Geol. Mag.: page 1 of 19 © *Cambridge University Press 2013*
doi:10.1017/S0016756813000393

Upper Silurian miospores from the Precordillera Basin, Argentina: biostratigraphic, palaeonvironmental and palaeogeographic implications

V. J. GARCÍA MURO*†, C. V. RUBINSTEIN* & P. STEEMANS‡

*IANIGLA-CCT CONICET-Mendoza, C.C. 131, 5500 Mendoza, Argentina
‡Palaeogeobiology – Palaeobotany – Palaeopalynology, Allée du 6 Août, Bât. B-18, parking 40, University of Liège, B-4000 Liège 1, Belgium

---

(*Received* 10 January 2013; *accepted* 2 May 2013)

Abstract – This study is concentrated on Ludlow (to Pridoli?) miospores from the Los Espejos Formation at the Quebrada Ancha locality, Central Precordillera, San Juan Province, Argentina. The Ludlow age is in agreement with the age based on acritarchs. The assemblage of continental palynomorphs is composed of 43 miospore species (29 trilete spores and 14 cryptospores). A new synonymy is proposed: *Chelinospora poecilomorpha* is here considered a junior synonym of *Clivosispora verrucata*. In addition, specimens belonging to *C. verrucata* var. *verrucata* and *C. verrucata* var. *convoluta* are included in a new morphon. This study represents the second Late Silurian miospore assemblage described from South America; the first was from the Urubu River, Amazon Basin, northern Brazil. The Quebrada Ancha assemblages allow a reasonably good correlation with biozones established for the Upper Silurian from the Cantabrian Mountains, northern Spain. The dendrogram analysis between coeval miospore assemblages from different localities shows a strong palaeogeographic affinity with the miospores recovered from northern Brazil and North Africa. Miospore assemblages from Spain show influences from Baltica and North Africa, demonstrating their intermediate position between these two continental plates. Conversely, dissimilarities recognized between Libya and Tunisia are most probably owing to local ecology and/or environmental conditions.

Keywords: trilete spores, cryptospores, taxonomy, Palaeozoic, palynostratigraphy, palaeobiogeography, palaeoenvironments

1. Introduction

Silurian deposits of the Central Precordillera Basin, in San Juan Province, Argentina, comprise the La Chilca and the Los Espejos formations, which combined constitute the Tucunuco Group. Beginning in the Hirnantian (uppermost Ordovician), the Tucunuco Group encompasses the entire Silurian, culminating at its top in the Ludow, Pridoli and even lowest Devonian (Lochkovian) at the northern outcrops.

These deposits have been intensely studied with various geologic disciplines, such us geodynamics, tectonics, sequence stratigraphy, facies analysis and palaeontology, in order to understand the evolution of the basin (i.e. Cuerda, 1969; Hünicken & Sarmiento, 1988; Sánchez, Waisfeld & Benedetto, 1991; Benedetto *et al.* 1992; Astini, Benedetto & Vaccari, 1995; Astini & Mareto, 1996; Rickards *et al.* 1996; Albanesi, Ortega & Hünicken, 2006).

Even though the Silurian of the Precordillera has yielded a very rich and diverse invertebrate fauna, including brachiopods, trilobites, bivalves and gastropods among others, fossils of recognized stratigraphic value, i.e. graptolites and conodonts, are sparse, particularly in the Upper Silurian strata.

Traditionally, the La Chilca Formation has been interpreted as Hirnantian–Llandovery in age and the overlying Los Espejos Formation probably as old as Wenlock to locally as young as Lochkovian. The age of the Los Espejos Formation is based mainly on correlation with known brachiopod faunas. However, the scarcity of biostratigraphic index fossils in the upper stratigraphic unit hinders accurate age determination, particularly for its contacts with the underlying La Chilca Formation and the overlying Talacasto Formation.

Palynological studies, mainly those concerning marine organic-walled phytoplankton, shed light on the age of this unit, thus allowing the interpretation of an age not older than Ludlow for the base of the Los Espejos Formation in different sections (Rubinstein & García Muro, 2011). These palynomorphs, however, did not confirm the Pridoli and Lochkovian ages for the uppermost part of the Los Espejos Formation (Rubinstein, 2001; Rubinstein & García Muro, 2011, 2013). Therefore, palynological data indicates a Late Silurian age for the formation.

The organic-walled phytoplankton assemblages from the Los Espejos Formation are abundant and diverse; terrestrial palynomorphs are, in comparison, subordinate (Rubinstein & García Muro, 2011) through all the Los Espejos Formation, in the studied sections.

---

†Author for correspondence: vgarcia@mendoza-conicet.gob.ar

Local exceptions occur in levels close to the upper boundary of the unit.

The occurrence of trilete spores in the Los Espejos Formation was first mentioned by Pöthe de Baldis (1981). She documented four species from the basal portion of the Los Azulejitos Section. Later, Rubinstein (1992) recorded trilete spores from the middle and upper parts of the Los Espejos Formation in the Las Aguaditas and Loma de Los Piojos sections (Rubinstein, 1995), with fewer than ten identified species.

The incorporation of detailed palynological studies from more sections of the Los Espejos Formation allows us to recognize the presence of miospore assemblages (trilete spores and cryptospores) in almost all of them, from the base to the top, with varying abundances, diversity and quality of preservation (Rubinstein, Le Hérissé & Steemans, 1996; Rubinstein & Brussa, 1999; Rubinstein, García Muro & Steemans, 2010, 2011; Rubinstein & García Muro, 2011, 2013).

Recent studies expanded our knowledge of the Los Espejos miospore assemblages by recording many taxa from levels corresponding to the lower, middle and upper parts of the unit at the Quebrada Ancha, Cerro La Chilca, Río Jáchal and Río de Las Chacritas sections. To date, only the palynomorphs of the Río de Las Chacritas section have been illustrated and analysed in detail (Rubinstein & García Muro, 2011). The most significant miospore assemblage owing to its diversity, abundance and preservation comes from the Quebrada Ancha area, near the Talacasto locality (Fig. 1). Therefore, the goal of this contribution is to evaluate the cryptospores and trilete spores coming from 14 productive levels from the Quebrada Ancha area, including a taxonomic reappraisal, evolution of the diversity and correlation with coeval microfloras worldwide as well as their biostratigraphic, palaeoenvironmental and palaeogeographic significance.

2. Geology and palaeontology

The evolution of the Siluro-Devonian Argentinean Precordillera Basin differs from other South American basins because it was affected by accretion of the Cuyania terrane with the Gondwana margin during the Mid–Late Ordovician (Benedetto, 2010). One of the main consequences of the collision was development of a flexural bending forming the Talacasto–Tambolar arch in the Central Precordillera (Astini, Benedetto & Vaccari, 1995), which underwent recurring relaxation and contraction events. Towards this arch, stratigraphic units become wedged and important interruptions of sedimentation occur. Therefore, the Siluro-Devonian succession of the Precordillera constitutes a typical foreland deposit, with a sequence stratigraphic arrangement interpreted as a consequence of lithosphere rheology and eustasy (Astini, Benedetto & Vaccari, 1995).

In the Precordillera Basin, the Silurian siliciclastic shelf consists of storm-dominated shallow-marine deposits, composed mainly of intercalated pelites and sandstones. The La Chilca and the Los Espejos formations both show evidence of a transgressive to sea-level highstand history. This interpretation is based on the presence of a thin ferruginous oolite layer and phosphate-rich chert conglomerates at the two units' bases, succeeded by shaly intervals with a gradual

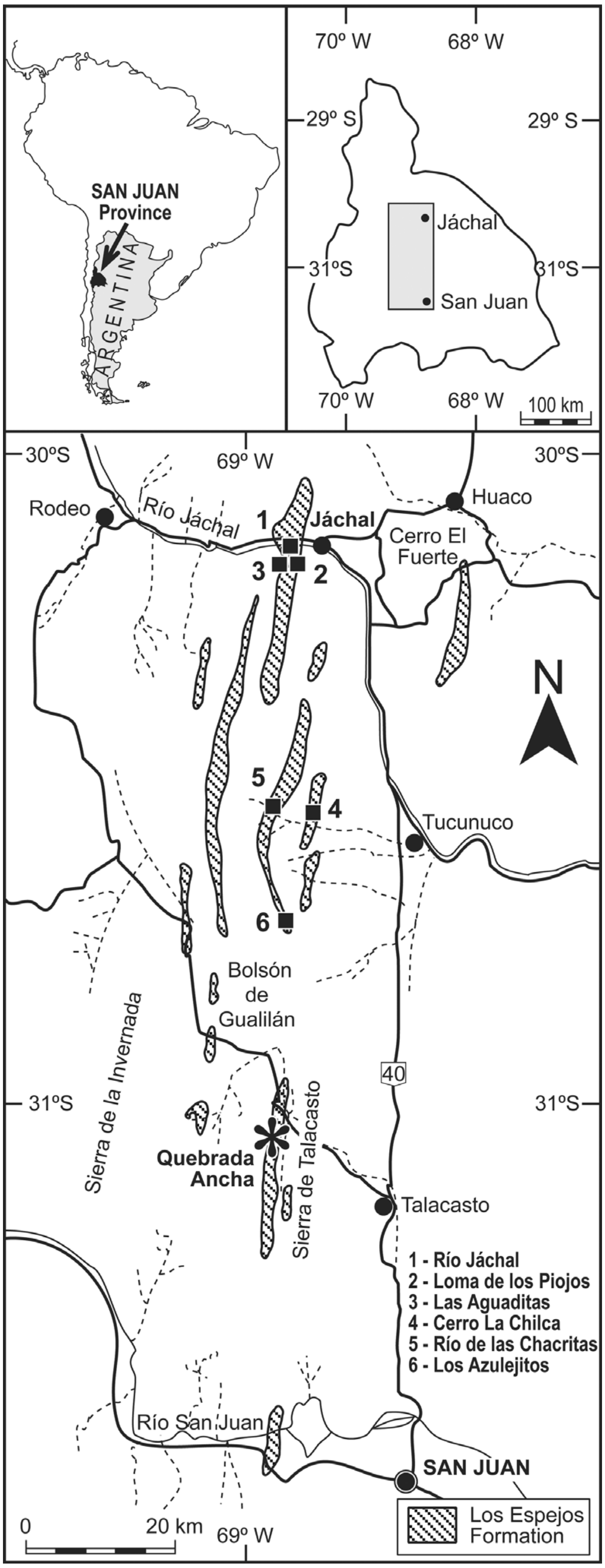

Figure 1. Location map of the Silurian Precordillera Basin showing the miospore assemblage localities sampled by the authors. The black asterisk indicates the section reported on here.

upward thickening and coarsening. Shaly-predominant sediments of the lower part of the Los Espejos Formation represent a low-energy open shelf environment, followed towards the top by an increasing amount of sandstone beds, representing storm-dominated shelf and shoreface environments. Shell-bearing storm beds tend to dominate from the middle to the upper part of the unit. The upper third of the Los Espejos Formation shows evidence of subaerial exposures at the top of the regression cycles. The internal cyclic stacking patterns are considered to have been generated by forced regressions (Sanchez, Waisfeld & Benedetto, 1991; Astini & Mareto, 1996).

The age of the Los Espejos Formation is mainly based on brachiopod faunas (Benedetto *et al.* 1992). Four faunas were assigned to the Wenlock?, Ludlow and Pridoli, and the younger one, at the top of the unit next to Jáchal (Fig. 1), to the early Lochkovian. Graptolite and conodont records are limited and they do not further constrain the overall age of the formation. Graptolites such as *Monograptus uncinatus notouncinatus* Cuerda, *Monograptus leintwardensis* var. *incipiens* Elles & Wood and *Monograptus argentinus* Cuerda have been identified near the middle part of the unit, allowing the Los Espejos Formation to be assigned to the late Llandovery – early Wenlock to the early–mid Ludlow (Cuerda, 1969). Rickards *et al.* (1996) recorded graptolites from Cerro del Fuerte, near Jáchal (Fig. 1), corresponding to the *Neodiversograptus nilssoni – Lobograptus scanicus* zones in the upper third of the unit, which indicate an early Ludlow age. Hünicken & Sarmiento (1988) recorded conodonts of the upper part of the *Polygnathoides siluricus* Zone and the lower part of the *Pedavis latialata* Zone, in the middle to upper part of the Los Espejos Formation in the Quebrada Ancha area, suggesting an age not older than Ludfordian for these levels. On the other hand, Albanesi, Ortega & Hünicken (2006) documented the *Kockelella variabilis variabilis* Zone of early Ludlow (Gorstian) age in shell beds of the middle–upper part of the Los Espejos Formation in the same area. The latter authors considered that the species recorded by Hünicken & Sarmiento (1988) do not confirm the proposed age. According to Benedetto *et al.* (1992), the lower to middle part of the Los Espejos Formation, in the Quebrada Ancha area, cannot be dated by means of brachiopods, whereas the uppermost part of the unit contains *Coelospira extensa* Benedetto & Toro that indicates a Pridoli age (Fig. 2). Summarizing, the previously studied fauna does not provide a precise age for the lower part of the formation while the top could probably be as young as Pridoli. Meanwhile, palynological studies carried out from the Los Espejos Formation allow its age to be constrained to the Ludlow (Rubinstein, 2001; Rubinstein & García Muro, 2011, 2013).

