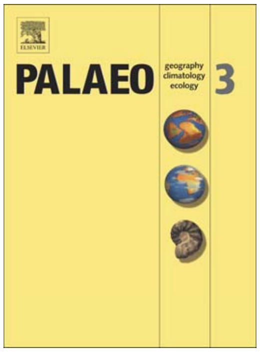

Early seed plants from western Gondwana: Palaeobiogeographical and ecological implications based on Tournaisian (Lower Carboniferous) records from Argentina

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Early seed plants from western Gondwana: palaeobiogeographical and ecological implications based on Tournaisian (Lower Carboniferous) records from Argentina.

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ABSTRACT

The oldest seed occurrences in western Gondwana have been recognized in a new stratigraphic section located in western Argentina (Precordillera Basin). Palynological evidence indicates an Early Mississippian (probably Tournaisian) age for this new succession. The two identified early seeds generas, *Pseudosporogonites* cf. *hallei* and *Warsteinia sancheziae* n. sp. were up to now considered as restricted to the Devonian of Laurussia. This finding suggests a dispersal of earliest spermatophytes between Laurussia and Gondwana during Devonian/Tournaisian times, thus accounting for the Rheic Ocean as a surmountable biogeographic barrier for continental biotas. Alternative, contrasting biogeographic hypotheses dealing with early spermatophytes rising in palaeotropics and then displacing herbaceous communities of non-spermatophytes typical from cool high latitudinal regions, are explored for explaining the recognized palaeobiogeographical pattern. The new information supports a weak impact of the Devonian/Carboniferous biotic crisis on earliest seed plant diversity. Based on preliminary evidences of niches differentiation and ecological dynamics probably affected by wildfires, Tournaisian Gondwanan plant communities from high latitudes are interpreted as being more complex than previously thought, and more similar to those reported from Laurussia. In addition, their discovery in a sedimentary environment associated to glacigenic deposits, show that this new record might be linked to the coeval glacial age widely recorded elsewhere in Gondwana.

Keywords: Spermatophytes, Carboniferous, Gondwana, Argentina, Palaeogeography.

1. Introduction

Seed plants (or spermatophytes) are the most successful modern group of plants. The seed habit is one of the key evolutionary acquisitions that allowed them to colonize new habitats and to reproduce without available free water (Bateman and DiMichele, 1994; Chaloner and Hemsley, 1991; Prestianni and Gerrienne, 2010). The most primitive seeds evolved during the Devonian, a time of rapid and important modifications in both the biosphere and the geosphere that completely transformed continental ecosystems throughout a long and complex geobiotic process known as terrestrialization (Algeo and Scheckler, 1998; Meyer-Berthaud and Decombeix, 2007; Mintz et al., 2010).

Although for the past twenty years our knowledge of the earliest origin of seed plants has been greatly increased, their origin and earliest diversification has been exclusively reconstructed based on information coming from palaeotropical records from Laurussia (Prestianni and Gerrienne, 2010). Seed plants seem to have colonised all latitudes by the Tournaisian (359–346 Ma), yet the understanding of their dispersal, a critical palaeobiogeographical event taking into account the major barrier of the Rheic Ocean, remains obscure and strongly biased by the lack of Late Devonian–earliest Mississippian data from the Southern Hemisphere.

In this paper, report is made of the earliest occurrences of seed plants in western Gondwana, based on ovules from Tournaisian strata of a new glacial-linked stratigraphic succession of western Argentina. They have been identified as *Pseudosporogonites* cf. *hallei* and *Warsteinia sancheziae* sp. nov., up to now two strictly Devonian genera from Laurussia.

A discussion is proposed about the palaeogeographical as well as biostratigraphical implications and major ecological evolutionary significances of this discovery.

2. Geological and stratigraphic settings

The study area is part of the Sierra de Las Minitas, a set of low mountains located in the north of the La Rioja Province, western Argentina (fig. 1). The Sierra de Las Minitas is located approximately 30 km to the southwest of the small town of Jagüé, and it is considered as the northern reach of the Argentine Precordillera in the context of the Central Andean foreland basin (Caminos et al., 1993).

The areas next to Sierra de Las Minitas were originally surveyed by Aceñolaza (1971) and Caminos et al. (1993), yet the studied area was mapped in detail by Coughlin (2000). The structure of the region is complex as the folded bedding were later faulted and intruded by igneous bodies. Except for certain Lower Devonian trilobite-bearing units cropping out to the north of the Sierra de Las Minitas (Rubinstein et al., 2010; Rustán et al., 2011; Holloway and Rustán, 2012), the bulk of the stratigraphic record of the region has been preliminary assigned to the poorly defined Jagüel Formation (González and Bossi, 1986). This formation is characterized by a wide range of sedimentary siliciclastic lithotypes, and might partially involve several other units recognized in the area (Fauqué and Limarino, 1991; Azcuy and Carrizo, 1995; Carrizo and Azcuy, 1998; Limarino et al., 2006; Rustán et al., 2011). It has been interpreted to include stratigraphic intervals that may, in part, fill in the regional gap that elsewhere in the Argentine Precordillera separates the Devonian from the Carboniferous. This set of strongly folded, faulted and intruded stratigraphic units, underlie the uncontroversial Pennsylvanian glacial rocks of the base of the Río del Peñón Formation (Fauqué and Limarino, 1991), thus allowing the interpretation of a complex story of uplift, erosion and onlapping for the region. Prior to the early Pennsylvannian, at least one important folding episode took place forming an angular unconformity named “Agua de Carlos unconformity” (see figure 1). A number of glacial diamictites can be recognized underlying this unconformity (Astini and Ezpeleta, 2008; Ezpeleta and Astini, 2009). Geochronological (Coughlin, 2000), and palaeontological data (Vaccari et al., 2008; Sterren et al., 2010, Rubinstein et al, 2010; Prestianni et al., 2011, 2012) seemed to point these glaciomarine deposits being Devonian to Mississippian, and thus different from the Pennsylvanian Río del Peñón glacial record (Astini and Ezpeleta, 2008).

