silurian postglacial deposits of the Lipeón Formation sharply truncate the underlying Cospalá Formation. Miospores, chitinozoans and acritarchs have been recorded across the Ordovician/Silurian boundary. Marine palynomorphs dominate the studied section. The Late Ordovician miospore assemblage is fairly diverse.

It contains permanent tetrads and dyads, spores physically separated from cryptospore polyads, laevigate and ornamented hilate spores, and trilete spores. The trilete spores *Ambitisporites avitus*, *Aneurospora?* sp., *Chelinospora* cf. *prisca* and *Leiotriletes* spp. occur in the Cospalá Formation together with chitinozoans dated as early to late Katian. If land-derived palynomorphs were considered autochthonous, their age would be Hirnantian. The trilete spores of the Cospalá Formation constitute their oldest record in South America, representing the advent of vascular plants in the region. The Lipeón Formation yielded Telychian trilete spores dated by chitinozoans, constituting the earliest evidence of Silurian vascular plants of Argentina. The diversity and abundance of miospores decrease in the Lipeón Formation in accordance with the disappearance of terrestrial ecosystems due to the global transgression after the melting of the Hirnantian glaciers. Acritarchs in both the Cospalá and the Lipeón formations support the chitinozoan dating. Whereas chitinozoans and acritarchs show affinities with Gondwanan and peri-Gondwanan regions, the studied miospores confirm the cosmopolitanism of Late Ordovician–earliest Silurian microfloras. The new miospore data, particularly those related to the incoming and evolution of hilate/trilete spores, question previous palaeogeographic and palaeoclimatic interpretations about the origin and adaptive radiation of vascular land plants.

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1. Introduction

In recent years, the scenario of the major events in the evolution of the earliest terrestrial flora has rapidly changed with new data coming from different palaeoplates and mostly independently dated by other fossils. The incoming of the cryptospores represents the first step in the colonization of lands by the embryophytes followed by the appearance of trilete spores considered as produced by vascular plants (tracheophytes and their ancestors the ‘protracheophytes’). The colonization of land by plants

irreversibly modified the Earth's biogeochemical conditions and diversification of life on land allowed terrestrialization.

Stemans et al. (2010) have provided key data in this matter, thus suggesting new palaeogeographic and palaeoclimatic hypothesis. However, these authors' proposals should be revised in the light of subsequent data including the new findings of the Central Andean Basin herein.

Since the milestone contributions of Gray and Boucot (1971), Strother and Traverse (1979), Richardson (1985, 1996), and Stemans (1999), among others, the origin, evolution and biological affinities of the earliest land plants throughout the spore record and the later megafossil record are still subject of controversy. Such subjects have thereafter been reviewed and profusely discussed by different authors (e.g. Stemans et al., 2009, 2010, 2012; Kenrick et al., 2012; Wellman et al., 2013, 2015; Edwards et al., 2014; Strother et al., 2015).

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Stemans (1999), Wellman and Gray (2000) and Stemans et al. (2009) considered the cryptospores as dispersed spores derived from the earliest terrestrial flora represented by the primitive embryophytes. On the other hand, Strother et al. (2015) defined cryptospores, following Strother and Beck (2000), as organic-walled microfossils of non-marine origin derived from cryptogams capable of producing a resistant spore-wall of sporopollenin or other organic polymers. Strother et al. (2015) also pointed out the importance of tetrahedral configuration of tetrads. According to these authors, other spore arrangements do not necessarily indicate an embryophytic (land plant) origin. Edwards et al. (2014) stated that cryptospore-producing plants are not strictly bryophytes, as generally accepted, because they exhibit a combination of features which are not found together in extant bryophytes. They propose the term ‘cryptophytes’ for these basal embryophytes.

The transition from cryptospores to hilate/trilete spores is considered a major event in the dispersed spore record because it represents the inception and adaptive radiation of the vascular plant lineage (Stemans et al., 2009). Even though their first appearance was generally admitted to occur in the Early Silurian, sparse laevigate trilete spores have also been recorded from Upper Ordovician strata of Turkey (Stemans et al., 1996) and Algeria (Spina, 2014). The discovery of well-preserved and diversified hilate and trilete spores in the Katian of Saudi Arabia (Stemans et al., 2009; Wellman et al., 2015) pushed back the origin and evolution of vascular land-plants and located their origin in western Gondwana (following palaeogeographical reconstructions such as the new one of Torsvik and Cocks, 2013a). It is worth noting that different authors have considered South America as part of the western margin of Gondwana. West Gondwana is defined as the part of the supercontinent represented today by South America, the Arabian plate, Africa and West Antarctica (Vaughan and Pankhurst, 2008). More precisely, South America refers to the western part of west Gondwana and the Arabian plate to the eastern part.

To date, the earliest fossil evidence of land-plants has been recorded from northwestern Argentina. The oldest cryptospore assemblage was recorded from Dapingian deposits (Middle Ordovician) of the Zanjón Formation in the Sierras Subandinas, Central Andean Basin. Its age is independently dated by chitinozoans (Rubinstein et al., 2010). Before this finding, Darriwilian cryptospore assemblages from the Czech Republic (Vavrdová, 1984) and Saudi Arabia (Strother et al., 1996) were recognized as the first proof of the advent of embryophytes. These data, together with the oldest plant fragments recorded from the Late Ordovician of Oman (Wellman et al., 2003), situated the origin of terrestrial life on the Gondwana palaeocontinent.

Other cryptospore assemblages have been recorded from the Middle and Upper Ordovician of Gondwana and peri-Gondwana terranes (Argentina, Czech Republic, Libya, Turkey), Avalonia (UK, Belgium) and China (Stemans et al., 2010 and references therein).

In Argentina, a few cryptospore tetrads have also been recorded in Darriwilian and Katian strata of the Precordillera Basin (Ottone et al., 1999; de la Puente and Rubinstein, 2013a) and in the Darriwilian of the Sierras Subandinas, where dyads and monads are also present (Rubinstein et al., 2011).

Recently, Late Ordovician cryptospore assemblages have been reported from different localities and palaeoplates. Vecoli et al. (2011) described well-preserved and independently dated cryptospore assemblages from the Hirnantian of Anticosti Island (Canada) and Estonia, giving evidence of latest Ordovician diverse floras in Laurentia and, for the first time, in Baltica. Even when located in different palaeoplates, both microfloras correspond to low palaeolatitudes. Subsequently, Badawy et al. (2014) documented the oldest cryptospore assemblage of Sweden (Baltica). These cryptospores coming from levels just above the early Katian graptolite *Dicellograptus complanatus*, are low-diverse but well preserved. Concerning high latitude Gondwana

and peri-Gondwana terranes, Mahmoudi et al. (2014) reported the first record of Hirnantian cryptospores from Iran. Their age proved well constrained by the presence of the chitinozoan *Spinachitina oulebsiri*. The Iranian assemblage is relatively diversified and moderately preserved.

Spina (2014) recorded the first fairly-diversified cryptospore assemblage from Hirnantian glacial-related deposits of Algeria. Cryptospores from the Upper Ordovician of northern Chad and southeastern Libya have also been reported (Le Hérisse et al., 2013).

Strother et al. (2015) described in detail the Darriwilian cryptospore assemblage from Saudi Arabia previously reported (Strother et al., 1996), analyzing the taxonomy, evolution and possible affinities of these Middle Ordovician well-preserved cryptospores.

Land derived palynomorphs are well represented in the Hirnantian throughout the Argentine Central Andean Basin. Particularly, in the Salar del Rincón Formation, in the Puna region, a fairly diversified and well-preserved cryptospore assemblage has been recorded (Rubinstein and Vaccari, 2004). This assemblage, previously dated as latest Hirnantian–earliest Llandovery, is now undoubtedly assigned to the Hirnantian based on chitinozoan studies (de la Puente et al., 2015). In the Sierras Subandinas, scarce cryptospores with tetrahedral tetrad configuration have been recorded in the Hirnantian Zapla Formation (Rubinstein, 2005).

No Ordovician records of land-derived palynomorphs have been recorded from other South American basins.