In the Quebrada Ancha area, the Los Espejos Formation is partially exposed in different sections and reaches a total thickness of 235 m. In this contribution, two sections representing the lower and the uppermost parts of the stratigraphic unit (Fig. 2) have been sampled and are considered the most significant for constraining the age and recognizing the differences with the underlying Lower Silurian La Chilca Formation and the overlying Lower Devonian Talacasto Formation.

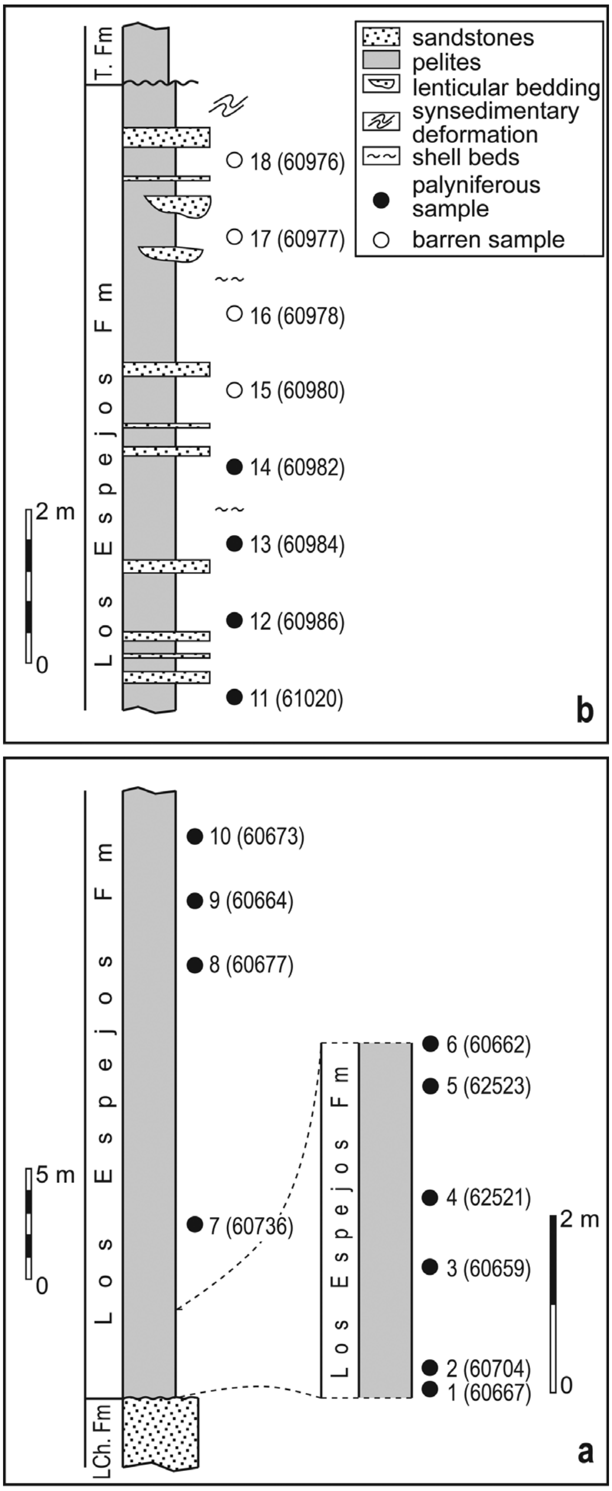

Figure 2. Stratigraphic sections of the studied of Los Espejos Formation in the Quebrada Ancha area. (a) Lower section. (b) Uppermost section. Location and identification numbers of palynological samples in both sections, and the position of the third faunal assemblage of Benedetto *et al.* (1992) – mainly represented by *Coelospira extensa* – are indicated.

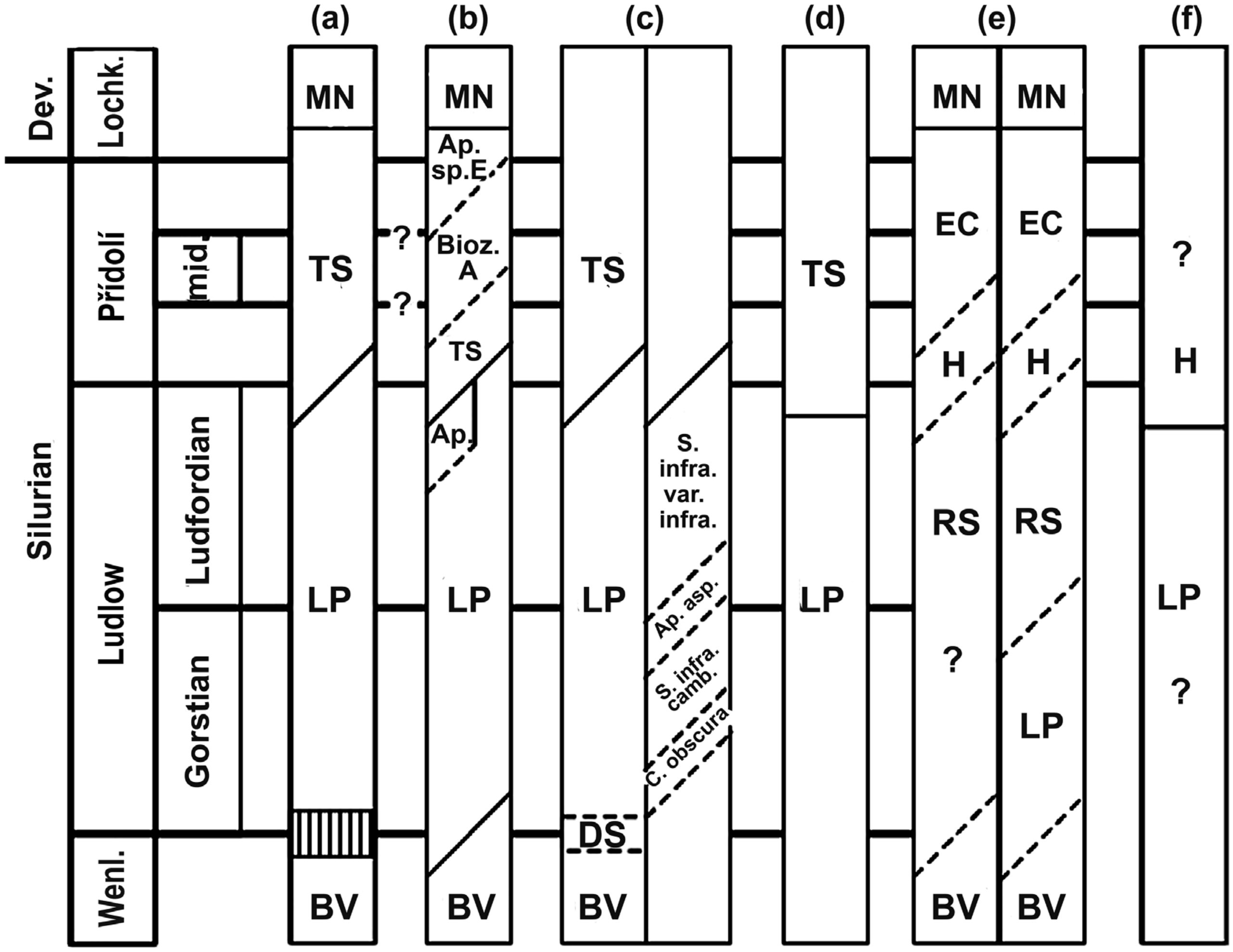

Figure 3. Miospore biostratigraphic zonal correlations in the Upper Silurian and the Lochkovian. (a) Richardson & McGregor (1986); (b) Richardson & Edwards (1989); (c) Burgess & Richardson (1995); (d) Rubinstein & Steemans (2002); (e) Richardson, Rodríguez & Sutherland (2001); (f) Hassan Kermandji (2007). Diagonal lines indicate boundaries revised herein. The exact position of biozones and sub-biozones and their correlation with series and stage boundaries remain doubtful because of the lack of reliable independent biostratigraphic control. BV – *brevicosta–verrucatus*; DS – *downiei–sagittarius*; LP – *libycus–poecilomorphus*; RS – *reticulata–sanpetrensis*; H – *hemiesferica*; TS – *tripapillatus–spicula*; EC – *elegans–cantabrica*; MN – *micrornatus–newportensis*.

The marine phytoplankton, including acritarchs and chlorophytes, is currently under investigation. Nevertheless, owing to the presence of taxa unknown below the Ludlow, from the lower levels of the Los Espejos Formation (i.e. *Fimbriaglomerella divisa* Loeblich & Drugg, 1968, *Ozotobrachion palidodigitatus* (Cramer) Playford, 1977 and *Stellinium rabians* (Cramer) Eisenack, Cramer & Díez, 1976) an age not older than Ludlow is interpreted for the unit. In the upper section, the diversity of the marine phytoplankton decreases significantly, and taxa considered indices of the Pridoli have not been recorded. Consequently, marine palynomorphs restrict the age to the Ludlow.

3. The miospore biostratigraphy of the Upper Silurian

Numerous studies on the stratigraphic distribution of miospores from the Upper Silurian and Siluro-Devonian boundary are available (Hassan Kermandji, 2007; Steemans, Rubinstein & Melo, 2008 and references therein; Spina & Vecoli, 2009 and references therein; Mehlqvist, Vajda & Steemans, 2012). Most of these are geographically concentrated on northwestern Gondwanan (North Africa) sections, with the remaining few from Euramerica. Among them, there are few sections complete enough to allow the creation of biozonations. Attempts have been made in combining data from Euramerica and Gondwana (Richardson & McGregor, 1986; Richardson & Edwards, 1989), or on Euramerican samples from the UK (Burgess & Richardson, 1995), on material from the Peri-Gondwanan terrane of Spain (Richardson, Rodríguez & Sutherland, 2001), or on Libyan (Rubinstein & Steemans, 2002) and Algerian (Hassan Kermandji, 2007) miospore assemblages from northwestern Gondwana (Fig. 3). The application of these biostratigraphic zonations to new studies remains somewhat problematic because of the lack of independent biostratigraphic control and differences in the composition of the assemblages depending on palaeogeography.

The boundary between the cf. *protophanus–verrucatus* Zone (*brevicosta–verrucatus* in Burgess & Richardson, 1995) and the *libycus–poecilomorphus* (LP) Zone (Richardson & McGregor, 1986) was interpreted to correspond, more or less, with the base of the Ludlow in Libya (Richardson & Ioannides, 1973). However, unequivocal evidence to confirm this correlation is unavailable. Burgess & Richardson (1995) clearly put the base of the LP Biozone in the lower part of the Gorstian in Wales, somewhere between the uppermost *nilssoni* and the lowermost *incipiens* graptolite zones, i.e. somewhere in the lower part of the Gorstian. Contrary to the biostratigraphic zonations established in Libya, the *brevicosta–verrucatus* (BV) Zone is not directly overlain by the LP Zone in Wales but by a new biozone defined by Burgess & Richardson (1995), the *downiei–sagittarius* (DS) Zone, and above the LP Zone. The base of this zone is correlated with the latest *ludensi*s or the early *nilssoni* zones (i.e. latest Homerian or earliest Gorstian). Burgess & Richardson (1995) noted that the DS Zone is only found in approximately 20 m of strata from the Rumney Borehole, and in North Africa there is a sampling gap of over 100 m at the critical part of the sequence.

The upper part of the LP Zone has been subdivided into an *Apiculiretusispora* spp. Subzone by Richardson & Edwards (1989). The LP Zone has also been subdivided into four Subzones by Burgess & Richardson (1995): *C. obscura*, *S. inframurinata* var. *cambrensis*, *A. asperata* and *S. inframurinata* var. *inframurinata* subzones. Independent biostratigraphic control is too imprecise to clearly correlate the Gostian–Ludfordian boundary with this miospore stratigraphic zonation, which probably lies in between the base of the *S. inframurinata* var. *cambrensis* and *S. inframurinata* var. *inframurinata* subzones.