2.1. Studied stratigraphic section

A new stratigraphic section (Fig. 2), devoid of structural complexity and including glacial diamictites, was surveyed in the eastern flank of a major syncline structure located to the southern area of the Sierra de Las Minitas (about 28° 48’ 35” S/ 68° 45’ 04”). Without exposed contact with the ancient most Lower Devonian trilobite-bearing units, this section embraces the upper interval of the set of stratigraphic units underlying the Pennsylvanian Río del Peñón Formation.

The stratigraphic column exposed at this new section is very thick and only its lowermost third was surveyed. The measured interval is nearly 300 m thick (Fig. 1), with the base covered by modern deposits. The lowermost part of the section starts with massive and laminated dark mudstones with dropstones. It continues with a nearly 12 m thick dark grey to black, stratified, matrix-supported polimictic diamictite, with stratified pebbly mudstones and thick beds of fine grained sandstones in its upper portion. Boulders in the diamictite are usually faceted and exhibit striation. This glacigenic interval is sharply succeeded by 65 m of a dominantly fine-grained interval with alternating green shale sand tabular to lenticular yellowish-greenish sandstones with rare fossils and bioturbations. This interval shows frequent slump features and a thickening-coarsening upward trend. A fertile palynological sample (P2) derives from the upper part of this stratigraphic interval. The succession continues with nearly 34 m of fine to medium grained fossiliferous sandstones, with increasing participation of mudstones toward the upper part. Fossils from this latter interval include brachiopods, bivalves, crinoids, orthoconic nautiloids, gastropods, scarce fish remains and plants. The sandstones are arranged in thick amalgamated and thoroughly laminated beds with thin lenses showing hummocky cross stratification and several levels of coquinas, predominantly composed of the brachiopod *Azurduya* sp. It continues with nearly 75 m of amalgamated and massive beds of medium to coarse scarcely fossiliferous sandstones. Above, another thickening-coarsening upward interval of nearly 80 m occurs, mainly composed of greenish to blackish green siltstones with relatively scarce interbedded fine-grained sandstones, which contains the sampled plant bearing levels (AQ-365 and AQ-380).

The upper part of the section surveyed (42 m thick) is characterized by a predominance of massive scarcely fossiliferous greenish-dark grey middle-grained sandstones with occasional interbedded middle and coarse conglomerates. The section has been studied up to the base of a thick greenish pebbly mudstone interval with marine faunal record.

3. Material and Methods

3.1 Provenance and Repository

All specimens come from a single stratigraphic level of the Agua Quemada section (see Cisterna and Isaacson, 2003) (AQ-365 collecting site, 28° 48’ 44.3” S/ 68° 45’ 01.8” W) within a thick massive greenish-dark grey siltstone interval, located about 250 m above the base of the surveyed column (Figure 2).

The reported palynological sample comes from a level (P2) located nearly 50 m above of the top of the diamictitic beds of the base of the column (see P2 on Fig. 2).

Illustrated plant specimens have been numbered PULR-158 to 162. Illustrated spore is PULR-166. They are housed in the palaeontological collections of the Museo de Ciencias Naturales at Universidad Nacional de La Rioja, La Rioja, Argentina.

3.2 Methods

Materials were referred to a geologic map, using GPS coordinates. Specimens were prepared mainly by dégagement (Fairon-Demaret et al., 1999) and photographed either dry or submersed in water, using a digital camera Canon Power Shot S50 mounted on a binocular loupe Leica MZ75.

4. Systematic palaeontology

More than 20 isolated ovules preserved as adpressions/compressions have been collected, being on the whole poorly preserved. They are very variable in shape, size and occurrence of diagnostic features, so that only the best preserved specimens were considered for morphological descriptions. The terminology is that used in Hilton and Bateman (2006) and in Prestianni et al. (2013).

4.1. Warsteinia sancheziae *sp. nov.*

Spermatophyta (following Rothwell and Serbet, 1994)

Hydrasperman seed-plants (following Hilton and Bateman 2006)

Genus *Warsteinia* Rowe 1997

Type species. *Warsteinia paprothii* Rowe 1997 from uppermost Famennian, Oese, Sauerland, Germany.

Emended diagnosis. Compressions of isolated ovules with four winged integumentary lobes. Nucellar region oval, pointed proximally and differentiated distally into apical salpinx with proximal differentiation of presumed pollen chamber. Integumentary lobes adnate or fused to nucellus to just below pollen chamber, comprising an inner dense sclerotesta composed of longitudinally aligned elements and an outer sarcotesta comprised of perpendicularly aligned anastomosing fibrous strands.

Species *Warsteinia paprothii*

Diagnosis. Ovule 3.3–4.7 mm long and 2.3–3.0 mm wide. Integumentary wings membranous. Nucellar region 1.1–1.4 mm large in broadest part at mid-level of ovule. Salpinx 0.5 by 0.5 mm.

Species *Warsteinia sancheziae* sp. nov

(Figure 3 a and b)

Derivation of the name. In honor of Pr. Dr. Teresa M. Sánchez.

Holotype. PULR-158 Sierra de Las Minitas, La Rioja Province, Argentina; Jagüel Formation; Tournaisian.

Diagnosis. Ovule 7.9 mm long and 4.0 mm wide. Integumentary wings robust. Nucellar region 6.2 mm long and 2.6 mm large in broadest part at mid-level of ovule. Pollen chamber, 1.9mm wide and 0.8 mm high. Salpinx 1.05 by 1.0 mm.