Similarities between Late Ordovician–earliest Silurian microfloras have been postulated by many authors (e.g. Stemans, 1999; Wellman and Gray, 2000; Rubinstein and Vaccari, 2004; Stemans et al., 2010; Vecoli et al., 2011; Wellman et al., 2013) and confirmed by new data suggesting that the earliest land plants were of cosmopolitan nature and then tolerant of diverse environmental conditions ranging from latitudes close to the palaeopole and to the equator, even during the Hirnantian glaciation. Minor differences between Ordovician microfloras could be related to local palaeoenvironmental conditions as well as taphonomic processes.

From the Early Silurian, cryptospore diversity and abundance diminish in coincidence with the expansion and diversification of trilete spores that dominated the vegetation from the Homerian (Wellman et al., 2015 and references therein). The notable decrease in cryptospore diversity was a consequence of the early Silurian global transgression that probably destroyed, reduced or moved the habitats of the earliest plants (Stemans et al., 2010).

Interestingly, the Llandovery deposits of the Precordillera Basin and the Central Andean Basin, which are respectively represented by the La Chilca Formation and the Lipeón Formation, had not yielded any trilete spores so far (Rubinstein and García Muro, 2013).

The first appearance of trilete spores in Argentina occurred in the basal part of the Los Espejos Formation in the Cerro La Chilca section (Precordillera Basin) which is assigned to the Wenlock (García Muro and Rubinstein, 2015). Trilete spores are known from Llandovery strata of Brazil and Paraguay (Le Hérisse et al., 2001; Stemans and Pereira, 2002).

This paper aims: (1) to describe the cryptospore and trilete spore assemblages that span the Ordovician/Silurian boundary in the Caspalá area of the Cordillera Oriental, Central Andean Basin, which is characterized by the transition between the Hirnantian “glacial horizon” and the post-glacial Lower Silurian deposits; (2) to present the oldest trilete spores of South America independently dated as Katian–Hirnantian; (3) to introduce the first trilete spores of the Early Silurian (Llandovery) of Argentina, (4) to discuss the origin and radiation of the trilete spores; (5) to interpret the palynomorphs distribution in relation to changing palaeoenvironmental conditions (glacial–post-glacial) based on detailed sedimentological observations and facies analysis; (6) and to compare our results with previous palaeogeographic and palaeoclimatic considerations.

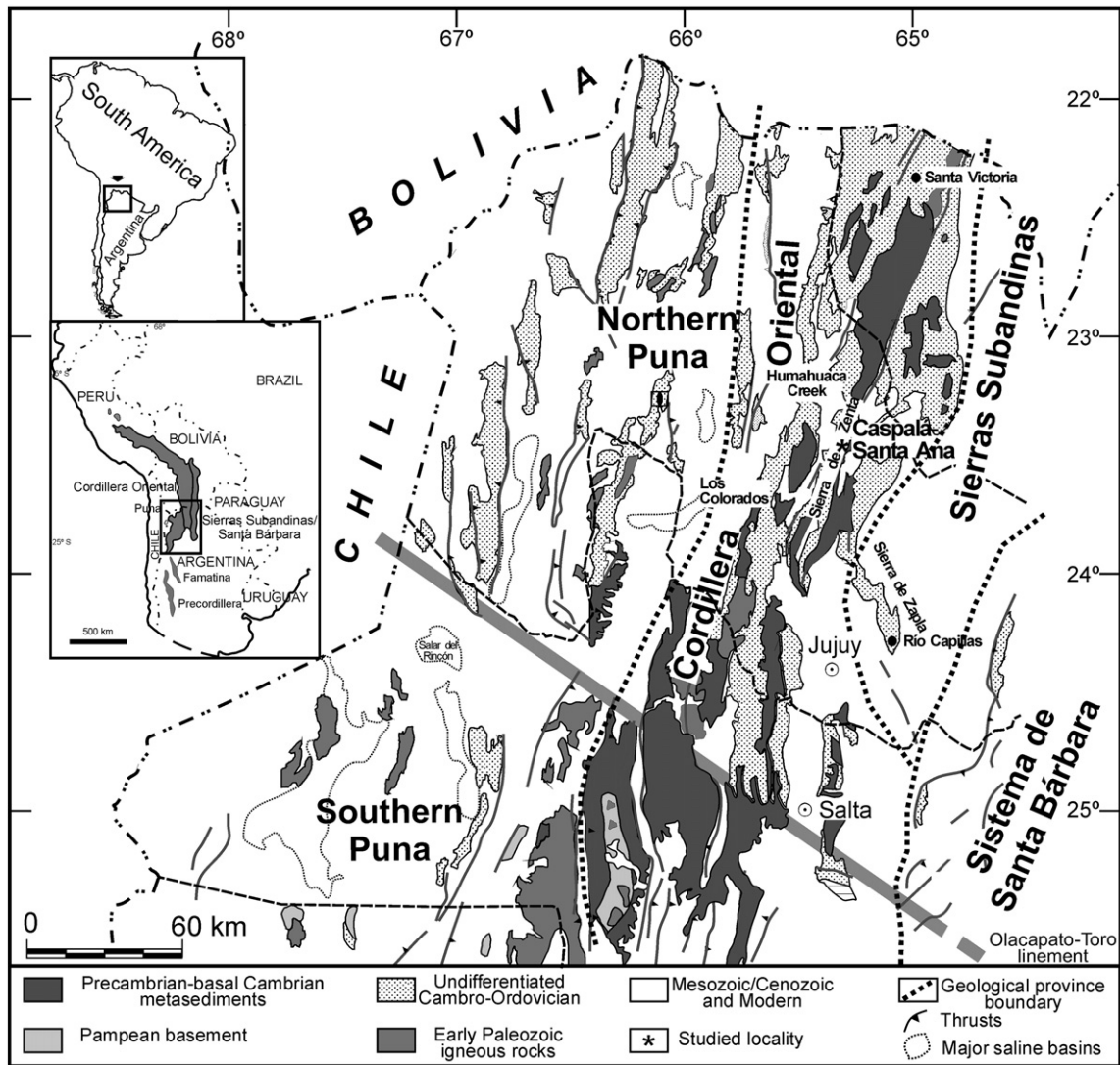


Fig. 1. Geological map of the Central Andean Basin, in northwestern Argentina, showing geological provinces and the studied locality. Modified from Astini (2008)