In Libya, the LP Zone is overlain by the *tripapillatus–spicula* (TS) Zone (Richardson & McGregor, 1986). In the UK, its base is immediately above the Ludlow Bone Bed (Richardson & Lister, 1969). The age of its base is thought to correspond to the Ludlow–Pridoli boundary and its top spans the Pridoli–Lochkovian boundary. However, the exact position of the base of the Pridoli in Britain cannot be confidently established. Conodont evidence from the Whitcliffe Formation in the UK suggests that the base of the Pridoli may be slightly higher than the base of the Downton Castle Sandstone Formation represented at its base by the Ludlow Bone Bed (Aldridge & Schönlaub, 1989; Miller, 1995). This is confirmed by independent dating based on chitinozoans (Jaglin & Paris, 2002) from Libya where a miospore assemblage correlated with the TS Zone is attributed to the latest Ludlow (Rubinstein & Steemans, 2002).

In Spain, Richardson, Rodríguez & Sutherland (2001) correlated the top of the LP Zone with the base of the overlying *reticulata–sanpetrensis* (RS) Zone in the Geras and the Argovejo outcrops. But they also correlated the top of the BV Zone with the base of the RS Zone in the La Peral outcrop creating a confusing stratigraphic correlation since the BV Zone had been defined as underlying the LP Zone in Richardson & McGregor (1986) and in Burgess & Richardson (1995). Richardson, Rodríguez & Sutherland (2001) considered that at least part of the RS Zone is of late Ludfordian age. The base of the overlying H Zone is observed above the first incoming of *Ramochitina villosa* Laufeld, 1974 in the Geras outcrop, a chitinozoan appearing close to the Gorstian–Ludfordian boundary (Nestor, 2009), and in the four outcrops studied in Spain below the first incoming of typical Pridoli chitinozoans such as *Urnochitina urna* Eisenack, 1934 (figs 10–13 in Richardson, Rodríguez & Sutherland, 2001). Thus, the latter authors believe that the base of the H Zone is Pridoli in age because the chitinozoans observed below the first incoming of *U. urna* may span the Pridoli. However, contrary to Richardson, Rodríguez & Sutherland (2001), we consider that a Ludfordian age cannot be excluded. The boundary between the H and the *elegans–cantabrica* (EC) zones is present in the four outcrops above the appearance of *U. urna* and in the La Vid section below the first incoming of *Margachitina elegans* Taugourdeau & de Jekhowski, 1960, which is characteristic of the mid Pridoli. The base of the *Aneurospora* Subzone in the upper part of the EC Zone is observed in layers containing *M. elegans*. Therefore, a mid Pridoli age cannot be excluded for its lower boundary. The *micrornatus–newportensis* (MN) Zone is observed in the lowermost Lochkovian characterized by *Eisenackitina bohemica* Eisenack, 1934. The base of the Devonian is around 30 m below the contact of the San Pedro and La Vid formations in the Argovejo outcrop. Priewalder (1997) considered that the presence of *M. elegans*, 10 m below the top of the San Pedro Formation in the La Vid outcrop (data from Cramer, 1967), constrained the age of the chitinozoan-bearing levels to be mid Pridoli, thus concluding that the San Pedro Formation does not extend into the Lochkovian. This result seems to be in contradiction with the one from Richardson, Rodríguez & Sutherland (2001), but perhaps there is a hiatus in the La Vid outcrop or the formation is diachronous. More analyses are required to solve this apparent contradiction. In their conclusions, Richardson, Rodríguez & Sutherland (2001) pointed out that there are some discrepancies between the age provided by the chitinozoans and those based on miospores. It must be remembered that miospores are absent, or of poor utility, in the Silurian stratotypes, which are marine. Therefore, miospore biozones should be calibrated with marine fossils present in the stratotypes, like chitinozoans. Hence, we cannot exclude an older age for the boundaries of the different biozones than those provided by Richardson, Rodríguez & Sutherland (2001).

The *sanpetrensis–triangulatus* is a spore zone established for the Ludlow by Hassan Kermandji (2007) in Algeria. This biozone is overlain by the H Zone of Richardson, Rodríguez & Sutherland (2001) and by a newly created *radiate–synorea* Zone. No independent age control is available to date these Algerian miospore biozones.

In the UK and other areas of the Euramerican continent, the MN Zone overlays the TS Zone in the lowermost Lochkovian (Richardson & McGregor, 1986; Steemans, 1989; Streel *et al.* 1987). Richardson & Edwards (1989) have created, intermediate between the TS and the MN zones, a Zone A and an *Apiculiretusispora* sp. E Zone separated by a 'no records' interval (*in* Wellman & Richardson, 1996, text-fig. 7). Richardson, Rodríguez & Sutherland (2001) have defined in Spain a *newportensis–argovejae* (NA) Subzone in the lower part of the MN Zone characterized by the incoming of *Streelispora newportensis* and *Leonispora argovejae*, and the absence of *Emphanisporites micrornatus*. The MN Zone is well known on the Euramerican plate. It has also been observed on Peri-Gondwanan terranes, in Spain (Richardson, Rodríguez & Sutherland, 2001) and in Brittany (Steemans, 1989). Only one specimen of *Streelispora newportensis* has been identified in Gondwana, in Libya (Loboziak *et al.* 1992). The definition of the Siluro-Devonian boundary based upon miospore zones is therefore problematic on this palaeocontinent.

4. Preparation and techniques

Eighteen samples were collected from two sections in the Quebrada Ancha area (Fig. 2a, b), representing the lower part (ten samples) and the uppermost part (eight samples) of the Los Espejos Formation. Fourteen samples were productive while the four samples closest to the upper boundary were barren.

The samples were processed in the University of Liège palynology laboratory (Belgium), using standard HCl–HF–HCl acid maceration techniques. The residues were oxidized with a Schulze solution (HNO_3+KClO_3) and then screened on a 12 μm sieve.

Miospore assemblages from different palaeogeographies were compared to the Quebrada Ancha assemblage through a cluster analysis, using Infostat 2009®.

The palynological slides are housed in the palynological collection of the IANIGLA, CCT CONICET Mendoza, Argentina. Specimen locations in the slides are located by England Finder coordinates.

5. Palynology

The miospore assemblage consists of 43 miospore species (29 trilete spores and 14 cryptospores). The lower part of the Los Espejos Formation is richer in trilete spore species (25 species) compared with the upper part (14 species), while cryptospore diversity undergoes a smaller decrease from 12 to 9 species (Fig. 4).

5.a. Cryptospores

Artemopyra urubuense Steemans, Rubinstein & Melo, 2008
Figure 5a

Remarks. This spore is known only from Gondwana. The other two localities where this species has been identified are from the Ludlow of Libya (Richardson & Ioannides, 1973) and from the lower Pridoli of Brazil (Steemans, Rubinstein & Melo, 2008).

Chelinohilates lornensis Wellman & Richardson, 1996
Figure 5b

Dyadospora murusattenuata/murusdensa morphon Steemans, Le Hérissé & Bozdogan, 1996
Figure 5c

Gneudnaspora divellomedia var. *minor* (Chibrikova) Breuer *et al.* 2007
Figure 5d

Hispanaediscus lamontii Wellman, 1993
Figure 5e

Hispanaediscus verrucatus (Cramer) Burgess & Richardson, 1991
Figure 5g

Remarks. This is one of the eponymous species of the BV Zone, Wenlockian in age (Burgess & Richardson, 1995; Richardson & McGregor, 1986).

Hispanaediscus wenlockensis Burgess & Richardson, 1991
Figure 5f

Remarks. This species has been identified in the type Wenlock area, England (Burgess & Richardson, 1991) and could be reworked here.

Imperfectotriletes patinatus Steemans, Higgs & Wellman, 2000
Figure 5h

Pseudodyadospora petasus Wellman & Richardson, 1993
Figure 5i

Rimosotetras problematica Burgess, 1991
Figure 5j

Rugosphaera sp.
Figure 5k

Sphaerasaccus glabellus Steemans, Higgs & Wellman, 2000
Figure 5l

Remarks. This species has been identified from the Ordovician of the UK (Wellman, 1996), the NW of Argentina (Rubinstein *et al.* 2010) and the Llandovery of Saudi Arabia (Steemans, Higgs & Wellman, 2000).

Tetrahedraletes medinensis (Strother & Traverse) Wellman & Richardson, 1993
Figure 5m

Tetrad sp. (ornamented with verrucae)
Figure 5n

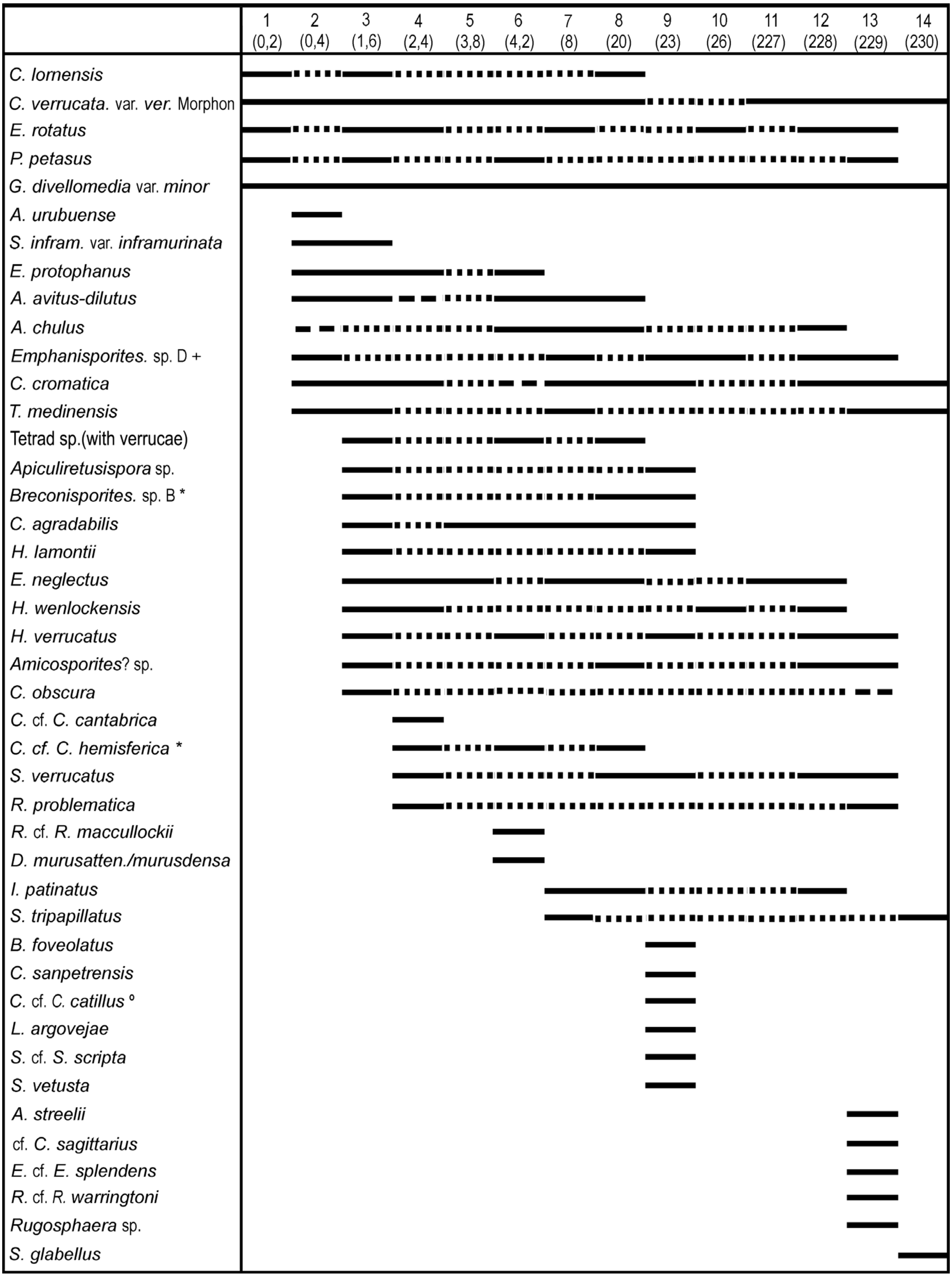

Figure 4. Stratigraphic distribution of trilete spore and cryptospore species in the studied levels. The numbers between brackets represent the metres from the base of the formation. Identified species are indicated in continuous lines; cf. species in dashed lines; supposed stratigraphic range in dotted lines. + in Richardson, Rasul & Al-Ameri (1981); * in Richardson, Rodríguez & Sutherland (2001); ° in Richardson & Lister (1969).