4.1.1. Description

One isolated specimen has been found (fig. 3a). Its overall shape is ovate. It measures 7.9 mm long and 4.00 mm wide. The nucellus measures 6.2 mm in length and 2.6 mm in width. It is pointed proximally and progressively broadens to the 2/3 of its length where it measures 3.8 mm wide. A very short 0.5 mm long chalaza is present proximally. Distally, near to the apex, an abrupt change in outline is observed (see arrow on fig. 3a and b). The change is interpreted this as the top of the pollen chamber. The pollen chamber is dome shaped and measures 1.9 mm wide and is 0.8 mm high. After a very clear shoulder it is extended by a “tube-like” 1.1 mm wide salpinx, which is broken distally but measures at least 1 mm in length.

The integument is formed by several lobes and completely surrounds the nucellus. Two lateral integumentary lobes are visible (number 1 and 2, fig. 3b). A third one, hidden by the nucellus, is only visible by its tip (fig. 3b). Considering the organization of these three lobes, the presence of a fourth one that was probably removed during the recovering of the specimen on the field is porposed. Lobes are laminar and curve around the outside of the nucellus. They are glabrous and lanceolate in shape. Tips are pointed and characterized by a curved outline. They show a peripheral continuation of organic matter interpreted here as a wing. Wings start at the chalazal level and progressively broaden up to the ovule mid-level where they progressively narrow up to the integument tips. Lobes measure 7.9 mm long and 1.9 mm wide at the broadest point which corresponds to the ovule mid-level. Wings are 0.65 mm wide at mid-level. The outline of the nucellus follows inner surface of the integument but the degree of fusion of the two structures is impossible to assess reliably.

This structure is interpreted as a seed plant ovule, as a result of the identification of a lobed integument and a hydrasperman nucellus. This organization is consistent with other coeval ovules from Laurussia.

4.1.2. Comparison

Upper Devonian and Tournaisian ovules represent a moderately diversified group. The acupulate state of this ovule as well as the occurrence of winged integumentary lobes immediately point toward the monospecific genus *Warsteinia*. *Warsteinia paprothii* Rowe 1997 has been described from the uppermost Famennian deposits of Sauerland in Germany (Rowe, 1992, 1997). It is characterized by 3.3–4.7 mm long and 2.3–3.0 mm wide ovules. Four winged integumentary lobes occur. The nucellus is hydrasperman and presents a wide salpinx. Despite very different preservation the general shape of the Argentinian specimen conforms to this genus. Integumentary lobes are winged and characterized by similar short pointed tips. The wings in our specimen are however thicker and do not present the characteristic membranous aspect of those of *W. paprothii*. The nucellus is proximally pointed and presents distally a wide salpinx. The Argentinian specimen is however twice as large as the described German specimens. The many similarities existing between the Argentinian specimen and the German material suggest that they are congeneric. However, the strong size differences as well as the differences in integument organisation led to consider the Argentinian specimen as part of a new species of the genus *Warsteinia, W. sancheziae*.

4.2. Pseudosporogonites *cf.* hallei *(Stockmans) Prestianni et al. 2013*

(Figures 3c–j, Figure 4)

4.2.1. Description

All specimens have similar outline regardless of their orientation. This suggests original radial symmetry (fig. 3c–j). Dimensions of most complete specimens vary from 4.1 to 5.9 mm long and 1.6 to 2.7 mm wide. It consists of a lobed integument proximally covered by a ridged cupule. They are all strongly variable according to fossilization orientation and compression.

In most specimens, the integument completely encloses the nucellus (fig. 3c,g–h). Due to a very brittle preservation of the organic matter nearly no preparation has been possible. One single specimen presents broken integumentary lobes that allow observation of the nucellus distal part (fig. 3d,f). It consists of a dome shape pollen chamber measuring 0.96 mm high and 1.32 mm wide. Above the pollen chamber is a short salpinx of 1 mm long and 0.9 mm wide. It is irregular at the extremity, suggesting it is slightly incomplete.

The integument form and arrangement is the most visible character of this ovule. It is very variable in shape; probably due to different taphonomic processes. It is formed by several lobes and completely covers the nucellus (fig. 3h). Each lobe is laminar and is curved. Lobes taper distally to the apex. They are glabrous and lanceolate in shape. They measure 1.4 mm wide at the broadest point which corresponds to the ovule mid-level. Integumentary lobes seem to be fused from 1/2 up to 2/3 of their total length. The total number of integumentary lobes is never shown directly. Most specimens show two or three lobes, however, a fourth one is inferred (fig. 3g–i). The tapering of integumentary lobes is variable among observed specimens. Most specimens show well differentiated lobes (fig. 3h). However, in three specimens the different lobes are impossible to distinguish (fig. 3c). They appear to be completely fused to each other and strongly tapper distally which gives a pointed shape to the ovule tip.

On some specimens, the chalazal third of the integument show a different organization (fig. 3g–j). The integument appears to be covered by a longitudinally striated structure that strongly contrasts with the glabrous aspect of the integument (fig. 3g). This structure is basally very narrow and flares out distally. It is 2.5 mm in length and 1.7 mm in width. It is here suggested to be a tightly addressed collaret cupule.

Only one specimen shows the distal most part of the branching system (fig. 3c). It is 7.0 mm long and 4.3 mm wide. It consists in one dichotomizing axis bearing two shortly stalked ovules. Stalks are 2.3 and 2.7 mm long and respectively 0.25 and 0.31 mm wide. This branching system notably bears ovules with fused integumentary lobes.

4.2.2. Comparison

Most Lower Mississippian ovules known until now have been described from Laurussia among which a large part comes from the Scottish Cementstone group (Barnard and Long, 1973; Gordon, 1941; Long, 1960a, b, c, 1961a, b, 1965, 1966, 1969, 1975, 1977a, b). Recently, a number of ovules have however been described from Gondwana (Carrizo and Azcuy, 1998; Césari, 1997; Erwin et al., 1994; Galtier et al., 2007).