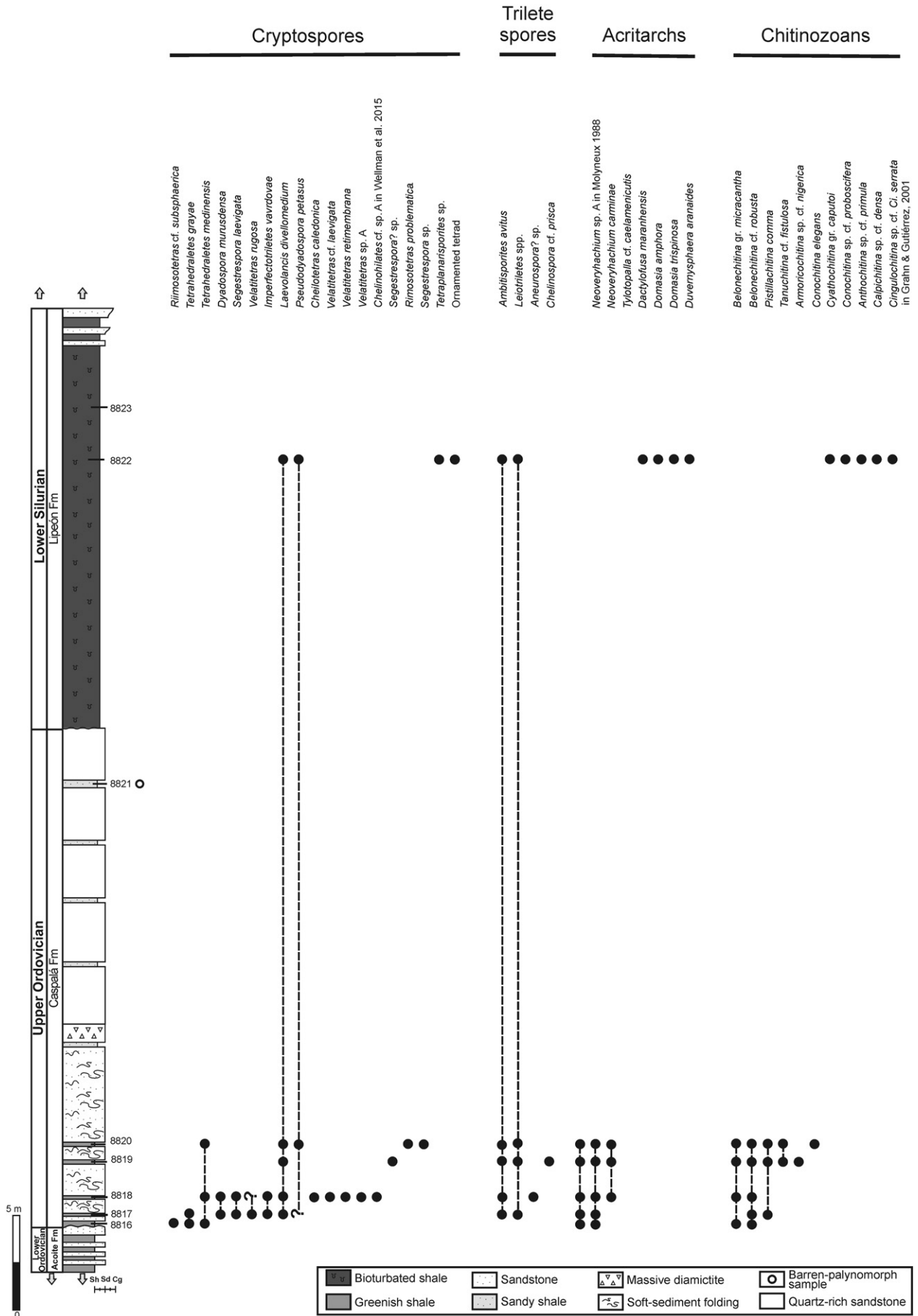
2. Geological setting

The Hirnantian “glacial horizon” has been recognized across the Lower Palaeozoic Central Andean Basin, which includes the Puna, Cordillera Oriental, Sierras Subandinas and Sistema de Santa Bárbara morphostructural provinces in northwestern Argentina (Fig. 1). It is represented by glaciofluvial to glaciomarine facies and unconformably overlies various Early to Middle Ordovician stratigraphic units. Due to the long hiatus and subtle angularity in some parts of the region, it once was considered a tectonic event (Ocolytic unconformity). The glacial record is covered by the transgressive Silurian deposits of the Lipeón Formation across a sharp boundary. In a few outcrops, such as in the Capillas River (Sierras Subandinas), this lower Silurian unit contains thin lenses of quartz pebble conglomerates in its base, immediately overlain by relatively fine-grained, mica-rich, thoroughly bioturbated, and open-marine facies related to a postglacial transgression episode.

In the Caspalá area (Jujuy Province), on the eastern margin of the Cordillera Oriental (Fig. 1), the glacial deposits are assigned to the Caspalá Formation (Starck, 1995), which is equivalent to the Zapla Formation or Mecoyita Formation in other areas of the region. Previous

sedimentological studies of the unit in the Caspalá area are scarce and data on its age are unknown. In this area, the glacially-related deposits of the Caspalá Formation are composed of a massive diamictite with few pebbles and oversized striated boulders overlying a strongly disturbed substrate, indicating soft-sediment folding, deformation, and partial reworking of the previous older sedimentary record, followed by graded quartz-rich arenites with a few fine-grained partitions toward the top. The postglacial early Silurian deposits of the Lipeón Formation sharply truncate the glacial deposits with both marked grain-size diminution and strong compositional change. The Lipeón Formation shows a more homogeneous appearance although its detailed inspection allows the recognition of a heterolithic stratofabric with interbedded dark gray shales and fine-grained lenticular to tabular thin beds of sandstones strongly mottled and affected by burrowing (intense bioturbation – Ichnofabric indexes 4 & 5 of Droser and Bottjer, 1986). Progressively toward the top, thicker beds of graded and laminated sandstones are more and more frequent indicating a progradational arrangement. One distinct characteristic apart from the strong bioturbation is the high content of white micas, showing unroofing of a basement source.

Fig. 2. Schematic stratigraphic column of the Caspalá and Lipeón formations from Caspalá area of northwestern Argentina, showing stratigraphical distribution of cryptospores, trilete spores, acritarchs and chitinozoans.



Cryptosporites

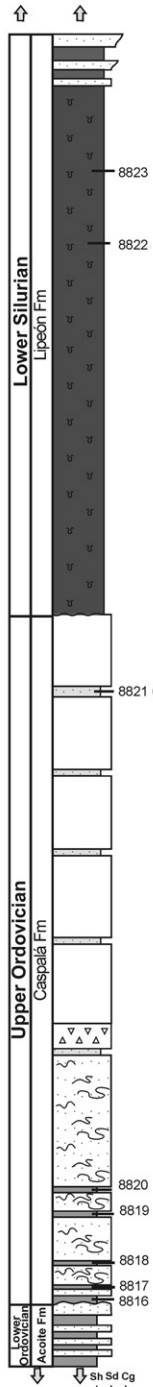
Trilete spores

Acritarchs

Chitinozoans

- Rimosoletes* cf. *subsphaerica*
Tetrahedraletes *grayae*
Tetrahedraletes *medinensis*
Dyadospora *murusdensa*
Segestrespora *laevigata*
Velatiertes *rugosa*
Imperfectobrietes *vavrdovae*
Laevolancis *divellomedium*
Pseudodyadospora *petasus*
Cheloleiras *caledonica*
Velatiertes cf. *laevigata*
Velatiertes *retimembrana*
Velatiertes sp. *A*
Chelinohialtes cf. sp. *A* in Wellman et al. 2015
Segestrespora? sp.
Rimosoletes *problematica*
Segestrespora sp.
Tetraplanisporites sp.
 Ornamented tetrad
- Ambisporites* *avilius*
Leiofrites spp.
Aneurospor? sp.
Chelinospora cf. *prisca*
- Neovevryhachium* sp. *A* in Molyneux 1988
Neovevryhachium *caminae*
Tylopalla cf. *caelamenicutis*
Dactylofusa *maranhensis*
Domasia *amphora*
Domasia *trispinosa*
Duvernysphaera *aranales*
- Belonechitina* gr. *micracantha*
Belonechitina cf. *robusta*
Pistillachitina *comma*
Tanuchitina cf. *fistulosa*
Amoricochitina sp. cf. *rigerica*
Conochitina *elegans*
Cyathochitina gr. *caputoi*
Conochitina sp. cf. *proboscifera*
Anthochitina sp. cf. *primula*
Calpichitina sp. cf. *densa*
Cingulochitina sp. cf. *Ci. serrata* in Grahn & Gutiérrez, 2001

5 m
0



Bioturbated shale	Sandstone	Massive diamictite	Barren-palynomorph sample
Greenish shale	Sandy shale	Soft-sediment folding	Quartz-rich sandstone

3. Material and methods

Palynomorph data of six levels from the glacially-related deposits of the Caspalá Formation and two levels from the transgressive deposits of the Lipeón Formation, were analyzed. The Late Ordovician is mainly represented by amalgamated coarse sandstones while the basal part of the Silurian deposits is seriously altered by post-diagenetic taphonomic factors (pervasive bioturbation). Therefore, only the levels that seemed suitable for palynological studies were selected for sampling. Among these, seven were productive, yielding miospores, marine phytoplankton (acritarchs and related forms) and chitinozoans. The uppermost sample (8821) of the Caspalá Formation was barren of palynomorphs (Fig. 2).