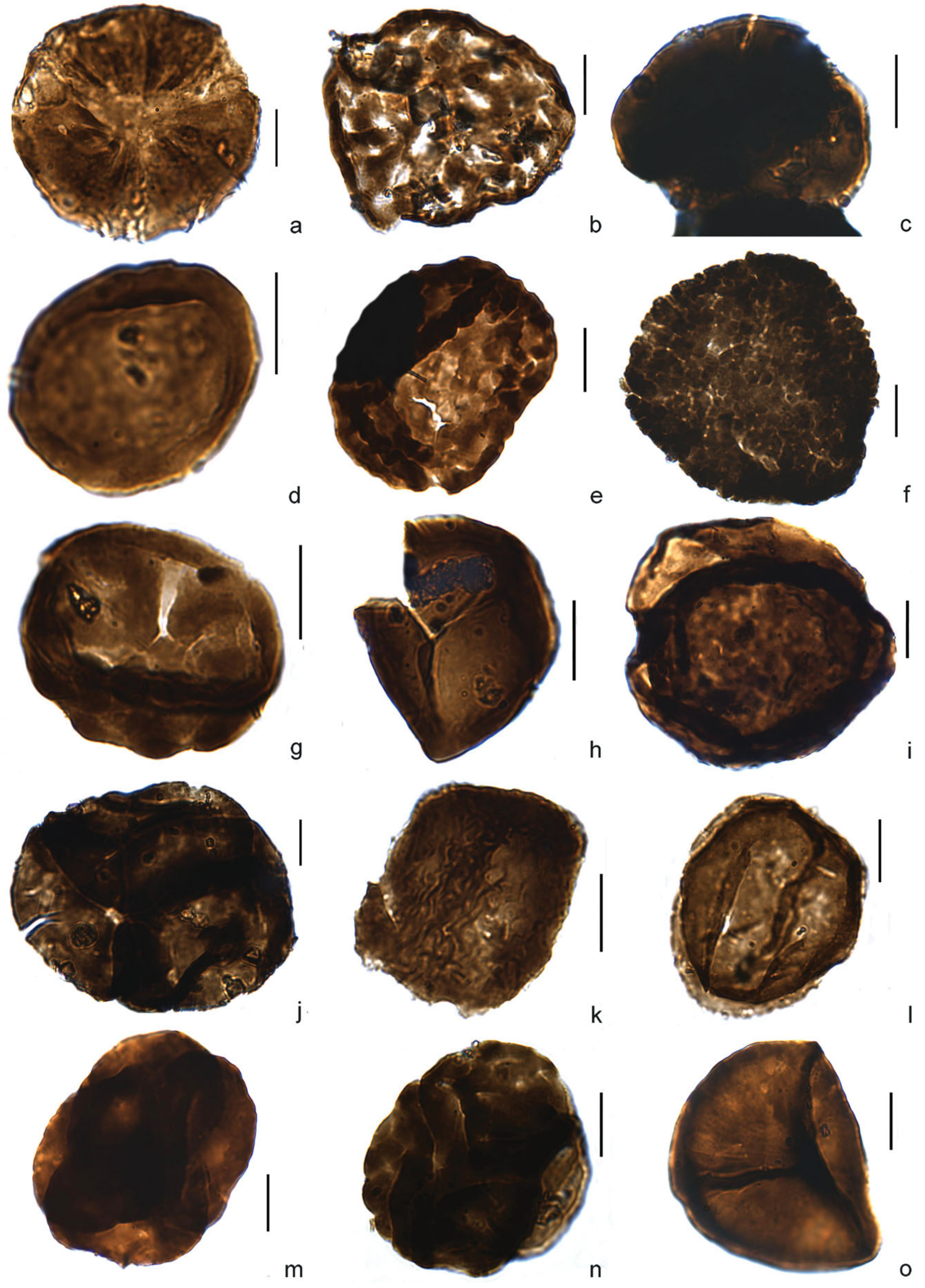

Figure 5. (Colour online) (a) *Artemopyra urubuense* Steemans, Rubinstein & Melo, 2008, diameter 43 μm, slide 60704, K35/3–4. (b) *Chelinohilates lornensis* Wellman & Richardson, 1996, slide 60677, Q36/1-2. (c) *Dyadaspora murusattenuata/murusdensa* morphon Steemans, Le Hérissé & Bozdogan, 1996, slide 60662, P39/1. (d) *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 var. *minor*

5.b. Trilete spores

Ambitisporites avitus/dilutus sensu Steemans,
Le Hérissé & Bozdogan, 1996
Figure 6a

Amicosporites streelii Steemans, 1989 partim
Figure 6c

Remarks. The specimens of *A. streelii* figured in Steemans (1989) include several with distal verrucae and specimens with only one large verrucae centred at the distal pole. It would seem that these represent two new species. In the Lower Devonian of Saudi Arabia (Breuer & Steemans, 2013), only specimens with one distal verrucae are known. Similar specimens are also known from the Saudi Arabian Upper Silurian (P. Breuer, pers. com. 2012).

Amicosporites? sp.
Figure 6b

Remarks. Several poorly preserved specimens are close to *Concentricosisporites agradabilis*. However, it has not been possible to see if there are radial muri on the proximal face. For this reason they have been tentatively placed in the genus *Amicosporites*.

Apiculiretusispora sp.
Figure 6d

Archaeozonotriletes chulus (Cramer) Richardson &
Lister, 1969
Figure 6e

Breconisporites sp. B in Richardson, Rodríguez &
Sutherland, 2001
Figure 6f, g

Remarks. Richardson, Rodríguez & Sutherland (2001) included in *Breconisporites*? spp. specimens with curvaturae extending equatorially onto a possible zona. These authors also observed rare laevigate or proximally rugulate zonate spores, more clearly bizonate, that they positively assigned to the genus *Breconisporites* (as *Breconisporites* sp. B, pl. 4, fig. 4), from the NA Subzone of the MN Zone in Spain of early Lochkovian age. They did not describe *Breconisporites* sp. B but from its illustration it appears very similar to our species.

Brochotriletes foveolatus Naumova, 1953
Figure 6h

Remarks. This species first appears in the Lochkovian and it is widely distributed over portions of Euramerica and Gondwana. The only previous older record is from the lower Pridoli of Brazil (Steemans, Rubinstein & Melo, 2008).

Chelinospora cf. *C. cantabrica* Richardson,
Rodríguez & Sutherland, 2001
Figure 7c

Chelinospora cf. *C. hemiesferica* (Cramer & Diez) *in*
Richardson, Rodríguez & Sutherland, 2001
Figure 7a, b

Remarks. C. hemiesferica is the eponymous species for the H Zone (Richardson, Rodríguez & Sutherland, 2001) of Ludfordian to Pridoli age, and *C.* cf. *C. hemieferica* first appears within the H Zone.

Chelinospora obscura Burgess & Richardson, 1995
Figure 7d

Chelinospora (*Clivosispora*) *verrucata* (McGregor)
comb. nov.
Figure 7f–j

Basionym. Clivosispora verrucata McGregor, 1973, pp. 54–5, pl. 7, figs 4, 5, 10. The following synonymy list includes only those references with descriptions and/or illustrations of Silurian specimens. Several other specimens have also been recorded from the Lower Devonian and are also listed here.

Synonymy and references.

1973 *Clivosispora verrucata* McGregor, pp. 54–5, pl. 7, figs 4, 5, 10.
1973 *Lophozonotriletes*? *poecilomorphus* Richardson & Ioannides, pp. 279–80, pl. 7, figs 9–15; pl. 8, figs 1, 4–6.
1975 *Lophozonotriletes*? *poecilomorphus* Richardson & Ioannides; Cramer & Diez, p. 342, pl. 1, fig. 1; pl. 2, fig. 33.
1976 *Clivosispora verrucata* var. *verrucata* McGregor & Camfield, p. 15, pls 3, 11–14.
1976 *Clivosispora verrucata* var. *convoluta* McGregor & Camfield, p. 15, pls 2, 13–21.
1995 *Lophozonotriletes*? *poecilomorphus* Richardson & Ioannides; Burgess & Richardson, pp. 22–3, pl. 9, figs 10–13.
1995 *Lophozonotriletes*? *poecilomorphus* Richardson & Ioannides; Steemans, pl. 3, fig. 9.
2001 *Lophozonotriletes*? *poecilomorphus* Richardson & Ioannides; Beck & Strother, p. 151, pl. 6, figs 8(?), 9,10, 12, 13.

Breuer *et al.* 2007, slide 60984, J32/1-3. (e) *Hispanaediscus lamontii* Wellman, 1993, slide 60664, S46/1. (f) *Hispanaediscus wenlockensis* Burgess & Richardson, 1991, slide 60659, K47/1. (g) *Hispanaediscus verrucatus* (Cramer) Burgess & Richardson, 1991, slide 60984, N31/1. (h) *Imperfectotriletes patinatus* Steemans, Higgs & Wellman, 2000, slide 60986, S39/1. (i) *Pseudodyadospora petasus* Wellman & Richardson, 1993, slide 60667, O42/0. (j) *Rimosotetras problematica* Burgess, 1991, slide 62521, P43/0. (k) *Rugosphaera* sp., 60984, Q47/4. (l) *Sphaerasaccus glabellus* Steemans, Higgs & Wellman, 2000, slide 60982, N36/1. (m) *Tetrahedraletes medinensis* (Strother & Traverse) Wellman & Richardson, 1993, slide 60704, G43/4. (n) Tetrad with coarse verrucae, slide 60659, S29/1. (o) *Stellatispora inframurinata var. inframurinata* (Richardson & Lister) Burgess & Richardson, 1995, slide 60659, S28/0. The scale bar represents 20 μm.

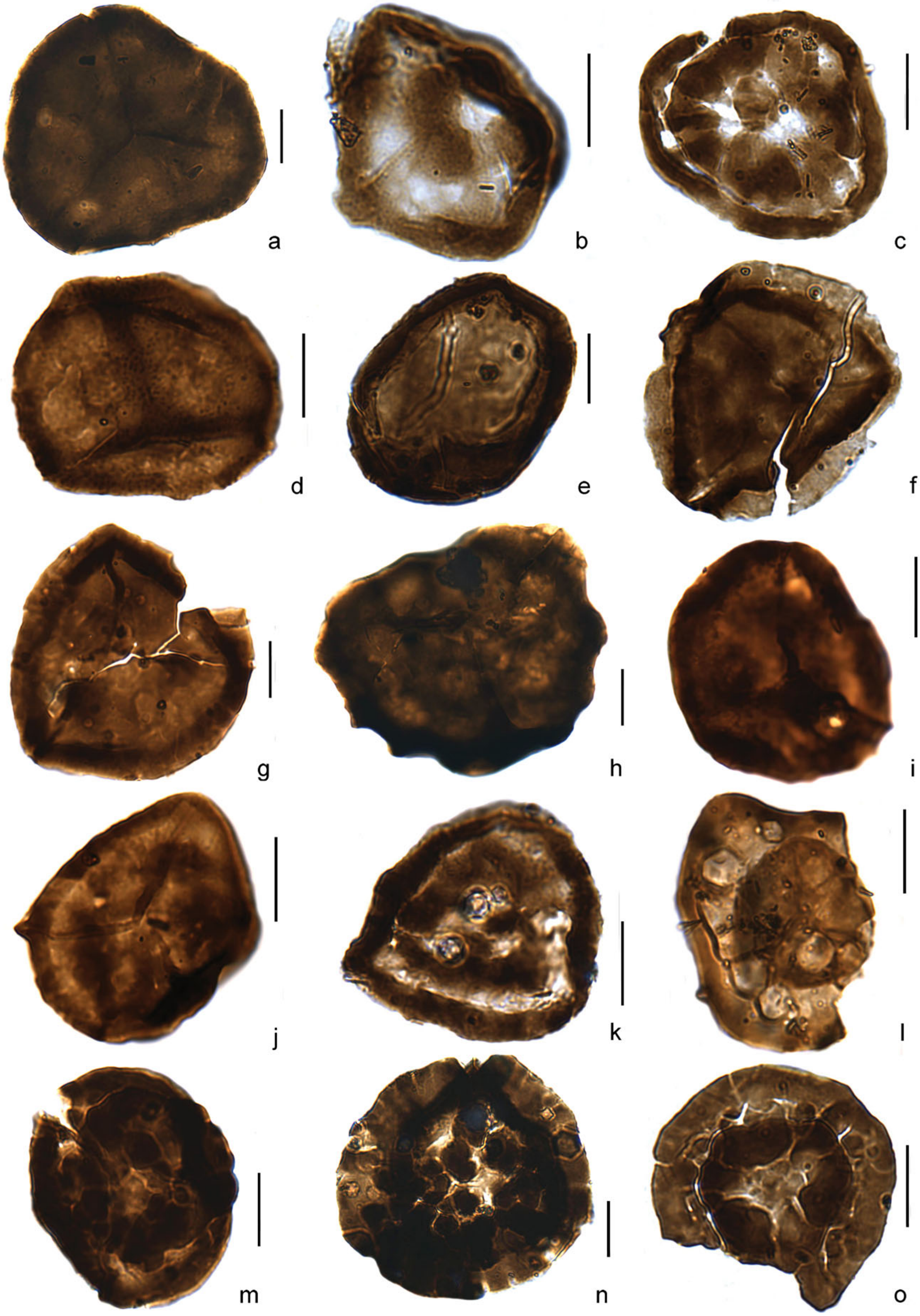

Figure 6. (Colour online) (a) *Ambitisporites avitus/dilutus sensu* Steemans, Le Hérissé & Bozdogan, 1996, slide 60659, K45/3. (b) *Amicosporites*? sp., slide 60986, M45/0. (c) *Amicosporites streelii* Steemans, 1989, slide 60984, S29/1. (d) *Apiculiretusispora* sp., slide 60664, F41/2. (e) *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, 1969, slide 60986, L29/4. (f, g) *Breconisporites* sp. B in