Ruxtonia minuta Galtier et al. (2007) was described from the Australian Tournaisian Ruxton Formation. It consists in multiovulate cupules. These are bilaterally symmetrical and contain up to two ovules. The integument presents between 8 and 10 terete lobes fused up to the level of the plinth. The occurrence of a bilaterally multiovulate cupule is the main character that distinguishes the Argentinian specimen from *Ruxtonia minuta* where the cupule is uniovulate and rather radially symmetrical. In addition, the presence basally of numerous terete integumentary lobes contrasts strongly with the up to four flat lobes occurring in our specimens.

Occloa cesariana Erwin et al. (1994) is a taxon that was established for compressed ovules from Peru. It is characteristically acupulate and presents 5 to 9 basally fused integumentary terete lobes. All these characters differentiate *Occloa cesariana* from the Argentinian specimens that present a small cupule and a flat integument.

Carrizo and Azcuy (1998) mentioned the occurrence in the Tournaisian of La Rioja Province (Argentina) of a possible other species of the genus *Occloa*. They briefly described it as pedicellate fructifications showing an ovate body. This body is basally surrounded by a tissue (the integument) that is deeply carved distally forming several flat lobes. A careful observation of the published figures led us to doubt of the attribution of this material to the genus *Occloa*. Indeed, they strongly remind us of the material described here. In addition to the integument that seem to form several flat lobes, noteworthy is the presence toward the base of the ovate body of an additional structure that could represent a badly preserved cupule similar to that described here (fig. 3 in Carrizo and Azcuy, 1998). It is however necessary to restudy this material before arriving to further conclusions.

Eonotosperma arrondoi Césari has been reported from the lower Mississippian deposits of the río La Troya Valley, La Rioja province, Argentina (Césari, 1997). It corresponds to fertile material associated with frond remains identified as *Diplothmema bodendenderi* (Kurtz) Césari. The fertile material is compared to *Genomosperma* Long. However, only one badly preserved specimen is reported. A close observation of this specimen prevents any comparison to be done as it lacks most characters commonly associated to ovules (i.e. cupule, integument ?, ovule). It is necessary to restudy this material or find more specimens before arriving to further conclusions.

With the exception of *Occloa* sp., none of the up to now described Tournaisian material appears convincingly similar to ours. Indeed, the occurrence in this material of a collaret uniovulate cupule and of an integument presenting four flat lobes more reliably conforms to the Devonian genus *Pseudosporogonites* Stockmans (1948). A recent revision of the genus led to a better definition of species within it. The four species now included are *Pseudosporogonites hallei*, *P. bertrandii*, *P. quadrapartitus* and *P. avonensis* (Prestianni et al., 2013). In addition to qualitative morphological differences, each species occupies a specific position in a morphospace formed by plotting length and width of the integument. According to this, the Argentinian specimens conform more reliably to *Pseudosporogonites hallei*. This determination is further supported by the lanceolate shape of integumentary lobes and by the characteristics of the pollen chamber. However, considering the poor preservation of this material, as well as the long time span separating it from the Devonian occurrences; we will here refer to it as *Pseudosporogonites* cf. *hallei.*

See figure 4 for a reconstruction of specimen illustrated figure 3c.

5. General discussions

5.1 Age of the plant-bearing strata and stratigraphic implications

The possibility of Upper Devonian/Lower Tournaisian sedimentary rocks cropping out in the Sierra de Las Minitas was suggested by radiometric dating of igneous bodies within the Jagüel Formation (Coughlin, 2000). The record of diamictites in these successions, along with preliminar palaeontological evidences, supported proposals by Astini and Ezpeleta (2008) and

Ezpeleta and Astini (2009), interpreting them as belonging to the Late Devonian glacial event recorded elsewhere in Gondwana (Caputo, 1985; Díaz-Martínez et al., 1999; Isaacson et al., 1999; 2008; Caputo et al., 2008; Wicander et al., 2011).

Further palaeontological results were, however, inconclusive regarding the age of these strata. An age close to the Devonian–Carboniferous boundary was suggested based on the presence of a basal species of the trilobite *Pudoproetus* in levels underlying the glacial diamictites (Vaccari et al , 2013), whereas palynological content from levels located nearly 30 m above the diamictites still indicated Middle Devonian ages (Rubinstein et al., 2010). In turn, records of the brachiopod *Azurduya* all along the figured sedimentary succession pointed out Early Mississippian ages (Sterren et al., 2010). In addition, the record of *Pseudosporogonites* and *Warsteinia* preliminarily supported a Late Devonian age for the stratigraphic interval located nearly 250 m above the diamicitites of the new studied section (Prestianni et al, 2011, 2012). However, *Pseudosporogonites* is a widespread genus that has a stratigraphical distribution ranging from Upper Famennian to very close to the Devonian/Carboniferous boundary in Pennsylvania, Great Britain and Belgium (Prestianni et al., 2013). *Warsteinia,* in turn, has been found in one single locality in Sauerland (Germany) within the Hangenberg sandstones, also very close to the Devonian/Carboniferous boundary. Our knowledge of their real stratigraphical range is strongly biased by the lack of suitable Tournaisian deposits on Laurussia.

New palynological findings indicate a Mississippian age for the studied plant levels in Argentina. They consist of extremely rare elements of the miospore *Waltzispora lanzonii* Daemon 1974, recovered from horizons located nearly 200 m below of the plant-bearing layers (P2 sample, see Stratigraphic Setting, Provenance and Repository and column in the Figure 2). The specimen recovered (Fig. 5) very closely resembles some specimens illustrated by Playford and Melo (2010), which show important morphological variation. *Waltzispora lanzonii* is a biostratigraphic marker for the Mississippian (Daemon, 1974; Melo and Loboziak 2003), being most probably confined to Tournaisian strata. Although it may extend slightly higher into the Visean, these rare occurrences are considered to be probably reworked (Playford and Melo, 2010). Current and previously published data indicate that this taxon is restricted to north-northwesthern Gondwana, with records in Brazil, Perú, Algeria and Libya (Playford and Melo, 2010) and Chile (Rubinstein, unpublished data).