The samples were processed in the Palaeopalynology laboratory of IANIGLA (Mendoza, Argentina), using standard HCl–HF–HCl acid maceration techniques. The organic residue was screened on a 10 µm sieve to remove fine organic particles. The phytoplankton and spores were mounted in Glycerin jelly as permanent palynological slides and examined using light microscopy with interference contrast. The chitinozoans were hand-picked and mounted on stubs for scanning electron microscope (SEM) examinations according to the technique described by Paris (1981).

The palynological slides are housed in the Palynological Collection of the IANIGLA, CCT Mendoza, CONICET, Argentina. Specimen locations are referred to by using England Finder coordinates.

4. Palynological results

The assemblages are dominated by marine palynomorphs (organic-walled phytoplankton and chitinozoans); miospores (cryptospores and trilete spores) constitute a minor proportion of the assemblages. The terrestrial palynomorphs are moderately to poorly preserved, flattened, broken and partly carbonized. However, the cryptospores, particularly those from the Ordovician section, are fairly diverse. Cryptospores outnumber trilete spores both in diversity and abundance except at level 8819. The uppermost Silurian sample (8823) has provided very poorly preserved palynomorphs, including small and simple acanthomorphic acritarchs and unidentifiable miospores.

The identified miospores (Plates 1, 2) include nineteen cryptospore species (seventeen species in the Ordovician samples and four in the Silurian samples) and four trilete spore species (four species in the Ordovician samples and two in the Silurian samples).

All the recognized spore taxa are grouped according to their main morphological features (Wellman and Richardson, 1993; Steemans et al., 2000; Wellman et al., 2015) and listed alphabetically hereafter (Appendix A). Some remarks are given for species considered of particular interest, species left in open nomenclature and doubtful species assignments.

Chitinozoan and acritarch (including algae) taxa, particularly those biostratigraphically relevant, are illustrated (Plates 2, 3) and discussed throughout the paper.

The stratigraphic distribution of palynomorph taxa is displayed in Fig. 2.

4.1. Chitinozoans

In the Caspalá Formation chitinozoans were recovered from the lower levels of the glacial deposits (samples 8816–8820; Fig. 2), characterized by extensive reworking. The assemblages yielded Katian chitinozoans mostly represented by broken specimens. The lower samples (8816, 8817 and 8818) contain an early Katian association mainly composed of *Belonechitina* gr. *micracantha* (Eisenack, 1931), *Belonechitina* cf. *robusta* (Eisenack, 1959) and *Pistillachitina comma* (Eisenack, 1959). The following samples, from upper levels (samples 8819 and 8820), additionally contain late Katian chitinozoan species, such as *Tanuchitina* cf. *fistulosa* (Taugourdeau and de Jekhowsky, 1960), *Conochitina elegans* (Eisenack, 1934) and *Armoricochitina* cf. *nigerica* (Bouché, 1965). *T. fistulosa* is a typical component of the late Katian of Northern Gondwana (Paris et al., 2000, 2015). *A. nigerica* has been recorded in the Katian of Western Gondwana (Grahn, 2006) and the late Katian and Hirnantian of Northern Gondwana (Paris et al., 2015 and references therein). This species, as well as *C. elegans*, are considered Polar taxa with a range south of 40° S (see Vandenbroucke et al., 2010; Paris et al., 2015). This Katian chitinozoan association has been frequently observed in Northern Gondwana, mixed with Darriwilian and Sandbian associations reworked by the different pulses of the Hirnantian glaciation (Paris et al., 2015, and references therein).

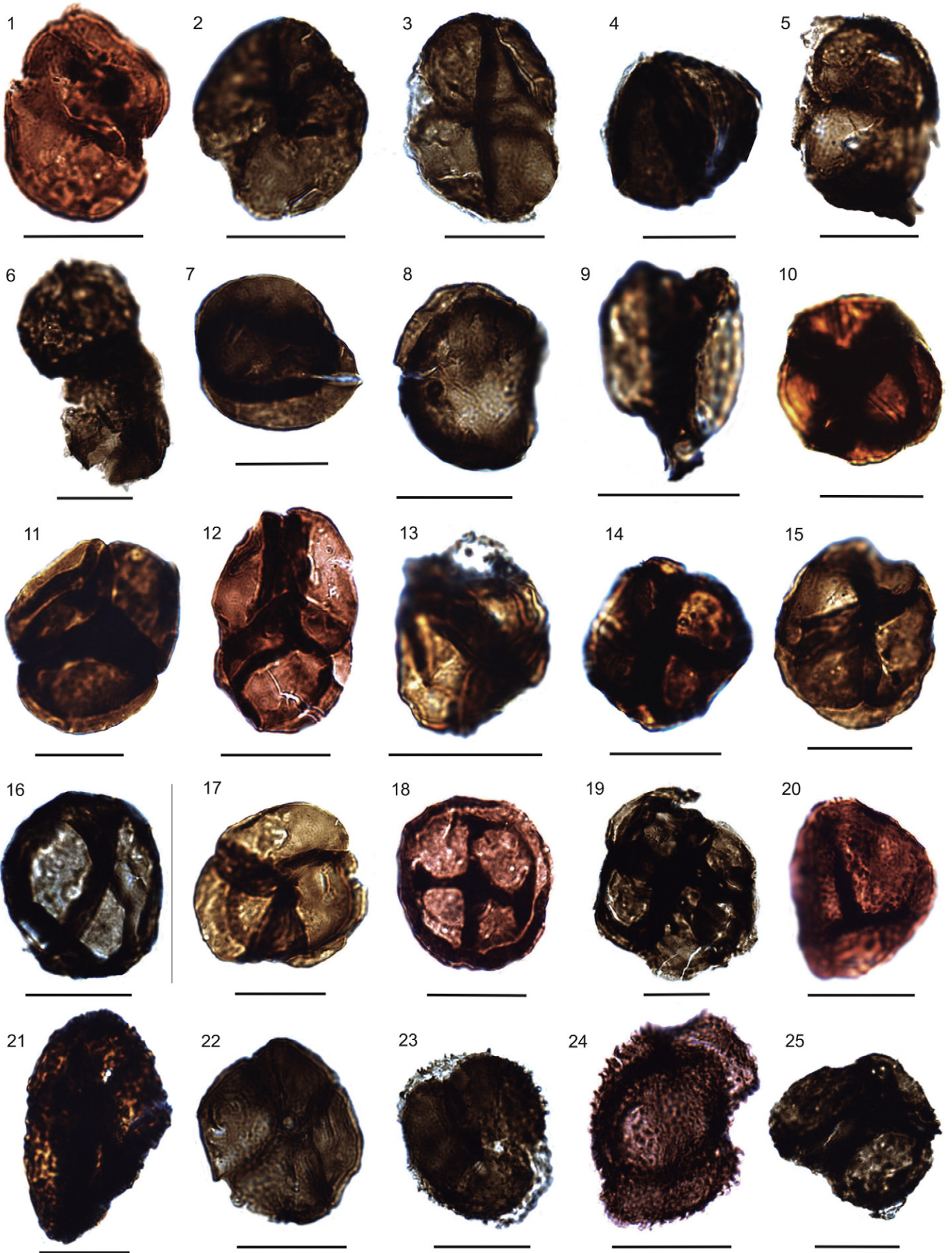
The samples analyzed from the outcrops of the Lipeón Formation derive from the finer-grain size levels from the lower half of the unit, which is characterized by intense bioturbation. The lower chitinozoan-bearing level (sample 8822, Fig. 2) contains *Cyathochitina* gr. *caputoi* Da Costa, 1971, *Conochitina* cf. *proboscifera* Eisenack, 1937, *Anthochitina* cf. *primula* Nestor, 1994, *Calpichitina* cf. *densa* (Eisenack, 1962), and *Cingulochitina* cf. *serrata* (Taugourdeau and de Jekhowsky, 1960) in Grahn and Gutiérrez, 2001. The recovered chitinozoan association indicates a Telychian age for the Silurian deposits in this area and correlates with the lower (but not basal) Lipeón Formation cropping out toward the east in the Sierras Subandinas region (de la Puente et al., 2013). The upper level (sample 8823) is barren of chitinozoans.