2001 *Chelinospora* (*Lophozonotriletes*?) *poecilomorpha* Richardson, Rodríguez & Sutherland, p. 159, pl. 10, figs 6, 7.
2002 *Lophozonotriletes*? *poecilomorphus* Richardson & Ioannides; Rubinstein & Steemans, pl. III, fig. 14.
2002 *Clivosispora verrucata* McGregor var. *convoluta* McGregor & Camfield; Rubinstein & Steemans, pl. II, fig. 6.
(?)2007 *Chelinospora poecilomorpha* Richardson, Rodríguez & Sutherland; Hassan Kermandji, pl. 1, figs 1, 4.
2007 *Clivosispora verrucata* McGregor; Breuer *et al.* figs 5, 13–14.
2008 *Chelinospora poecilomorpha* Richardson, Rodríguez & Sutherland; Steemans, Rubinstein & Melo, fig. 7(3–4).
2008 *Clivosispora verrucata* McGregor var. *convoluta* McGregor & Camfield; Steemans, Rubinstein & Melo, fig. 7(7).
2008 *Clivosispora verrucata* McGregor var. *verrucata* McGregor & Camfield; Steemans, Rubinstein & Melo, fig 7(8).
2009 *Chelinospora poecilomorpha* Richardson, Rodríguez & Sutherland; Spina & Vecoli, pl. III, fig. 5.

Remarks. We consider *Chelinospora* (*Lophozonotriletes*?) *poecilomorpha* (Richardson & Ioannides, 1973) Richardson, Rodríguez & Sutherland (2001) as a junior synonym of *Chelinospora* (*Clivosispora*) *verrucata* (McGregor, 1973) comb. nov.; the latter was published in July 1973 and the former in April of the same year. Both show exactly the same type of ornamentation and patina. The diameter ranges in the original descriptions show differences between both taxa (23–45 μm for *C. poecilomorpha* and 39–80 μm for *C. verrucata*). Even though *C. verrucata* can be larger, it could represent phenotypic (particular environmental) variation. Subsequent literature mentions smaller specimens of *C. verrucata* (e.g. Gao, 1981; Wellman *et al.* 1998; Rubinstein & Steemans, 2002; Wellman, 2006; Steemans, Rubinstein & Melo, 2008; Spina & Vecoli, 2009). Rare specimens of *C. verrucata* show a cingulum with radial depressions resembling coalescent verrucae, which is why McGregor (1973) assigned this species to *Clivosispora*. Personal observations (P. Steemans) of this species from various Silurian and Devonian samples suggest this character is most probably an artefact of the thick distal verrucae observed through the patina at the equator. A similar artefact may also be due to specimen compression during fossilization (see pl. 10, fig. 7 in Richardson, Rodríguez & Sutherland, 2001).

Chelinospora verrucata var. *verrucata* morphon

Remarks. A morphon, *Chelinospora verrucata* var. *verrucata* morphon, is created on the basis of the distal ornamentation for these miospores. It includes the varieties *verrucata* var. *verrucata* and *verrucata* var. *convoluta* of McGregor & Camfield (1976). These taxa are very similar having a subtriangular to subcircular amb. Equatorial thickenings are well developed, ranging from 2–15 μm in width (most not exceeding 4 μm), laevigate or with rounded humps and intervening radial depressions that may resemble coalescent verrucae. The trilete mark, when present, extends three-quarters to the total radius of the spore. All spores included in this morphon have a proximal face that is thin, laevigate and folded along the trilete mark. The distal face has coarse verrucae 1–15 μm wide, separated by depressions with a maximum width of 3 μm (Fig. 6f), but commonly they are more closely packed, sometimes even fused, giving the appearance of coarse convoluted muri (see Fig. 6i, j). In some specimens the verrucae overlap the cingulum.

The specimens found in Quebrada Ancha have a triangular to subtriangular amb. Equatorial crassitudes range from 2–4 μm in width. In most specimens the trilete mark is not preserved; when it is preserved it extends over the equatorial crassitude. The distal face has coarse verrucae of 2–6 μm wide, frequently collapsed, and often overlapping the equatorial crassitude.

Dimensions. 28–52 μm (36 μm average; 17 Quebrada Ancha specimens measured).

Occurrence. Ludlow to Emsian from localities on the Gondwana, Avalonia, Armorica and Baltica palaeoplates.

Chelinospora sanpetrensis (Rodriguez) Richardson,
Rodríguez & Sutherland, 2001
Figure 7e

Concentricosisporites agradabilis (Rodriguez)
Rodriguez, 1983
Figure 6i–k

Remarks. Poorly preserved specimens may be confused with *Amicosporites* sp.

cf. *Concentricosisporites sagittarius* (Rodriguez)
Rodríguez, 1983
Figure 6l

Coronaspora cromatica (Rodríguez) Jansonius &
Hills, 1979
Figure 6m–o

Richardson, Rodríguez & Sutherland, 2001; (f) slide 60659, T295/1-2; (g) slide 60664, O40/1. (h) *Brochotriletes foveolatus* Naumova, 1953, slide 60664, H27/1. (i, j) *Concentricosisporites agradabilis* (Rodriguez) Rodriguez, 1983, (i) slide 60664, T39/0; (j) slide 60664, V30/4. (k) cf. *Concentricosisporites agradabilis* (Rodriguez) Rodriguez, 1983, slide 60677, H38/0. (l) cf. *Concentricosisporites sagittarius* (Rodriguez) Rodriguez, 1983, slide 600984, M37/2. (m–o) *Coronaspora cromatica* (Rodríguez) Richardson, Rodríguez & Sutherland, 2001; (m) slide 62521, L39/4 (distal face); (n) slide 60664, G37 (proximal face); (o) slide 60984, J28/4 (proximal face). The scale bar represents 20 μm.

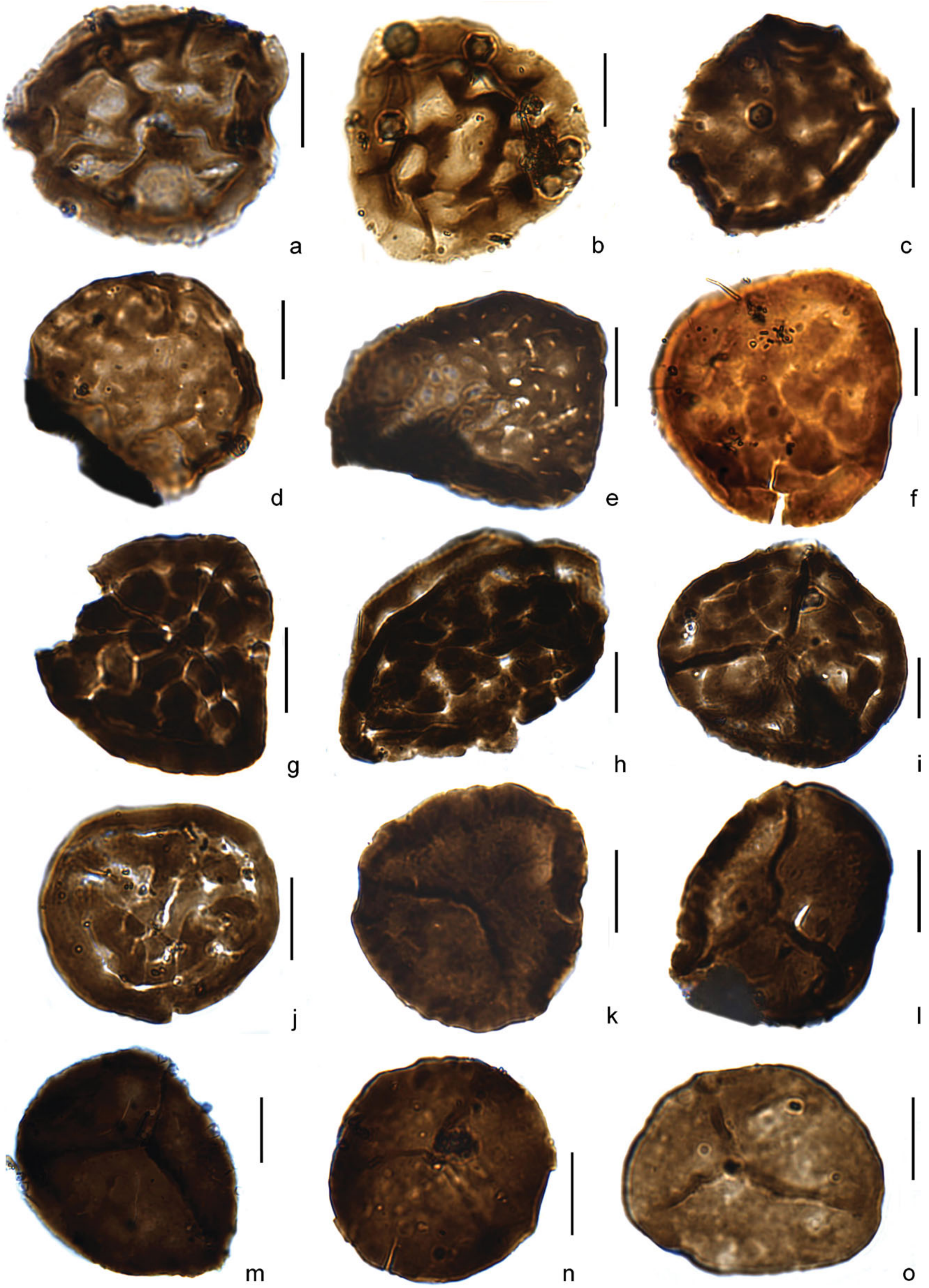

Figure 7. (Colour online) (a, b) *Chelinospora* cf. *C. hemisferica* in Richardson, Rodríguez & Sutherland, 2001; (a) slide 60677, K33/3; (b) 62521, S31/2. (c) *Chelinospora* cf. *C. cantabrica* Richardson, Rodríguez & Sutherland, 2001, slide 62521, O30/3. (d) *Chelinospora obscura* Burgess & Richardson, 1995, slide 60659, J25/2. (e) *Chelinospora sanpetrensis* (Rodríguez) Richardson, Rodríguez & Sutherland, 2001, slide 60664, W45/2. (f–j) *Chelinospora verrucata* var. *verrucata* morphon; (f) slide 60984, H39/2; (g) slide 60704,

Cymbosporites cf. *C. catillus* in Richardson & Lister, 1969
Figure 7k–l

Emphanisporites neglectus Vigran, 1964
Figure 8a

Emphanisporites protophanus Richardson & Ioannides, 1973
Figure 8b

Emphanisporites rotatus (McGregor) McGregor, 1973
Figure 8c–e

Emphanisporites cf. *E. splendens* Richardson & Ioannides, 1979
Figure 8g–i

Description. Amb subtriangular to subcircular; proximal face shows an annular thickening formed by joined circular to elongated verrucae, 5 μm wide. Separated verrucae, up to 5 μm wide, are distributed on the proximal face forming a ring between the annular thickening of joined verrucae and the equatorial outline. Radial muri extend from almost the proximal pole to the equatorial margin.