The palynological association containing *Waltzispora lanzonii* is composed of up to 99% of Devonian taxa, implying that, save exceptions, the content recovered is completely reworked. This fact could explain previous reports on Devonian ages for this stratigraphic interval based on palynological content (Rubinstein et al., 2010; Prestianni et al., 2011). Conspicuous reworking is in agreement with similar observations from a number of Gondwanan units embracing the Devonian–Carboniferous boundary, usually related to strong glacial erosion (Streel et al., 2000).

Hence, plantbearing stratas probably correspond to the Tournaisian, thus becoming interesting in discussions related to the coeval glacial-linked records in Gondwana (Caputo, 1985; Díaz-Martínez et al., 1999; Isaacson et al., 1999; 2008; Caputo et al., 2008; Wicander et al., 2011) and particularly on the potential recognition of the Devonian–Carboniferous transition in southern South America (Amenábar, et al., 2009).

5.2 Palaeobiogeography: crossing the Rheic Ocean

Tournaisian ages, interpreted on biostratigraphical evidences confirm that *Pseudosporogonites* cf. *hallei* and *Warsteinia sancheziae* represent the earliest evidences of spermatophytes in Western Gondwana. Indeed, the most ancient evidences for hydrasperman spermatophytes are derived from the Upper and uppermost Famennian of Laurussia (Hilton, 1998; Prestianni, 2005; Prestianni and Gerrienne, 2010). Up to now there was no real evidence of their presence in Western Gondwana during this period, and therefore, *Pseudosporogonites* and *Warsteinia* were considered endemic to Laurussia (Hilton, 1999). Their occurrence in the Tournaisian of Argentina raises some interesting palaeobiogeographic issues.

There have been two main schools regarding the closure of the Rheic Ocean between Laurussia and Gondwana. The first is centered on palaeomagnetic and tectonic evidences and postulates a wide Devonian ocean and a progressive closure in the Carboniferous (Stampfli and Borel, 2002; Stampfli et al., 2002; Van der Voo, 1988). The second is more focused on the palaeobiogeographic information and places the two continents already in close proximity during the Devonian (Benedetto, 1984; Cocks and Torsvik, 2004, 2006, 2011; McKerrow et al., 2000). The contrast between these two reconstructions has been noted many times and the question has been addressed using several fossil groups, namely miospores (Streel et al., 1990), plants (Meyer-Berthaud et al., 1997), fishes (Ahlberg et al., 2001), and early tetrapods (Blieck et al., 2007). All these groups are characterized by continental life habit and and their biogeographic analyses gave similar results.

Tournaisian plant assemblages from Gondwana are rare. They are known in Northern Africa (Morocco), Southern America [Argentina (Sessarego and Césari, 1989), Brazil (Dolianiti, 1980)], Southern Africa (Streel and Theron, 1999) , and Australia (Galtier et al., 2007; Decombeix et al., 2011b). Mostly coming from marine sedimentary rocks, they provide very fragmentary information with often badly preserved drifted material. Up to now seed plants have very rarely been found in these deposits.

Very little is known about early seed plants dispersal and what is known is only based on morphological interpretations (Prestianni and Gerrienne, 2010). The colonization rate/potential is therefore impossible to assess reliably. Unlike *P.* cf. *hallei*, *W. sancheziae* had wings that probably increased slightly its dispersal range. However, ovules are big diaspores and are naturally dispersed on limited distances (maximum 50 km in exceptional long distance dispersal, according to Higgins and Richardson, 1999). Their dispersal is further limited by natural barriers such as oceans and mountains. This suggests that, despite its scarcity, the information provided here tend to be more consistent with contact or near-contact between Laurussia and Gondwana than with wide separation between these continents. However, islands and island arcs have been largely omitted from the different reconstructions (Cocks and Torsvik, 2004). Their introduction in the different palaeobiogeographical models, would probably give a less contrasted answer. This seems to be confirmed by latest palaeogeographic reconstructions (Stampfli et al., 2013).

5.3 A delay in high latitudinal floras distribution during the Devonian/Carboniferous transition?

The marine environments around the Devonian/Carboniferous boundary are worldwide marked by an important diversity crisis and a mass extinction (Sallan and Coates, 2010). This extinction is commonly thought to be one of the consequences of the terrestrialization process and the increase in biomass production that came with it (Algeo and Scheckler, 1998). A global crisis in terrestrial plants is also suggested to have occurred mainly on basis of palynological evidences (Streel et al., 2000). In such configuration, the Tournaisian witnessed a diversification of lignophytes (i.e., wood plants) as a consequence of the niches left empty by the extinction of the once dominating Devonian progymnosperms (e.g., *Archaeopteris*). Recently, a new scenario for the changes affecting the vegetation around the Devonian/Carboniferous proposed by Decombeix et al. (2011a) challenged this idea. These authors suggested that the presence of lignophyte trees is continuous across the Devonian–Carboniferous transition. Thus, there was little diversity drop close to the system boundary, and Early Tournaisian communities were more diverse than previously thought.

The presence of typical Devonian taxa in Tournaisian deposits tends to confirm the second scenario. Spermatophytes indeed seem to pass the Devonian/Carboniferous boundary without important diversity loss. They rather diversified continuously between the two periods suggesting that the Tournaisian together with the Famennian record the first diversification of seed plants with a very restricted (if any) effect of the Devonian/Carboniferous boundary.