4.2. Acritarchs

Acritarch assemblages from the glacial-related Caspalá Formation are relatively diverse, with scarce Late Ordovician (Katian–Hirnantian) diagnostic species such as *Neoveveryhachium carminae* (Cramer) Cramer, 1970 (levels 8816 to 8820, in Fig. 2), *Neoveveryhachium* sp. A in Molyneux, 1988 (levels 8816 to 8820, in Fig. 2) and *Tylotopalla* cf. *caelamenicuttis* Loeblich, 1970 (levels 8818 to 8820, in Fig. 2) and high participation of Early and Middle Ordovician taxa (Rubinstein et al., 2008). The overlying Lipeón Formation, which represents the transgression after glacial waning, yielded a diverse acritarch assemblage. Among these acritarchs, index-taxa such as *Dactylofusa maranhensis* Brito and Santos, 1965, *Domasia amphora* Martin, 1969, *Domasia trispinosa* Downie, 1960 and *Duvernaysphaera aranaides* (Cramer) Cramer and Díez, 1972 can be highlighted.

Neoveveryhachium carminae and *Neoveveryhachium* sp. A were recorded from all the Ordovician studied levels. *N. carminae* first appears in the early–middle Katian of high latitude Gondwanan and peri-

Plate 1. Miospores of the Caspalá Formation (Late Ordovician) and the Lipeón Formation (early Silurian). The scale bars represent 20 µm. 1. *Dyadospora murusdensa* Strother and Traverse, 1979; Caspalá Formation, 8817b, R40/1. 2. *Dyadospora murusdensa* Strother and Traverse, 1979; Caspalá Formation, 8818d, U31/2. 3. *Segestrespora laevigata* Burgess, 1991; Caspalá Formation, 8817b, K29/3. 4. *Segestrespora laevigata* Burgess, 1991; Caspalá Formation, 8818d, J27/0. 5. *Segestrespora* sp.; Caspalá Formation, 8820b, Y29/0. 6. *Segestrespora*? sp.; Caspalá Formation, 8819a, U30/0. 7. *Pseudodyadospora petasus* Wellman and Richardson, 1993; Caspalá Formation, 8820d, C32/4. 8. *Pseudodyadospora petasus* Wellman and Richardson, 1993; Lipeón Formation, 8822b, L35/1. 9. *Pseudodyadospora petasus*? Wellman and Richardson, 1993; Caspalá Formation, 8817a, S23/0. 10. *Cheilotetras caledonica* Wellman and Richardson, 1993; Caspalá Formation, 8818a, Q32/3. 11. *Rimosotetras problematica* Burgess, 1991; Caspalá Formation, 8820b, V37/3. 12. *Rimosotetras* cf. *subsphaerica* Strother et al., 2015; Caspalá Formation, 8816b, H35/0. 13. *Tetrahedraletes grayae* Strother, 1991; Caspalá Formation, 8816'd, G34/0. 14. *Tetrahedraletes grayae* Strother, 1991; Caspalá Formation, 8817b, H37/0. 15. *Tetrahedraletes medinensis* Strother and Traverse, 1979; Caspalá Formation, 8816a, P37/0. 16. *Tetrahedraletes medinensis* Strother and Traverse, 1979; Caspalá Formation, 8818b, L38/0. 17. *Tetrahedraletes medinensis* Strother and Traverse, 1979; Caspalá Formation, 8820c, U33/3. 18. *Tetraplanarisporites* sp.; Lipeón Formation, 8822c, T42/1. 19. *Velatitetras* cf. *laevigata* Burgess, 1991; Caspalá Formation, 8818c, O29/0. 20. *Velatitetras retimembrana* (Miller and Eames) Wellman and Richardson, 1996; Caspalá Formation, 8818a, S42/2. 21. *Velatitetras rugosa* (Strother and Traverse) Steemans et al., 1996; Caspalá Formation, 8817a, W29/0. 22. *Velatitetras rugosa*? (Strother and Traverse) Steemans et al., 1996; Caspalá Formation, 8818d, S30/4. 23. *Velatitetras* sp. A; Caspalá Formation, 8818d, H26/1. 24. Ornamented tetrad; Lipeón Formation, 8822b, O24/3. 25. Tetrad sp.; Caspalá Formation, 8818a, D30/2.



Gondwanan areas (Vecoli and Le Hérisse, 2004; Paris et al., 2007; Delabroye et al., 2011a) while the biocron of *Neoveryhachium* sp. A, firstly recorded from the Ashgill of Lybia (Molyneux, 1988), is generally understood to be Hirnantian (e.g. Le Hérisse et al., 2013; Thusu et al., 2013). However, as observed in the studied samples (Rubinstein, unpublished data), similar morphological features (the main difference is the number of striae on the vesicle) between *N. carminae* and *Neoveryhachium* sp. A, may be the consequence of intraspecific variability. Moreover, there are not many records of *Neoveryhachium* sp. A. Therefore, a Katian occurrence for the latter cannot be excluded.

Tylotopalla cf. *caelamenicutis* has been recorded from the level 8818 until the uppermost Caspalá productive level (8820). Despite poor preservation, the Argentine specimens of *Tylotopalla* cf. *caelamenicutis* would seem to present more heteromorphic processes than the North Gondwana specimens of *T. caelamenicutis* Loeblich, 1970. The latter first appears in the Hirnantian syn-glacial climatic period in high latitude Gondwanan areas of the *Tanuchitina elongata* chitinozoan Zone (Vecoli and Le Hérisse, 2004; Delabroye et al., 2011a).

The genus is also represented in the Late Ordovician low latitude areas of Anticosti Island (Canada) by the species *Tylotopalla heterobrachiifera* nomen nudum. This species appears at the Vauréal–Ellis Bay transition (Delabroye et al., 2011a) of Katian–Hirnantian age.

Based on the comparison of palynological data from Canada (Anticosti), Estonia and Gondwana Delabroye et al. (2011b) recognized two Late Ordovician palaeophytoprovinces: the Baltic/Laurentian and the Gondwanan one. The Gondwanan palaeophytoprovince includes high latitude Gondwanan and peri-Gondwanan assemblages characterized by the presence of e.g. *Tylotopalla caelamenicutis*, *Neoveryhachium carminae* and *Neoveryhachium* sp. A in Molyneux, 1988. The presence of these species in the Caspalá Formation locates the Central Andean Basin, northwestern Argentina, in the Gondwanan palaeophytoprovince.

Domasia amphora and *Domasia trispinosa* were recovered from level 8822 (Fig. 2). They represent Silurian species stratigraphically ranging from the Aeronian (middle Llandovery) to the Wenlock–Ludlow. *Duvernaysphaera aranoides* (level 8822) first appears in successions of middle Llandovery and ranges to the Early Devonian (Rubinstein and García Muro, 2011 and references therein).

Dactylofusa maranhensis (level 8822) is a useful biostratigraphic and palaeogeographic marker. It exclusively occurs in Gondwanan and peri-Gondwanan areas (e.g. North Africa, Saudi Arabia, Jordan, Brazil, Argentina) ranging from the late Aeronian to the Ludlow (Le Hérisse et al., 2001; Rubinstein, 2005; García, 2014).

4.3. Miospores

Cryptospores recovered from the lower levels of the Caspalá Formation (8816, 8817 and 8818) are represented by permanent tetrads and dyads (see Appendix A). Moreover, spores physically separated from cryptospore polyads, laevigate and ornamented hilate spores, and trilete spores (see Appendix A) are present at levels 8817 and 8818. These glacial-related beds also contain chitinozoans dated as early Katian with strong evidences for reworking. Upward, the uppermost

Ordovician productive levels (8819 and 8820) yielded cryptospores less diverse than those of the lower levels. These levels also contain trilete spores represented by simple unornamented species with the addition of *Chelinospora* cf. *prisca* (see Appendix A), a new species described from the Katian of Saudi Arabia (Wellman et al., 2015). The abovementioned levels additionally yielded late Katian chitinozoan species.