Dimensions. 36 μm, measured on one specimen.

Discussion. According to the original description by Richardson & Ioannides (1973), the species shows equatorial thickening, simple trilete rays, a quite uniform and continuous annular thickening (incipient, irregular or prominent) and radial ribs beyond the annular thickening (pl. 4, figs 1–4, 7). The specimen recorded in Quebrada Ancha is similar to *Emphanisporites splendens* but the annular thickening is formed by coalescent verrucae and it also has separated verrucae distributed on the proximal face. Richardson, Rodríguez & Sutherland (2001) noted that the Cantabrian and North African specimens are highly variable.

Stratigraphic and geographic occurrences. Richardson & Ioannides (1973) first described the species as Downtonian (Pridoli) in North Africa. Richardson, Rodríguez & Sutherland (2001) recorded *E. splendens* for the upper portion of the *Coronaspora reticulata – Chelinospora sanpetrensis* (RS) spore biozone, dated as early Pridoli, up to the base of the H Zone, in North Africa and the Cantabrian zone.

Emphanisporites sp. D *in* Richardson, Rasul & Al-Ameri, 1981
Figure 8f

Remarks. There is no description for the original specimens, only illustrations have been published by Richardson, Rasul & Al-Ameri (1981).

Leonispora argovejae Cramer & Diez, 1975
Figure 8j

Retusotriletes cf. *R. maccullockii* Wellman & Richardson, 1996
Figure 7m

Retusotriletes cf. *R. warringtoni* Richardson & Lister, 1969
Figure 7n

Scylaspora cf. *S. scripta* in Richardson, Rodriguez & Sutherland, 2001
Figure 8m

Scylaspora vetusta (Rodriguez) Richardson, Rodriguez & Sutherland, 2001
Figure 8n, o

Stellatispora inframurinata var. *inframurinata* (Richardson & Lister) Burgess & Richardson, 1995
Figure 5o

Synorisporites tripapillatus Richardson & Lister, 1969
Figure 8l

Synorisporites verrucatus Richardson & Lister, 1969
Figure 8k

6. Miospore biostratigraphy

Chelinospora (*Clivosispora*) *verrucata* comb. nov, placed here in synonymy with *Clivosispora verrucata*, occurs since the lowest sample (60667). Its presence demonstrates that the base of the section is not older than the base of the LP Biozone (see Section 3, i.e. latest Homerian or earliest Gorstian). It should also be noted that the presence of *Chelinohilates lornensis*, in the same level, has been previously recorded from the lowest Lochkovian of Scotland (Wellman & Richardson, 1996).

Just 40 cm above the formation base, sample 2 (60704) contains, among others, *Stellatispora inframurinata* var. *inframurinata*. This is the eponymous species of the youngest subzone of the LP Zone. Its age ranges from the latest Gorstian or earliest Ludfordian up to latest Ludfordian or earliest Pridoli. In the same sample and above (up to the sample 13 (60984) in the upper Los Espejos Formation), *Emphanisporites* sp. D has been recorded. This species is known from the Ludlow of Libya, the Downton Group of the UK (Richardson, Rasul & Al-Almeri, 1981) and from the lower Pridoli of Brazil (Steemans, Rubinstein & Melo, 2008). The other species in samples 2 (60704) and 3 (60659) are stratigraphically *in situ*, except *Hispanaediscus wenlockensis*, which could be reworked; that species has only been observed in the Wenlock of the UK (Burgess & Richardson, 1991). *Coronaspora cromatica* and *Concentricosisporites agradabilis* also

---

V37/2; (h) slide 60659, U43; (i) slide 60677, V34/0–3; (j) slide 60984, H26/1. (k, l) *Cymbosporites* cf. *C. catillus* in Richardson & Lister, 1969; (k) slide 60664, X27/1; (l) slide 60664, P27/2. (m) *Retusotriletes* cf. *R. maccullockii* Wellman & Richardson, 1996, slide 60662, F25/1. (n) *Retusotriletes* cf. *R. warringtoni* Richardson & Lister, 1989, slide 60984, K28/1. (o) *Retusotriletes* sp., slide 60984, R29/1. The scale bar represents 20 μm.

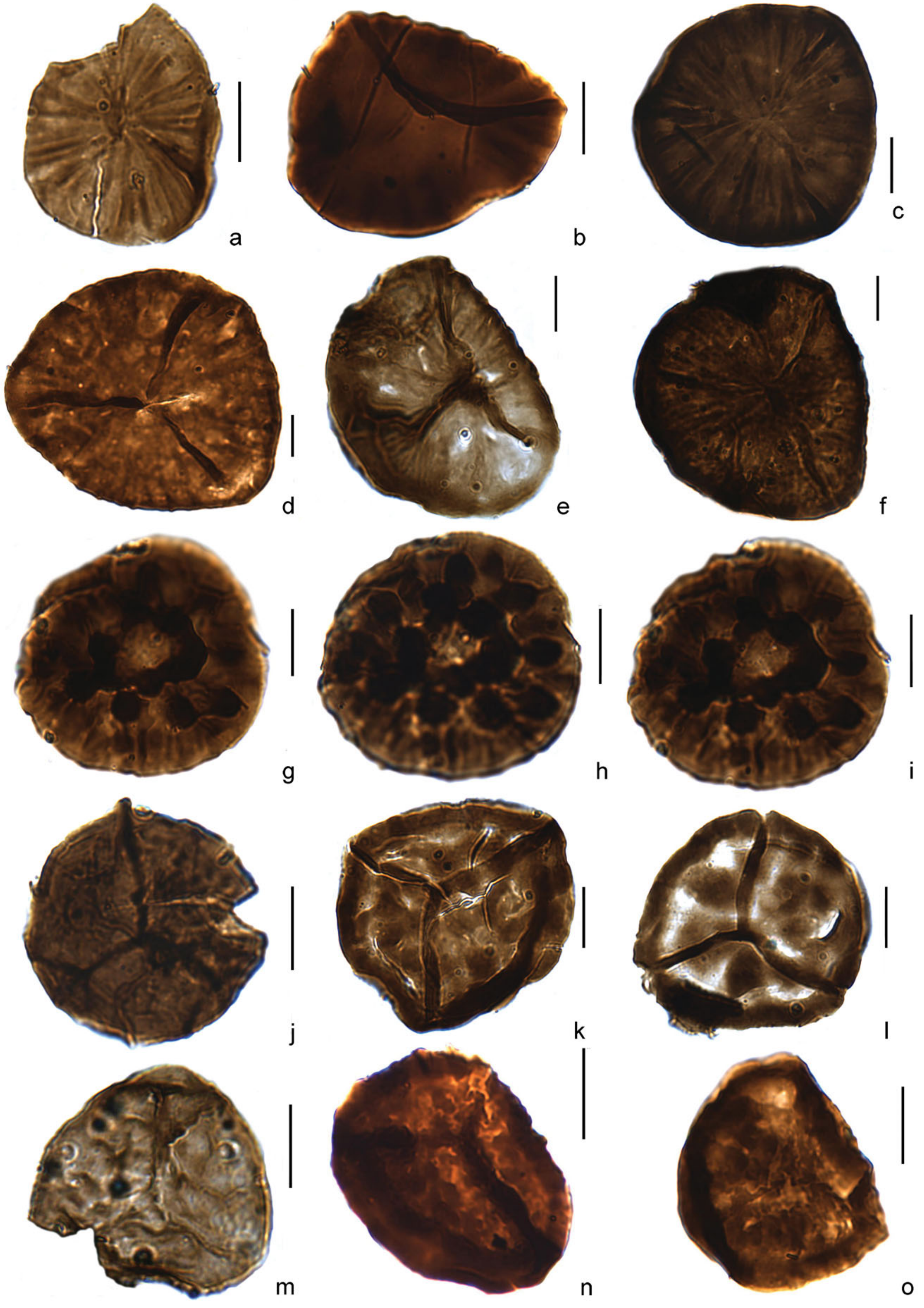

Figure 8. (Colour online) (a) *Emphanisporites neglectus* Vigran, 1964, slides 60986, W26/1. (b) *Emphanisporites protophanus* Richardson & Ioannides, 1973, slide 60984, V36/4. (c) *Emphanisporites rotatus* (McGregor) McGregor, 1973, slide 60659, Q41. (d, e) *Emphanisporites* cf. *E. rotatus* (McGregor) McGregor, 1973; (d) slide 60673, P26/3; (e) slide 60736, B32/4. (f) *Emphanisporites* sp. D

appear in sample 2 (60704). Both are accessory species of the RS Zone and H Zone of Richardson, Rodríguez & Sutherland (2001), respectively, thus pointing to a latest Ludfordian age.

Surprisingly, *Breconisporites* sp. B in Richardson, Rodríguez & Sutherland (2001) first occurs in sample 3 (60659) and extends up to the upper part of the lower section. *Breconisporites*, a genus formerly unknown below the Lochkovian, based on few data points, was recorded in the lower and middle Pridoli of Libya (*B. simplex* Wellman, 1993 *in* Rubinstein & Steemans, 2002).

In sample 4 (62521), *S. verrucatus* appears for the first time in the outcrop. Although that species was believed not to occur below the Pridoli (Richardson & McGregor, 1986), it has been shown that it exists also in the late Ludlow (Rubinstein & Steemans, 2002; Steemans, Rubinstein & Melo, 2008). In addition, the identification of that species is problematic as *Synorisporites libycus*, which is recorded from the Wenlock (Richardson & Ioannides, 1973), and *S. verrucatus* are very close and most probably are the end member morphologies of a morphon. In the same sample, *C.* cf. *C. hemiesferica* has been identified. That species appears in the H Zone in Spain, considered late Ludfordian and/or early Pridoli in age. In this sample *Chelinospora* cf. *C. cantabrica* also occurs. This species is known to appear in the RS Zone, thus supporting this age.

Samples 5 (62523) and 6 (60662) do not display first appearances of biostratigraphically relevant taxa.

In sample 7 (60736) *S. tripapillatus*, which is characteristic of the TS Zone, supports an age very close to the boundary between the Ludlow and Pridoli.

The occurrence of *B. foveolatus*, in sample 9 (60664), could be surprising in possible Late Silurian samples. However, this species, which is previously only known from the Lower Devonian of the Old Red Sandstone Continent, has also been identified from the lower Pridoli of Brazil (Steemans, Rubinstein & Melo, 2008), therefore supporting the Late Silurian age. *Leonispora argovejae* occurs in the same sample. It is the eponymous species of the NA Subzone in the lower part of the MN Zone of Spain (Richardson, Rodríguez & Sutherland, 2001). Even if its presence suggests a Lochkovian age, the definition of the Silurian–Devonian boundary, based on spores, remains uncertain.

In the upper part of the Los Espejos Formation, in sample 13 (60984), the occurrence of *Amicosporites streelii* indicates a Lochkovian age. However, it should be taken into account that specimens similar to *A. streelii* have also been found in the Upper Silurian of Saudi Arabia (P. Breuer, pers. com. 2012).

According to the identified miospore species in the Los Espejos Formations, it is difficult to attribute accurate biozones to the analysed samples. Besides, the lower part of the Los Espejos Formation is richer in trilete spore species than the upper part, and the same trend is shown for the marine phytoplankton. Therefore, the lower part has more potential to be more accurately age dated.

Despite the incertitude around the age of the samples, based on miospore assemblages, it seems clear that the studied part of the Los Espejos Formation would have been deposited during the Late Silurian. The marine phytoplankton biostratigraphy also supports this age (Rubinstein, 2001; Rubinstein & García Muro, 2011 and unpub. data).

7. Palaeoecology and palaeobiogeography

The presence of miospore assemblages in the Quebrada Ancha area proves the existence of emergent land near to this locality. This information needs to be considered for the compilation of future palaeogeographic maps.

The distribution and diversity of terrestrial palynomorphs such as miospores, as well as marine palynomorphs, are controlled mainly by palaeoenvironments and palaeogeography. The Precordillera Late Silurian miospores come from a basin developed in an active continental margin of Gondwana, where the sedimentary deposits indicate a foreland basin, as noted above.