The finding of Devonian spermatophytes in the Lower Carboniferous of Western Argentina may also shed light on the early biogeographic evolution of plant assemblages. In addition to *Pseudosporogonites* and *Warsteinia*, Tournaisian floras from Western Argentina record other typically Devonian or Devonian-like taxa such as the lycophytes *Gilboaphyton* Arnold 1937 and *Frenguellia* Arrondo et al. 1991. *Gilboaphyton/Archaeosigillaria* is clearly Devonian in Laurussia and it is never present in the Carboniferous elsewhere (Berry and Edwards, 1997) but Western Gondwana (Carrizo and Azcuy, 2006); while *Frenguellia* is a protolepidodendralean genus with a simple and "primitive" appearance (Arrondo et al., 1991) resembling typically Devonian taxa such as *Leclercqia* Banks et al. or *Colpodexylon* Banks. Considering the homogeneity of the imbedding matrix, the "good" preservation state of some morphological details as well as the large size of some plant parts a reworking of macro-remains is here considered as impossible. The Devonian affinities of Tournaisian western Gondwanan plant assemblages contrasts with coeval Laurussian and eastern Gondwana floras that record a completely different kind of assemblages containing large spermatophytes and "true" lycophytes (Decombeix et al. 2011a). As a result, there is a pattern of apparent diachronism in the evolution of fossil floras between western Gondwana and other regions during the Tournaisian. This pattern could be explained by two different, though related, scenarios. On the one hand, it is possible that such Devonian floras where virtually absent during the Late Devonian in high southern latitudes (i.e. western Gondwana), while they were dominant in the palaeotropics (i.e. Laurussia and eastern Gondwana). When more complex assemblages evolved, these Devonian-like communities were displaced towards higher latitudes; a similar scenario has been proposed for the onshore-offshore displacement pattern observed in some marine clades (Jablonski et al., 1983). On the other hand, Devonian-like assemblages could have had a world-wide distribution during the Late Devonian, being present in Laurussia eastern Gondwana and western Gondwana. Later, during the Tournaisian, more complex floras could have evolved in low latitudes (Laurussia and eastern Gondwana) overcompeting Devonian taxa in this region while they still dominated high latitude environments.

Unfortunately, the poor fossil record of Late Devonian macrofloras from Gondwana, impedes a definitive assessment of these two hypotheses. Nevertheless, the presence of similar floras (even the same species) between Gondwana and Laurussia during the Middle Devonian (Meyer-Berthaud, 2003) suggests that the latter scenario is the most plausible one. A careful study and analysis of Late Devonian Gondwana floras, together with new findings, might clarify these contrasting biogeographic patterns observed during the Tournaisian, and the actual process driving them.

5.4 The Pseudosporogonites *and* Warsteinia *life habit and the earliest Gondwanan spermatophytes communities:*

The recorded preovules occur as a dense patch within a single silty bed devoid of marine fauna. They are profusely accompanied by plant remains including lycophytes and fragmentary *incertae sedis* stems. Absence of marine fauna, high fragmentation levels, and presence of patches and clusters at the top of a thick predominantly sandy progradational interval, suggests a very shallow marine or even transitional sedimentary environment ,with high terrigeneous and freshwater input. Plants are thus all transported making ecological interpretations difficult.

Most plant remains in AQ-365 are preserved as compressions/impressions and have faded black to brown colour probably due to bad preservation of the organic matter. By contrast, the preovules are black, friable and present a silky luster suggesting exposition to wildfire (Scott, 2001). They very likely overcame a different story before deposition. The dense patch in which they have been found is here interpreted as a raft coming from a different area in the landscape.

Earliest spermatophytes have repeatedly been interpreted as opportunistic plants inhabiting areas with frequent disturbance and physical stress (Cressler, 2006; DiMichele et al., 1989; Prestianni and Gerrienne, 2010; Rothwell and Scheckler, 1989). Their record here as rare charcoalified remains among a diversified herbaceous background assemblage is consistent with these hypotheses. The herbaceous remains would represent the dominating vegetation that inhabited the wetter parts of the environment, while preovules-bearing plants very likely inhabited seasonally dry, higher areas subject to wildfire events. Therefore, such an ecological structure in plant communities, recording niche differentiation between spermatophytes and non-spermatophytes, clearly was also present at high latitude regions of Western Gondwana during the lowermost Carboniferous. Furthermore, wildfires as important driver-forces, account for a greatly overlooked, very complex ecological dynamics in these communities.

6. Conclusions

This paper documents the, most probable, earliest occurrence of seed plants in western Gondwana based on the Tournaisian ovules *Warsteinia sancheziae* sp. nov. and *Pseudosporogonites* cf. *hallei*, from western Argentina.

These taxa are typical from the type sections of the Upper Devonian of Laurussia. Their occurrence in the Tournaisian of Gondwana considerably extends their stratigraphical range, while also rises many palaeobiogeographical and palaeoecological evolutionary questions.

Glacial diamictites beds from the section studied would be linked to the Tournaisian glacial age widely recognized from a number of coeval records throughout Gondwana. Detailed palynological studies from the plant-bearing stratigraphic levels confirm strong reworking of Middle–Late Devonian intervals through glacial erosion and redeposition.

Although little is known about the dispersion capabilities of early seed-bearing plants, the presence of typical Laurussian taxa in Western Gondwana during the Tournaisian, implies that the Rheic ocean constituted a surmountable palaeobiogeographical barrier for continental biotas.