The lower level of the Lipeón Formation (8822) yielded less diverse and abundant miospores than the Ordovician ones, while the uppermost level (8823) only contained very poorly preserved unidentifiable miospores. Cryptospores are represented by tetrads and dyads, and hilate and trilete spores by simple unornamented forms. Chitinozoans from this stratigraphic unit are dated as Telychian.

5. Discussion

The inception of trilete spores is the main subject to be discussed after this new finding in the Caspalá Formation.

The “glacial horizon” has been proved to be Hirnantian (Monaldi and Boso, 1987; de la Puente et al., 2012; de la Puente and Rubinstein, 2013b; de la Puente, 2014). It is represented within the Caspalá Formation in the studied area and correlated with other stratigraphic units in the Central Andean Basin (e.g. Zapla Formation).

In the present study, the first record of trilete spores occurs at the levels 8817 and 8818 where the early Katian chitinozoan species (*Belonechitina* gr. *micracantha*, *Belonechitina* cf. *robusta*, *Pistillachitina comma*) occur together with representatives of the acritarch genus *Neoveryhachium* and other reworked taxa. *Tylotopalla* cf. *caelamenicutis* first appears in level 8818. No definitive evidences of Hirnantian markers have been found in these levels. The chitinozoan association was most likely recycled during the Hirnantian glacial pulses observed in northern Gondwana localities (Paris et al., 2015 and references therein).

Cryptospores and trilete spores of these levels could have consequently been reworked as the other palynomorphs. If land-derived palynomorphs had also been reworked, the age of the spores would be early Katian or even older. If the miospores were in situ, they would be Hirnantian.

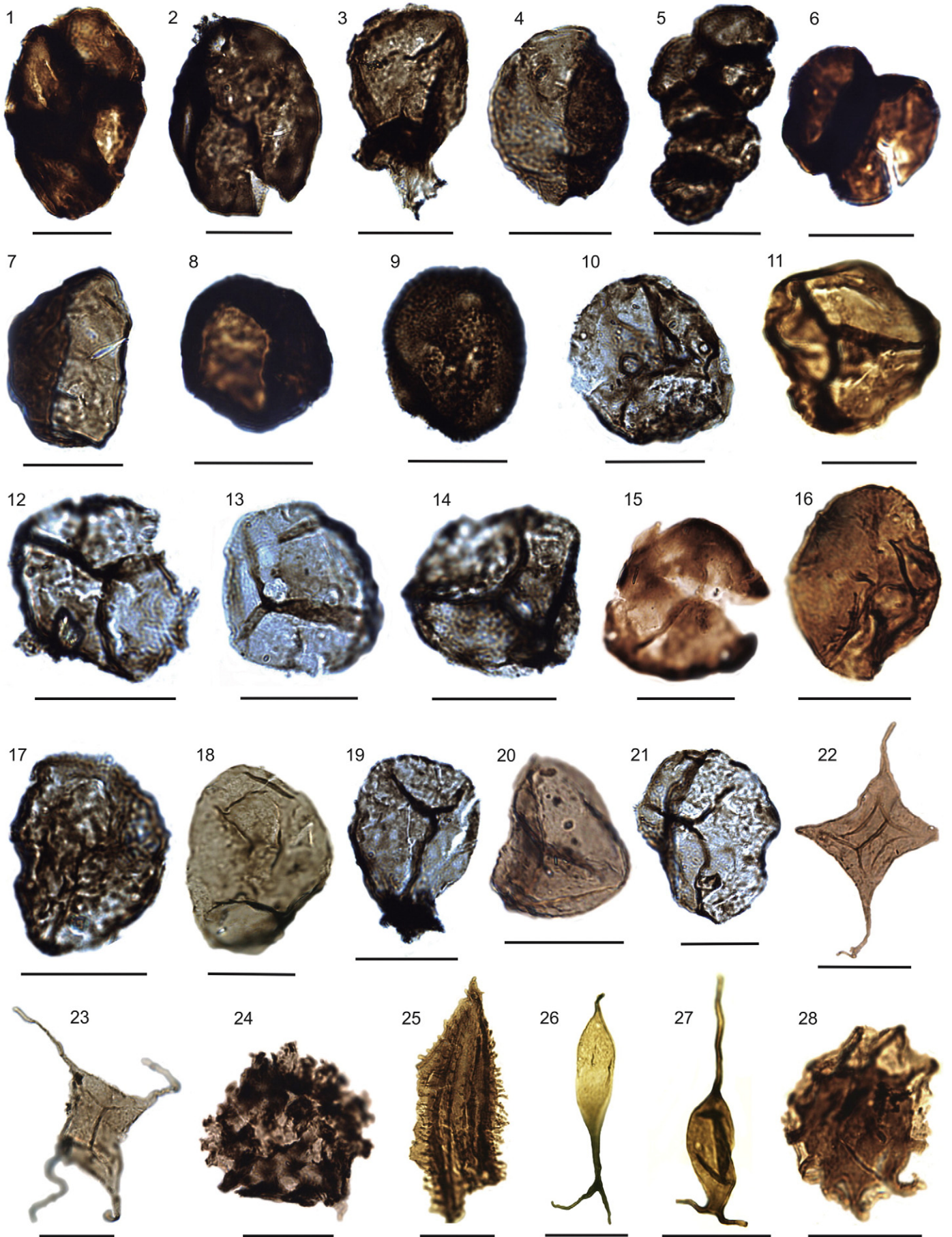
The subsequent level (8819) is characterized by reworked late Katian chitinozoan species (*Tanuchitina* cf. *fistulosa*, *Armoricochitina* sp. cf. *nigerica*) and the first appearance of *Chelinospora* cf. *prisca*, compatible with a late Katian age.

Hilate spores mainly represented by *Laevolancis divellomedium*, first occur at the same level as the trilete spores and range to the Telychian of the Lipeón Formation.

Summarizing, the hilate and trilete spores of the Caspalá Formation should have an age ranging from early–late Katian to Hirnantian.

If Katian, this miospore assemblage would be almost coeval with the oldest trilete spores known from Saudi Arabia, dated as middle–late Katian (Wellman et al., 2015). The assemblage presently studied is less diverse and presents less complex morphological features, probably indicating a more primitive degree of evolution.

Plate 2. Miospores and acritarchs of the Caspalá Formation (Late Ordovician) and the Lipeón Formation (early Silurian). The scale bars represent 20 µm. 1. Tetrade sp.; Caspalá Formation, 8818d, U30/2. 2. *Imperfectotriletes* (?*Ambitisporites*) *varvdovae* Steemans et al., 2000; Caspalá Formation, 8818a, O26/2. 3. *Imperfectotriletes* (?*Ambitisporites*) *varvdovae* Steemans et al., 2000; Caspalá Formation, 8817b, K26/2. 4. *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991; Caspalá Formation, 8817c, K38/1. 5. *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991; Caspalá Formation, 8818a, G30/1. 6. *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991; Caspalá Formation, 8818a, Q33/4. 7. *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991; Caspalá Formation, 8819a, C40/2. 8. *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991; Lipeón Formation, 8822b, M35/4. 9. *Chelinohilates* cf. sp. A in Wellman et al., 2015; Caspalá Formation, 8818c, T35/2. 10. *Ambitisporites avitus* Hoffmeister, 1959 sensu Steemans et al., 1996; Caspalá Formation, 8817c, O24/4. 11. *Ambitisporites avitus* Hoffmeister, 1959 sensu Steemans et al., 1996; Caspalá Formation, 8818'b, T10/0. 13. *Ambitisporites avitus* Hoffmeister, 1959 sensu Steemans et al., 1996; Caspalá Formation, 8819a, T31/0. 14. *Ambitisporites avitus* Hoffmeister, 1959 sensu Steemans et al., 1996; Caspalá Formation, 8820d, T30/0. 15. *Ambitisporites avitus* Hoffmeister, 1959 sensu Steemans et al., 1996; Lipeón Formation, 8822b, V39/0. 16. *Aneurospora*? sp.; Caspalá Formation, 8818c, P35/4. 17. *Chelinospora* cf. *prisca* Wellman et al., 2015; Caspalá Formation, 8819a, H28/0. 18. *Leiotriletes* sp.; Caspalá Formation, 8819a, R23/2. 19. *Leiotriletes* sp.; Caspalá Formation, 8820d, H40/0. 20. *Leiotriletes* sp.; Lipeón Formation, 8822b, E30/3. 21. *Leiotriletes* sp.; Caspalá Formation, 8817a, S28/3. 22. *Neoveryhachium carminae* (Cramer, 1964) Cramer, 1970; Caspalá Formation, 8817b, Q42/3. 23. *Neoveryhachium* sp. A in Molyneux, 1988; Caspalá Formation, 8818c, F38/0. 24. *Tylotopalla* cf. *caelamenicutis* Loeblich, 1970; Caspalá Formation, 8820a, O33/2. 25. *Dactylofusa maranhensis* Brito and Santos, 1965; Lipeón Formation, 8822a, H32/4. 26. *Domasia amphora* Martin, 1969; Lipeón Formation, 8822a, H24/0. 27. *Domasia trispinosa* Downie, 1960; Lipeón Formation, 8822a, R40/2. 28. *Duvernaysphaera aranoides* (Cramer) Cramer and Díez, 1972; Lipeón Formation, 8822a, M32/0.