For all of the sections studied throughout the basin, palynomorph diversity decreases stratigraphically upwards quite similarly for both marine and terrestrial palynomorphs, in the middle to upper part, culminating with the complete disappearance of palynomorphs near the top (Rubinstein & García Muro, 2013). This decrease in palynomorph preservation could be a consequence of the predominance of storm-dominated platform facies to shoreface facies, including subaerial exposures, at the top of regressive cycles, in the upper third of the unit (Astini & Maretto, 1996) represented in Figure 2b.

In this context, the miospores of the Los Espejos Formation, in Quebrada Ancha, display a moderate diversity with 29 trilete spores and 14 cryptospores. The diversity of coeval Ludlow–Pridoli palynological assemblages (considering only those that are relatively continuous and well-dated sections) was compared with the Precordillera assemblage and quantitatively analysed using cluster analysis (Fig. 9). In Libya, northern Gondwana, the miospore assemblage is richer than that of the Quebrada Ancha assemblage, having 71 species of trilete spores and 13 species of

---

in Richardson, Rasul & Al-Ameri, 1981, slide 60736, M31/1. (g–i) *Emphanisporites* cf. *E. splendens* Richardson & Ioannides, 1979, slide 60984, J47/1; (g) proximal focus; (h) distal focus; (i) intermediate focus. (j) *Leonispora argovejae* Cramer & Diez, 1975, slide 60664, E26/4. (k) *Synorisporites verrucatus* Richardson & Lister, 1969, slide 60986, V30/3. (l) *Synorisporites tripapillatus* Richardson & Lister, 1969, slide 60736, O32/0–2. (m) *Scylaspora* cf. *S. scripta* in Richardson, Rodríguez & Sutherland, 2001, slide 60664, M44/2. (n, o) *Scylaspora vetusta* (Rodriguez) Richardson, Rodríguez & Sutherland, 2001; (n) slides 60664, F28/0; (o) slide 60664, M26/1. The scale bar represents 20 μm.

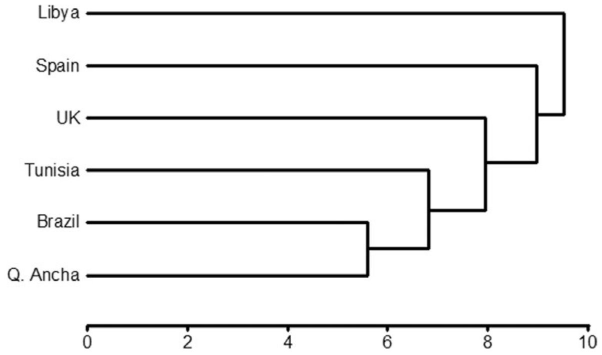

Figure 9. Dendrogram (cluster analysis) comparing Upper Silurian miospore assemblages of Brazil (Steemans, Rubinstein & Melo, 2008), Libya (Rubinstein & Steemans, 2002), Spain (Richardson, Rodríguez & Sutherland, 2001), Tunisia (Spina & Vecoli, 2009), the UK (Richardson & Lister, 1969; Richardson & McGregor, 1986; Burgess & Richardson, 1995) and Quebrada Ancha (present study). *x*-axis represents the Euclidean distance.

cryptospores (Rubinstein & Steemans, 2002). In Tunisia, also in northern Gondwana and close to the former locality, Spina & Vecoli (2009) recorded a less diverse miospore assemblage, with 32 species of trilete spores and 13 species of cryptospores. In northern Spain, located in the Peri-Gondwanan terrane of Armorica, Richardson, Rodríguez & Sutherland (2001) recorded 41 species of trilete spores and 12 species of cryptospores. The northern Brazilian basin is palaeogeographically closest to the Precordillera Basin. It contains 29 species of trilete spores and 8 species of cryptospores (Steemans, Rubinstein & Melo, 2008) displaying similar diversity to that of the Precordillera (Fig. 9). It is also noteworthy that the composition of both microfloras has 70 % of species in common.

Even though the available distribution information is incomplete, because of the few and widely dispersed assemblages, including the total lack of information from some palaeoplates, it is possible to propose some preliminary palaeobiogeographical and palaeoecological conclusions.

The cryptospores are quite comparable in all the assemblages and are usually less represented (in abundance and diversity) in relation to trilete spores. Even if the diversity of trilete spores is variable, for example comparing those from Libyan and Precordilleran assemblages, cryptospores are more uniform in occurrence. Thus, cryptospores seem to be more constant in abundance and diversity, probably owing to the cosmopolitism of cryptospore producing plants, which are apparently more tolerant to climatic variations, as suggested by Steemans, Wellman & Filatoff (2007).

Conversely, trilete spore-producing plants inhabited a wider variety of biotopes but were more sensitive to climatic variations (Steemans, Wellman & Filatoff, 2007). Therefore, palaeoplate setting and resulting palaeolatitudinal position or climatic differences, although significant, might not be the only determinant factor for the distribution of primitive vascular floras. The relatively high degree of similarity between northern Brazil and Argentina, situated at a high palaeolatitude (*c*. 70° S) and Tunisia, located at a mid-latitude (*c*. 40° S) supports this interpretation. Contrary to this, pronounced differences between Tunisian and Libyan assemblages can be easily observed on the dendrogram (Fig. 9). No palaeogeographic observation can easily explain this degree of difference. Consequently, spore-producing plants seem to have been especially sensitive to local sedimentology and/or ecology, and thus peculiarities of the local conditions were probably a major factor in controlling their distribution and evolution that overrode palaeogeographic influences. The hydrologic systems, which transport sediment to depositional basins, are important factors controlling sedimentation of miospore assemblages. Transport distance, sediment load and hydrodynamics of drainage basins are all factors that affect transport and resedimentation of miospores and the admixing of assemblages from different local floras. If long-shore currents are insignificant, there would be little mixing of sediments from different river catchments even if estuaries/deltas are relatively near.

Nevertheless, the strong relationship between Brazilian and Argentinean basins must be noted, both of them located at high palaeolatitudes under colder climatic conditions, and very similar in diversity as well as common species.

The miospore assemblage of the Los Espejos Formation contains a striking number of species with coarse ornamentation such as those included in the *Chelinospora verrucata* var. *verrucata* morphon, *Hispanediscus verrucatus* and *Synorisporites verrucatus*. Those species and other miospores such as *Amicosporites* spp., several *Coronaspora* spp. and *Chelinospora* spp. are frequently difficult to differentiate from each other. However, the presence of this coarse ornamentation could be an adaptation to local environmental conditions.

Interestingly, there is a degree of similarity between miospore assemblage compositions from Spain (Armorica), Libya (Gondwana) and the UK (Avalonia), which is thought to be a result of the palaeogeographic position of the Armorican/Iberic plate (Spain) situated between Baltica and Gondwana. Miospore assemblages from Spain and Brittany contain species characteristic of Baltica like *S. newportensis* and *E. micrornatus* (Steemans; 1989; Richardson, Rodríguez & Sutherland, 2001). Those species are unknown from Gondwana, except for rare specimens from Tunisia (Loboziak *et al*. 1992). On the other hand, *E. splendens*, well known from North Africa and Saudi Arabia and recorded from Spain (Richardson, Rodríguez & Sutherland, 2001), is absent from Baltica.

6. Conclusions

The recovery of miospores in a palynological assemblage, rich in marine acritarchs and chlorophytes, demonstrates the presence of emerged land close to the Quabrada Ancha locality, San Juan Province, Argentina.

Correlations of the Quabrada Ancha assemblages with the miospore biozones from Spain allow recognition of a Ludlow age in agreement with the age based on acritarchs; however, a Pridoli age cannot be excluded for the youngest samples.

The miospore diversity is relatively low, in comparison to localities from the UK, Spain and North Africa, but similar to that from north Brazil. The Argentinean and Brazilian localities are both from relatively high palaeolatitudes (i.e. 70° S); this may explain the strong similarities between both miospore assemblages. The lower diversity of these assemblages may also be a function of their palaeolatitudinal positions, especially when compared to those assemblages from land masses present in lower palaeolatitudes. The comparison between those miospore assemblages also shows that assemblages from Spain are influenced by the vegetation from Baltica and Gondwana, reflecting Spain's intermediate position between these two palaeocontinents and its role as bridge between them.

Acknowledgements. This paper is the result of scientific collaboration between the Ministry of Science, Technology and Productive Innovation of Argentina (MINCYT) and the National Funds for Scientific Research of Belgium (NFSR). (International Cooperation Project MINCYT/NFSR, BE/09/08). Financial support for this study was also provided by the CONICET (PIP 2010-11220090100921) and FONCYT (PICT 2006-1272 and PICT 2005-33630). R. Astini (CONICET, National University of Córdoba) is acknowledged for his collaboration on the fieldwork. We thank M. Giraldo (Liège) for palynological laboratory processing and Rafael Bottero for drafting the figures. We thank Florencia Carotti for helping us to improve the English. We are very grateful to Merrell Miller for the thorough review and linguistic improvement of the manuscript before submission. We also thank Jenny Morris and Charles Wellman for critically reviewing, and improving the manuscript, and Kat Piper for the final review.

References

ALBANESI, G. L., ORTEGA, G. & HÜNICKEN, M. A. 2006. Bioestratigrafía de conodontes y graptolitos silúricos en la sierra de Talacasto, Precordillera de San Juan, Argentina. *Ameghiniana* **43**, 93–112.

ALDRIDGE, R. J. & SCHÖNLAUB, H. P. 1989. Conodonts. In *A Global Standard for the Silurian System* (eds C. H. Holland & M. G. Bassett), pp. 274–9. Cardiff: National Museum of Wales Geological Series no. 9.

ASTINI, R. A., BENEDETTO, J. L. & VACCARI, N. E. 1995. The Early Paleozoic evolution of the Argentine Precordillera as a Laurentian rifted, drifted and collided terrane: a geodynamic model. *Geological Society of America Bulletin* **107**, 253–73.

ASTINI, R. A. & MARETTO, H. M. 1996. Análisis estratigráfico del Silúrico de la Precordillera Central de San Juan y consideraciones sobre la evolución de la cuenca. *13° Congreso Geológico Argentino and 2° Congreso de Exploración de Hidrocarburos*. Actas 1, pp. 351–68.

BECK, J. H., & STROTHER, P. K. 2001. Silurian spores and cryptospores from the Arisaig Group, Nova Scotia, Canada. *Palynology* **25**, 127–77.

BENEDETTO, J. L. 2010. *El Continente de Gondwana a Través del Tiempo. Una Introducción a la Geología Histórica*. Córdoba: Academia Nacional de Ciencias, 384 pp.

BENEDETTO, J. L., RACHEBOEUF, P. R., HERRERA, Z. A., BRUSSA, E. D. & TORO, B. A. 1992. Brachiopodes et biostratigraphie de la Formation de Los Espejos, Siluro-Dévonien de la Précordillère (NW Argentine). *Geobios* **25**, 599–637.

BREUER, P., AL-GHAZI, A., AL-RUWAILI, M., HIGGS, K. T., STEEMANS, P. & WELLMAN, C. H. 2007. Early to Middle Devonian miospores from northern Saudi Arabia. *Revue de Micropaléontologie* **50**, 27–57.

BREUER, P. & STEEMANS, P. 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy. *Special Papers in Palaeontology* **89**, 163 pp.

BURGESS, N. D. 1991. Silurian cryptospores and miospores from the type Llandovery area, south west Wales. *Palaeontology* **34**, 575–99.

BURGESS, N. D. & RICHARDSON, J. B. 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology* **34**, 601–28.

BURGESS, N. D. & RICHARDSON, J. B. 1995. Late Wenlock to early Přídolí cryptospores and miospores from south and southwest Wales, Great Britain. *Palaeontographica B* **236**, 1–44.

CRAMER, F. H. 1967. Chitinozoans of composite section of Upper Llandoverian to basal Lower Gedinnian sediments in northern León, Spain. A preliminary report. *Bulletin de la Société Belge de Géologie* **75**, 69–129.

CRAMER, F. H. & DIEZ, M. DEL C. R. 1975. Earliest Devonian miospores from the province of León, Spain. *Pollen et Spores* **17**, 331–44.

CUERDA, A. 1969. Sobre las graptofaunas del Silúrico de San Juan, Argentina. *Ameghiniana* **22**, 233–41.

EISENACK, A. 1934. Neue Mikrofossilien des baltischen Silurs III und neue Mikrofossilien des böhmischen Silurs I. *Palaeontologische Zeitschrift* **16** (1–2), 52–76.