Since early seed plants are found in association with typical Devonian-like herbaceous lycophytes such as *Haplostigma*, *Frenguellia* and *Gilboaphyton*, we hypothesized two related scenarios during Devonian–Carboniferous transition to explain this unusual Tournaisian Gondwanan assemblage. According to the first one, early spermatophytes and herbaceous lycophytes communities would have risen in the palaeotropics (i.e. Laurussia) during the Devonian while later during the Early Carboniferous they were displaced towards southern latitudinal refuges (i.e.Gondwana) by more complex floras; the alternative one implies that such Devonian-like communities were already present at high latitudes during the Late Devonian and remained there as relict during the Early Carboniferous. Evidence is so far inconclusive with respect to either scenario, although scare Middle Devonian records seem to support the second one.

In addition, from a palaeoecological evolutionary point of view, evidences account for little influence of the Devonian–Carboniferous biotic crisis on the earliest diversification burst of seed plants. Furthermore, we recognize an unexpected complexity in early plant communities from Western Gondwana, including niche differentiation between early spermatophytes and herbaceous lycophytes, as well as a probable influence of fires in their ecological dynamics.

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Figure captions.

Fig. 1. Simplified map of the Sierra de Las Minitas and location of the studied stratigraphical section (A) (modified from Coughlin 2000).

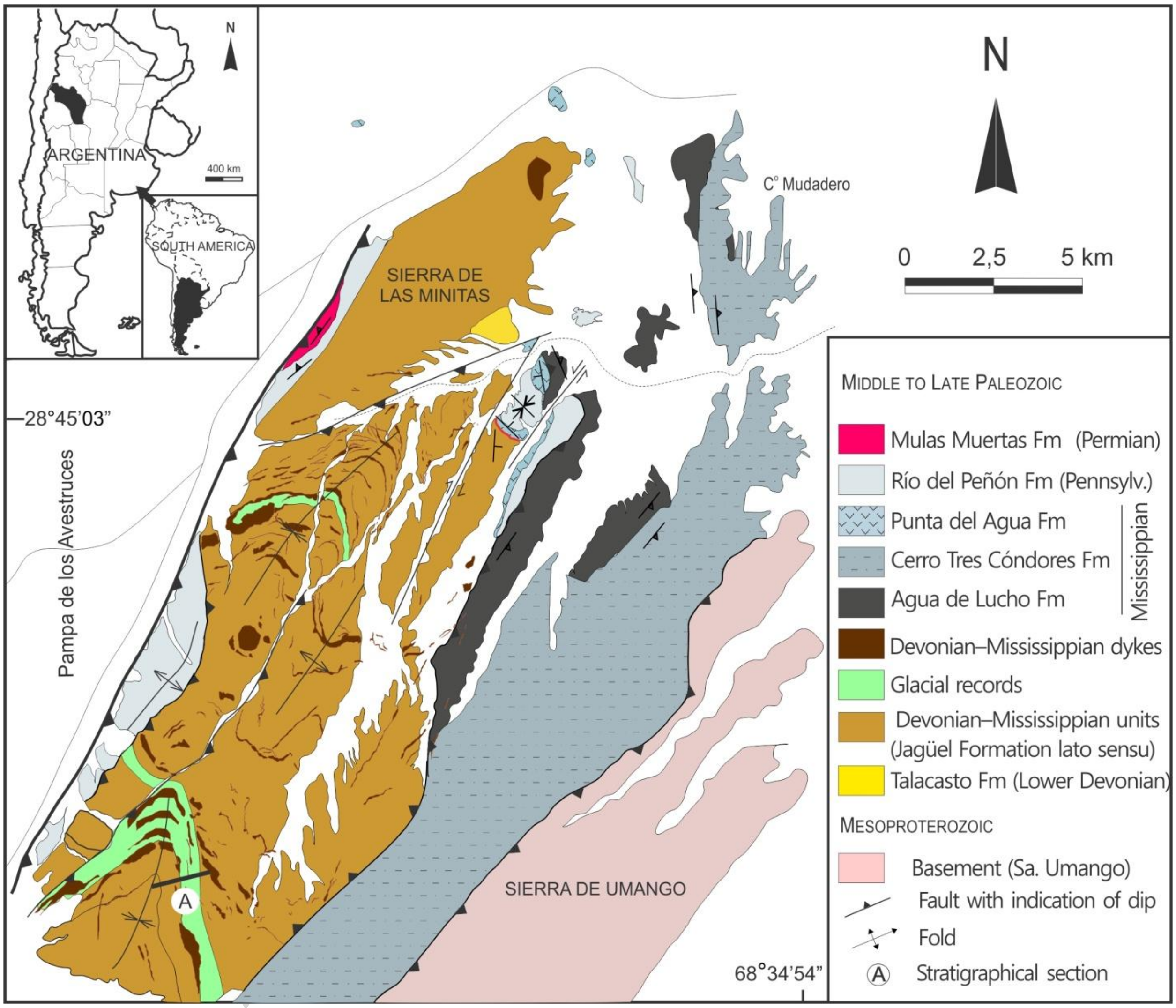
Fig. 2. Stratigraphical log of the here studied interval with localisation of plant beds and palynological samples.

Fig. 3. (a) *Warsteinia sancheziae* sp. nov.; Jagüel Formation (La Rioja Province, Argentina), Tournaisian, PULR-158, holotype; carbonaceous compression of entire ovule showing two wings and dome shaped pollen chamber; scale bar = 1 mm. (b) camera lucida drawing of specimen fig. 3a showing more clearly the winged integumentary lobes (number 1 and 2); same scale as fig. 3a.
(c–j) *Pseudosporogonites* cf. *hallei*; Jagüel Formation (La Rioja Province, Argentina), Tournaisian; scale bars = 1 mm. (c) PULR-159, ultimate dichotomy of the lateral branching system, two ovules are present. (d–f) PULR-160. (d) specimen with broken integument showing the organisation of the nucellus apex. (e) detail of specimen fig. 3d showing the dome shaped pollen chamber and broken salpinx. (f) camera lucida drawing of fig. 3e; PCF, pollen chamber floor; PC = pollen chamber; S = salpinx; same scale as fig. 3e. (g) PULR-161; specimen showing two tightly adpressed integumentary lobes. (h–j) PULR-162. (h) Most complete specimen showing the colaret cupule and three integumentary lobes. (i) camera lucida drawing of fig. 3h; same scale as fig. 3h. (j) detail of specimen fig. 3h showing organisation of the cupule (arrow).