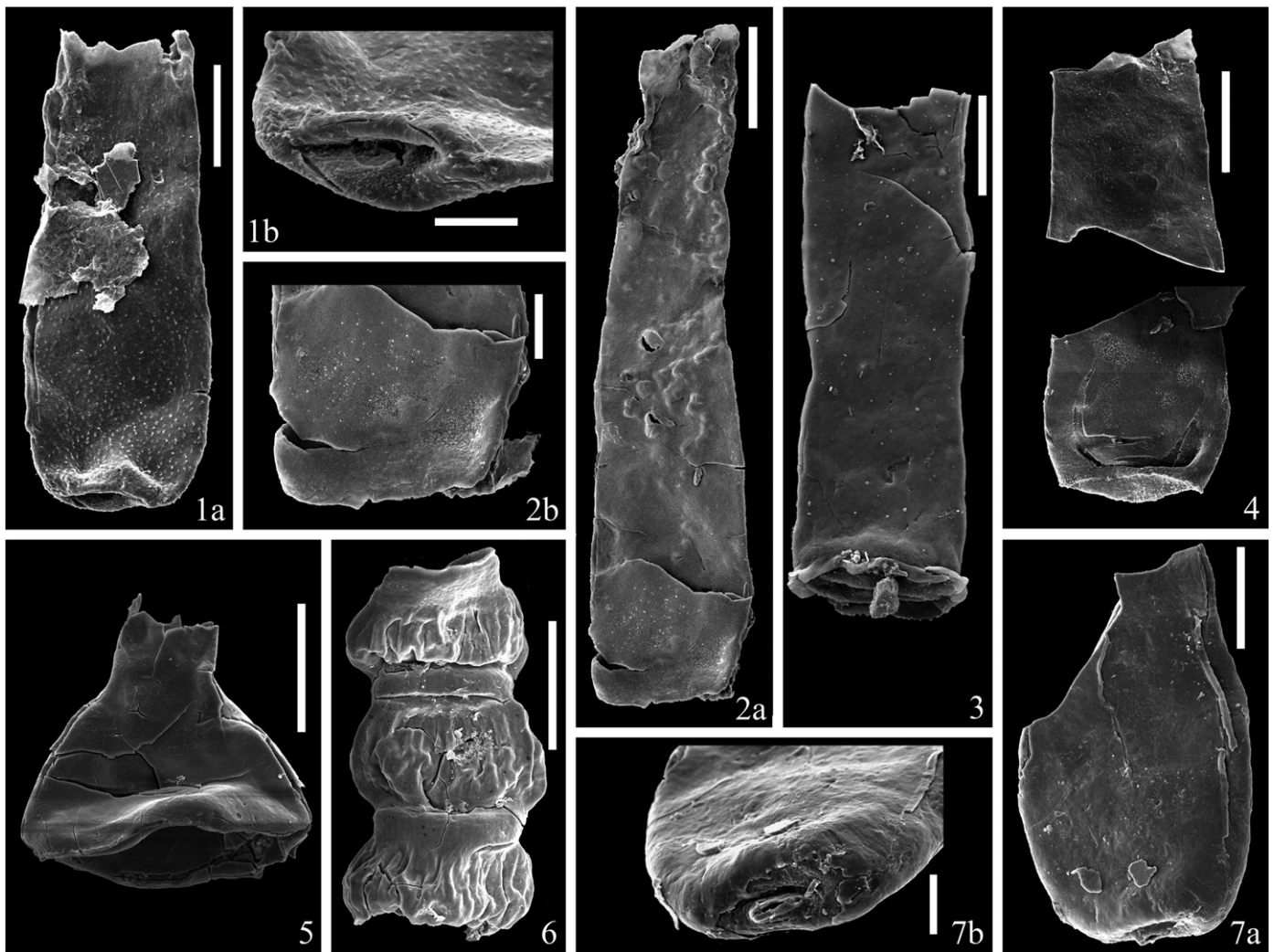


Plate 3. Late Ordovician chitinozoans from the Caspalá Formation (1–4) and early Silurian chitinozoans from the Lipeón Formation (5–7) of the Caspalá area in northwestern Argentina. Scale bars 50 μm for 1a, 2a, 3–7a; 20 μm for details 1b, 2b and 7b. 1a–b. *Belonechitina* cf. *robusta* (Eisenack, 1959). Sample 8819; 1b. Detail of the base of 1a. 2a–b. *Pistillachitina* *comma* (Eisenack, 1959). Sample 8819; 2b. Detail of 2a showing the spine ornamentation developed on the base. 3. *Tanuchitina* cf. *fistulosa* (Taugourdeau and de Jekhowsky, 1960). Sample 8820. 4. *Armoricochitina* sp. cf. *nigerica* (Bouché, 1965). Sample 8819. Specimen broken; the pieces are shown with opposite views. The bottom piece has been flipped (length of the chamber is approx. 155 μm). 5. *Cyathochitina* gr. *caputoi* Da Costa, 1971. Sample 8822. 6. *Calpichitina* cf. *densa* (Eisenack, 1962). Sample 8822. 7a–b. *Conochitina* cf. *proboscifera* Eisenack, 1937. Sample 8822; 7b. Detail of the base of 7a.

The Central Andean Basin had a complex evolutionary history as foreland basin during the early–middle Palaeozoic with an active subduction zone to the west (Astini, 2008; de la Puente and Rubinstein, 2013b; Rubinstein and García Muro, 2013) which was probably inducing unfavorable palaeoenvironmental conditions for the development of land vegetation.

The transgressive Telychian deposits of the Lipeón Formation show a notable decrease in abundance and diversity of terrestrial palynomorphs in agreement with adverse palaeoenvironmental conditions established at the end of the glaciation (Stee mans, 1999; Stee mans et al., 2010). According to Stee mans et al. (2010), the Aeronian is characterized by a high rate of miospore extinctions and, during the Aeronian and Telychian, their diversity curve reaches a minimum.

Remarkably, the trilete spores of the Lipeón Formation in the Caspalá area constitute the first record of Llandovery trilete spores in Argentina.

Stee mans et al. (2010) postulated that the invasion of land by plants is related to the palaeogeography. They considered that the migration and collision of palaeoplates, in addition to oceans probably not sufficiently large to constitute barriers for the dispersion of spores, allowed

the colonization of continents by vegetation. As explained by these authors, land plants first evolved on the Gondwana plate and subsequently colonized Avalonia. Afterwards, colonization progressed toward Laurentia and Baltica, when in close proximity (Ashgill–Llandovery).

Under the light of current worldwide data exposed above, together with data from the Argentine Central Andean Basin, the origin and radiation of embryophytes and earliest vascular land plants based on the cryptospore and hilate/trilate spore records should be reevaluated.