EISENACK, A., CRAMER, F. H. & DÍEZ, M. DEL C. R. 1976. *Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien. Band IV Acritarcha 2. Teil. E.* Stuttgart: Schweizertbart'sche Verlagsbuchhandlung, 863 pp.

GAO, L. 1981. Devonian spore assemblages of China. *Review of Palaeobotany Palynology* **34**, 11–23.

HASSAN KERMANDJI, A. M. H. 2007. Silurian-Devonian miospores from the western and central Algeria. *Revue de Micropaléontologie* **50**, 109–28.

HÜNICKEN, M. A. & SARMIENTO, G. N. 1988. Conodontes Ludlovianos de la Formación Los Espejos, Talacasto, provincia de San Juan, R. Argentina. *4º Congreso Argentino de Paleontología y Bioestratigrafía (Mendoza).* Actas 3, pp. 225–33.

JAGLIN, J. C. & PARIS, F. 2002. Biostratigraphy, biodiversity and palaeogeography of Late Silurian chitinozoans from A1–61 borehole (north-western Libya). *Review of Palaeobotany and Palynology* **118**, 335–58.

JANSONIUS, J. J. & HILLS, L. V. 1979. Genera file of fossil spores, supplement. *Special Publication, Department of Geology, University of Calgary*. Calgary: University of Calgary.

LAUFELD, S. 1974. Silurian Chitinozoa from Gotland. *Fossils and Strata* **5**, 1–120.

LOBOZIAK, S., STEEMANS, P., STREEL, M. & VACHARD, D. 1992. Biostratigraphie par miospores du Dévonien inférieur à supérieur du sondage MG-1 (Bassin d'Hammadah, Tunisie). Comparaison avec les données des faunes. *Review of Palaeobotany and Palynology* **74**, 193–205.

Loeblich, A. Jr. & Drugg, W. 1968. New acritarchs from the Early Devonian (Late Gedinnian) Haragan Formation of Oklahoma, U.S.A. *Tulane Studies in Geology* **6**, 129–37.

McGregor, D. C. 1973. Lower and Middle Devonian spores of Eastern Gaspé, Canada. *Palaeontographica Abteilung B* **142**, 1–77.

McGregor, D. C. & Camfield, M. 1976. Upper Silurian? to Middle Devonian spores of the Moose River Basin, Ontario. *Geological Survey of Canada Bulletin* **263**, 1–63.

Mehlqvist, K., Vajda, V. & Steemans, P. 2012. Early land plant spore assemblages from the Late Silurian of Skåne, Sweden. *GFF* **134**, 133–44.

Miller, C. G. 1995. Ostracode and conodont distribution across the Ludlow/Přídolí boundary of Wales and the Welsh Borderland. *Palaeontology* **38**, 341–84.

Naumova, S. N. 1953. Spore-pollen complexes of the Upper Devonian of the Russian Platform and their stratigraphic significance. *Trudy Geologicheskogo Institut, Akademiia Nauk SSSR* **43**, 1–204.

Nestor, V. 2009. Biostratigraphy of the Ludlow chitinozoans from East Baltic drill cores. *Estonian Journal of Earth Sciences* **58**, 170–84.

Playford, G. 1977. Lower to Middle Devonian acritarchs of the moose River Basin, Ontario. *Geological Survey of Canada, Bulletin* **279**, 1–87.

Pöthe de Baldis, D. 1981. Paleomicroplancton y mioesporas del Ludloviano Inferior de la Formación Los Espejos en el perfil Los Azulejitos, en la Provincia de San Juan, República Argentina. *Revista Española de Micropaleontología* **13**, 231–65.

Priewalder, H. 1997. SEM-revision of a chitinozoan assemblage from the Uppermost San Pedro Formation (Přídolí), Cantabrian Mountains (Spain). *Jahrbuch der Geologischen Bundesanstalt – A* **140** (1), 73–93.

Richardson, J. B. & Edwards, D. 1989. Sporomorphs and plant megafossils. In *A Global Standard for the Silurian System* (eds C. H. Holland & M. G. Bassett), pp. 216–26. Cardiff: National Museum of Wales Geological Series no. 9.

Richardson, J. B. & Ioannides, N. S. 1973. Silurian palynomorphs from the Tanezzuft and Acacus formations, Tripolitania, North Africa. *Micropaleontology* **19**, 257–307.

Richardson, J. B. & Ioannides, N. S. 1979. Emphanispoirites splendens, a new name for Emphanisporites pseudoerraticus Richardson & Ioannides, 1973 (preoccupied). *Micropaleontology* **25**, 111.

Richardson, J. B. & Lister, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology* **12**, 201–52.

Richardson, J. B. & McGregor, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geological Survey of Canada, Bulletin* **364**, 1–79.

Richardson, J. B., Rasul, S. M. & Al-Ameri, T. 1981. Acritarchs, miospores and correlation of the Ludlovian-Downtonian and Silurian-Devonian boundaries. *Review of Palaeobotany and Palynology* **34**, 209–24.

Richardson, J. B., Rodríguez, R. M. & Sutherland, S. J. E. 2001. Palynological zonation of Mid-Palaeozoic sequences from the Cantabrian Mountains, NW Spain: implications for inter-regional and interfacies correlation of the Ludford/Prídolí and Silurian/Devonian boundaries, and plant dispersal patterns. *Bulletin of the Natural History Museum, Geology Series* **57**, 115–62.

Rickards, B., Brussa, E., Toro, B. & Ortega, G. 1996. Ordovician and Silurian graptolite assemblages from Cerro del Fuerte, San Juan Province, Argentina. *Geological Journal* **31**, 101–22.

Rodriguez, R. M. 1983. *Palinología de las Formaciones del Silúrico superior-Devónico Inferior de la Cordillera Cantábrica*. Servicio de Publicaciones, Universidad de León, 1–231.

Rubinstein, C. V. 1992. Palinología del Silúrico Superior (Formación Los Espejos) de la Quebrada de Las Aguaditas, Precordillera de San Juan, Argentina. *Ameghiniana* **29** (3), 231–48.

Rubinstein, C. V. 1995. Acritarchs from the Upper Silurian of Argentina: their relations with Gondwana. *Journal of South American Earth Sciences* **8**, 103–15.

Rubinstein, C. 2001. Microflora y microplancton silúricos de la Precordillera Central de San Juan, Argentina. In *Palinología: Diversidad y Aplicaciones* (eds M. A. Fombella Blanco, D. Fernández González & R. M. Valencia Barrera), pp. 45–54. Secretariado de Publicaciones, Universidad de León.

Rubinstein, C. V. & Brussa, E. D. 1999. A palynomorph and graptolite biostratigraphy of the Central Precordillera Silurian basin, Argentina. In *Studies in Palaeozoic Palynology*. Selected papers from the CIMP Symposium at Pisa, 1998 (eds M. Tongiorgi & G. Playford). *Bolletino della Società Paleontologica Italiana* **38** (2–3), 257–66.

Rubinstein, C. V. & García Muro, V. J. 2011. Fitoplancton marino de pared orgánica y mioesporas silúricos de la formación los espejos, en el perfil del Río de Las Chacritas, Precordillera de San Juan, Argentina. *Ameghiniana* **48** (4), 618–41.

Rubinstein, C. V. & García Muro, V. J. 2013. Silurian to Early Devonian organic-walled phytoplankton and miospores from Argentina: biostratigraphy and diversity trends. *Geological Journal* **48**, 270–83.

Rubinstein, C. V., García Muro, V. J. & Steemans, P. 2010. Edad de las esporas de la Formación Los Espejos, Silúrico de la Precordillera de San Juan, Argentina. *XIII Simpósio Brasileiro de Paleobotânica e Palinologia*. Salvador, Bahia, Brasil. Anais, p. 142.

Rubinstein, C. V., García Muro, V. J. & Steemans, P. 2011. Miospores from Ordovician-Silurian Argentinean basins: evolution and relationships with other South American basins. *44th Annual Meeting of the American Association of Stratigraphic Palynologists, Southampton, U.K.* Programme and Abstracts, p. 40.

Rubinstein, C. V., Gerrienne, P., de la Puente, G. S., Astini, R. A. & Steemans, P. 2010. Early middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist* **188**, 365–9.

Rubinstein, C., Le Hérissé, A. & Steemans, P. 1996. Lower Devonian palynomorphs from the Talacasto Formation, Cerro del Fuerte Section, San Juan Precordillera, Argentina. *International Meeting and Workshop – C.I.M.P.* Prague, Abstract, p. 19.

Rubinstein, C. V. & Steemans, P. 2002. Miospore assemblages from the Silurian-Devonian boundary, in borehole A1–61, Ghadamis Basin, Libya. In *Paleozoic Palynology: a special issue in honour of Dr. Stanislas Loboziak* (eds P. Steemans, T. Servais & M. Streel). *Review of Palaeobotany and Palynology* **118**, 397–421.

SANCHEZ, T. M., WAISFELD, B. & BENEDETTO, J. L. 1991. Lithofacies, taphonomy, and brachiopod assemblages in the Silurian of western Argentina: a review of Malvinokaffric Realm communities. *Journal of South American Earth Science* **4**, 307–29.

SPINA, A. & VECOLI, M. 2009. Palynostratigraphy and vegetational changes in the Siluro-Devonian of the Ghadamis Basin, North Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **282**, 1–18.

STEEMANS, P. 1989. Palynostratigraphie de l'Eodévonien dans l'ouest de l'Europe. *Mémoires Explicatifs pour les Cartes Géologiques and Minéralogiques de la Belgique, Bruxelles* **27**, 1–453.

STEEMANS, P. 1995. Silurian and Lower Emsian spores in Saudi Arabia. *Review of Palaeobotany and Palynology* **89**, 91–104.

STEEMANS, P., HIGGS, K. T. & WELLMAN, C. H. 2000. Cryptospores and trilete spores from the Llandovery, Nuayyim-2 Borehole, Saudi Arabia. In *Stratigraphic Palynology of the Palaeozoic of Saudi Arabia* (eds S. Al-Hajri & B. Owens), pp. 92–115. Bahrain: Special GeoArabia Publication 1, Gulf PetroLink.

STEEMANS, P., LE HÉRISSÉ, A. & BOZDOGAN, N. 1996. Ordovician and Silurian cryptospores and miospores from southeastern Turkey. *Review of Palaeobotany and Palynology* **93**, 35–76.

STEEMANS, P., RUBINSTEIN, C. & MELO, J. H. G. 2008. Siluro-Devonian miospore biostratigraphy of the Urubu River area, western Amazon Basin, northern Brazil. *Geobios* **41**, 263–82.

STEEMANS, P., WELLMAN, C. H. & FILATOFF, J. 2007. Palaeophytogeographical and palaeoecological implications of a miospore assemblage of earliest Devonian (Lochkovian) age from Saudi Arabia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **250**, 237–54.

STREEL, M., HIGGS, K., LOBOZIAK, S., RIEGEL, W. & STEEMANS, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenno-Rhenish regions. *Review of Palaeobotany and Palynology* **50**, 211–29.

TAUGOURDEAU, P. & DE JEKHOWSKY, B. 1960. Répartition et description des Chitinozoaires Siluro-Dévoniens de quelques sondages de la C.R.E.P.S. de la C.F.P.A. et de la S.N. Repal au Sahara. *Revue de l'Institut Français du Pétrole, Paris* **15**, 1199–260.

VIGRAN, J. O. 1964. Spores from Devonian deposits, Mimerdalen, Spitsbergen. *Norsk Polarinstitutt Skrifter* **132**, 1–32.

WELLMAN, C. H. 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. *Journal of Micropalaentology* **12**, 47–66.

WELLMAN, C. H. 1996. Cryptospores from the type area for the Caradoc Series (Ordovician) in southern Britain. *Palaeontology* **55**, 103–36.

WELLMAN, C. H. 2006. Spore assemblages from the Lower Devonian 'Lower Old Red Sandstone' deposits of the Rhynie outlier, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **97**, 167–211.

WELLMAN, C. H. & RICHARDSON, J. B. 1993. Terrestrial plant microfossils from Silurian inliers of the midland valley of Scotland. *Palaeontology* **36**, 155–93.

WELLMAN, C. H. & RICHARDSON, J. B. 1996. Sporomorph assemblage from the "Lower Old Red Sandstone" of the Lorne, Scotland. *Palaeontology* **55**, 41–101.

WELLMAN, C. H., THOMAS, R. G., EDWARDS, D. & KENRICK, P. 1998. The Coheston Group (Lower Old Red Sandstone) in southwest Wales: age, correlation and palaeobotanical significance. *Geological Magazine* **135**, 397–412.