The Dapingian cryptospore assemblage from the Sierras Subandinas (Central Andean Basin) represents the earliest unequivocal fossil evidence of the presence of plants on emerged lands (Rubinstein et al., 2010).

The oldest trilete spores record in South America, representing the advent of vascular plants in the region, is described herein. This trilete spore assemblage, dated as possible early to late Katian or Hirnantian, could be more or less coeval in age with the current world's oldest one from Saudi Arabia (Stee mans et al., 2009; Wellman et al., 2015).

Before the present study, the oldest trilete spores of South America were recorded from the Aeronian of Brazil and Paraguay (Stemans et al., 2010).

Under the current state of knowledge, there is no doubt that land plants originated and first evolved on the Gondwana continent. The cryptospore advent seems to have occurred in the western margin of west Gondwana (Argentina) and the origin of hilate and trilete spore plant-producers could have occurred in the eastern part of west Gondwana (Wellman et al., 2015) or, perhaps, in Argentina, in the same region where embryophytes originated (Rubinstein et al., 2010).

If the Argentine trilete spores were considered Hirnantian, they would have appeared almost at the same time than the trilete spores in Turkey and Algeria, though being more complexly ornamented than Turkish and Algerian forms.

The earliest vascular plants seemed to have emerged at high to middle latitudes in Gondwanan and peri Gondwanan areas (Saudi Arabia, Argentina, Turkey and Algeria) under cold climatic conditions (see Fig. 12, in Torsvik and Cocks, 2013b). Likewise, such Gondwanan and peri Gondwanan affinities have been also demonstrated by chitinozoans and acritarchs that accompanied the trilete spores in the bearing marine deposits.

6. Conclusions

The Ordovician/Silurian boundary in the Caspalá area of the Cordillera Oriental, northwestern Argentina, is represented by the Hirnantian glacial-related deposits of the Caspalá Formation and the overlying transgressive early Silurian (Telychian) deposits of the Lipeón Formation.

Palynomorph assemblages across the transition are mainly marine, exhibiting a clear predominance of chitinozoans and organic-walled phytoplankton (acritarchs).

Land-derived palynomorphs of the cryptospore group are present in all the productive levels. However, hilate and trilete spores do not occur in the lowermost studied level.

The Late Ordovician cryptospore assemblage is fairly diverse while Late Ordovician trilete spores are low in both abundance and diversity. However, there are ornamented spores among them, which is uncommon for primitive trilete spores.

The recovered trilete spores of the Caspalá Formation constitute their oldest record in South America. Their age is considered to be Hirnantian.

The Lipeón Formation in the studied locality yielded trilete spores dated as Telychian, therefore revealing the earliest evidence of Silurian vascular plants of Argentina. The low diversity and abundance of miospores are in agreement with the disappearance of terrestrial ecosystems due to the global transgression after the melting of the Hirnantian glaciers.

The new miospore data, particularly those related to the incoming and evolution of hilate and trilete spores, question previous palaeogeographic and palaeoclimatic proposed models for the origin and adaptive radiation of vascular land plants.

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Appendix A. Annotated list of miospores

Cryptospore dyads

Dyadospora murusdensa Strother and Traverse, 1979 (Plate 1, 2)

Segestrespora laevigata Burgess, 1991 (Plate 1, 3, 4)

Segestrespora sp. (Plate 1, 5)

Remarks: The dyad is enclosed in an envelope but, due to poor preservation, it is not possible to determine if the envelope is laevigate or ornamented.

Segestrespora? sp. (Plate 1, 6)

Remarks: The specimen is tentatively assigned to this genus because the characteristic envelope of the dyad is not clearly observed due to its bad preservation.

Pseudodyadospora petasus Wellman and Richardson, 1993 (Plate 1, 7, 8)

Remarks: *Pseudodyadospora petasus?* (Plate 1, 9) seems to be a torn fused dyad, preserved in a roughly equatorial view showing an equatorial constriction and spores with invaginated distal wall.

Cryptospore tetrads

Cheilotetras caledonica Wellman and Richardson, 1993 (Plate 1, 10)

Rimosotetras problematica Burgess, 1991 (Plate 1, 11)

Rimosotetras cf. *subspaebrica* Strother et al., 2015 (Plate 1, 12)

Remarks: The single specimen is a tetrad with the spore member's outline more sub-circular than sub-triangular. Admittedly, the shape is strongly conditioned by preservation.

Tetraedraletes grayae Strother, 1991 (Plate 1, 13, 14)

Tetraedraletes medinensis Strother and Traverse, 1979 (Plate 1, 15–17)

Tetraplanarisporites sp. (Plate 1, 18)

Remarks: The single specimen is a planar fused tetrad with a cross-tetrad configuration. This allows the unquestionable assignment to the new erected genus *Tetraplanarisporites* Wellman et al., 2015

Velatitetras cf. *laevigata* Burgess, 1991 (Plate 1, 19)

Remarks: The poor preservation of the single specimen recorded inhibits the confident assignment to the species.

Velatitetras retimembrana (Miller and Eames) Wellman and Richardson, 1996 (Plate 1, 20)

Velatitetras rugosa (Strother and Traverse) Stemans et al., 1996 (Plate 1, 21)

Remarks: The specimen figured in Plate 1, 22 is questionably assigned to *Velatitetras rugosa* as it is unclear whether the permanent tetrad is enclosed in a closely-adpressed rugulate envelope.

Velatitetras sp. A (Plate 1, 23)

Remarks: Permanent tetrahedral tetrad enclosed within a loosely envelope ornamented with spinae. The spore member's outline is sub-circular and it is unclear whether they are laevigate or ornamented. The ornamentation of the envelope differentiates this specimen from other species of this genus.

Ornamented tetrad (Plate 1, 24)

Remarks: Tetrad of closely adherent spores densely ornamented with coarse, biform elements.

Tetrad spp. (Plate 1, 25; Plate 2, 1)

Remarks: Poorly preserved, loosely to tightly attached tetrads, laevigate or ornamented, naked or with some possible remains of a lost envelope.

Spores physically separated from cryptospore polyads

Imperfectotriletes (?*Ambitisporites*) *varvdovae* Stemans et al., 2000 (Plate 2, 3)

Remarks: Laevigate monads, sub-circular to sub-triangular in outline, equatorially thickened, with the proximal face displaying irregular trilete splits. These spores are similar to *Ambitisporites*; however, they are considered cryptospores because they are physically and not naturally separated from polyads and have no true trilete marks.

Hilate cryptospores

Laevolancis divellomedium (Chibrikova) Burgess and Richardson, 1991 (Plate 2, 4–8)

Remarks: The laevigate hilate cryptospores of this study are preserved in loosely attached dyads (Plate 2, 5, 6) or dissociated in monads (Plate 2, 4, 7, 8). All of them have an equatorially and distally thickened wall surrounding the hilum.

Chelinohilates cf. sp. A in Wellman et al., 2015 (Plate 2, 9)

Remarks: The only present specimen is similar to *Chelinohilates* sp. A, described by Wellman et al. (2015), in dimensions and ornamentation outside the hilum. However, poor preservation inhibits a positive assignment.

Trilete spores

Ambitisporites avitus Hoffmeister, 1959 sensu Steemans et al., 1996 (Plate 2, 10–15)

Aneurospora? sp. (Plate 2, 16)

Remarks: Trilete spore with sub-triangular amb and distal and equatorial areas covered by small conical spines, less than 1 µm in height. The equatorial thickening of the single specimen is unclear; therefore, attribution to the genus *Aneurospora* is questionable.

Chelinospira cf. *prisca* Wellman et al., 2015 (Plate 2, 17)

Remarks: Trilete spore, distal face ornamented with dense and low convolute muri. Even though this single specimen has the dimensions and characteristic features of *Chelinospira prisca*, the state of preservation does not permit an undoubtedly assignment to this species.

Leiotriletes spp. (Plate 2, 18–21)

Remarks: Spores sub-triangular in outline, laevigate, with trilete marks of different extensions, simple or accompanied by thin lips, extending to the margin or close to the margin. No equatorial thickening has been observed.

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