Fig. 4. *Pseudosporogonites* cf. *hallei*; reconstitution based on specimen illustrated on figure 3c. Scale bar = 2 mm.

Fig. 5. The Gondwanan Lower Mississippian (Tournaisian) guide spore *Waltzispora lanzonii*; PULR-166; scale bar = 10 µm.

Figure 1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ARGENTINA
400 km
SOUTH AMERICA
N
0
2,5
5 km
C° Mudadero
SIERRA DE
LAS MINITAS
—28°45'03"
Pampa de los Avestruces
A
SIERRA DE UMANGO
68°34'54"
MIDDLE TO LATE PALEOZOIC
Mulas Muertas Fm (Permian)
Río del Peñón Fm (Pennsylv.)
Punta del Agua Fm
Cerro Tres Cóndores Fm
Agua de Lucho Fm
Mississippian
Devonian–Mississippian dykes
Glacial records
Devonian–Mississippian units (Jagüel Formation lato sensu)
Talacasto Fm (Lower Devonian)
MESOPROTEROZOIC
Basement (Sa. Umango)
Fault with indication of dip
Fold
Ⓐ Stratigraphical section

Figure 2

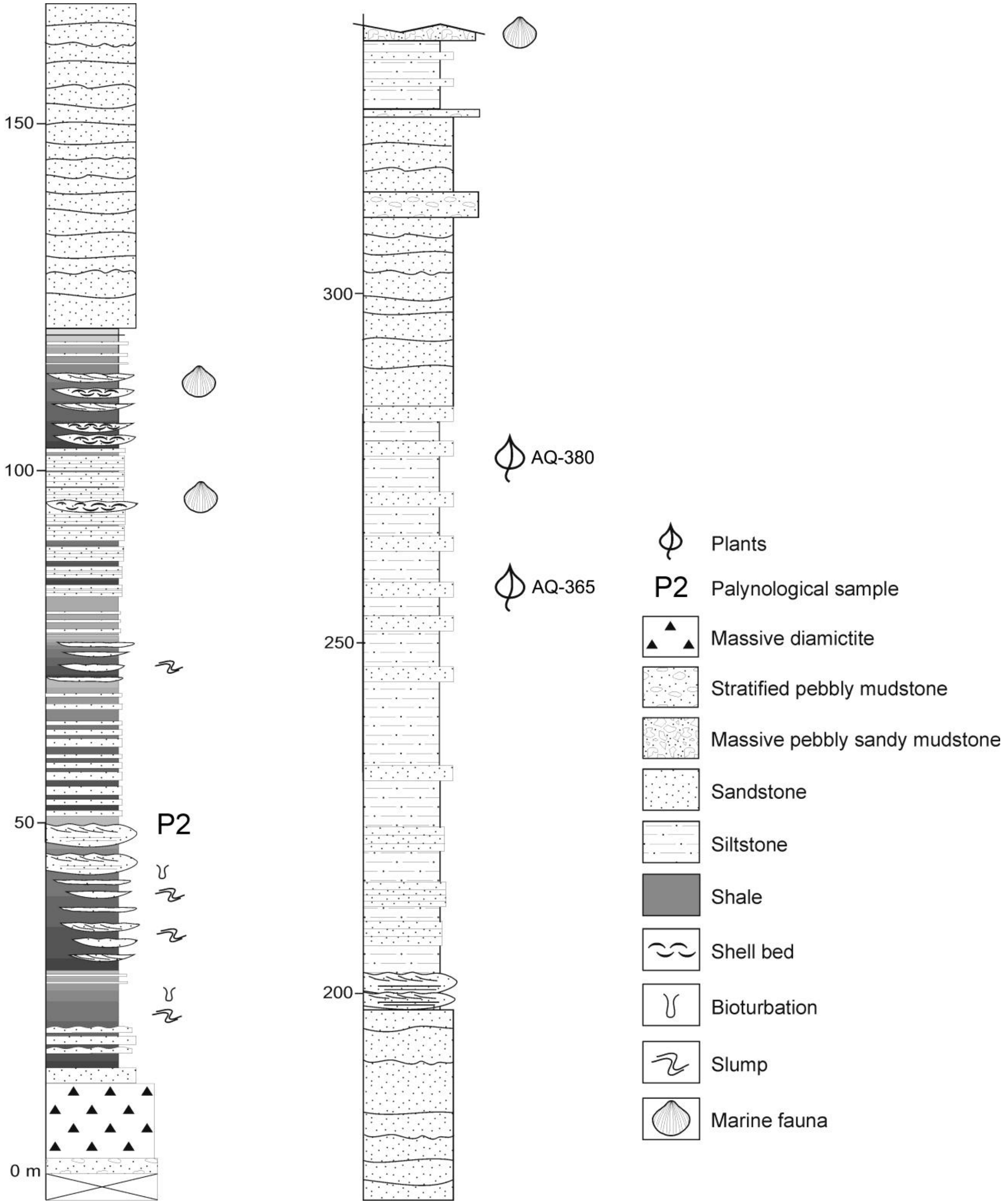

150
100
50
0 m
300
250
200
P2
AQ-380
AQ-365
Plants
P2 Palynological sample
Massive diamictite
Stratified pebbly mudstone
Massive pebbly sandy mudstone
Sandstone
Siltstone
Shale
Shell bed
Bioturbation
Slump
Marine fauna

Figure 3

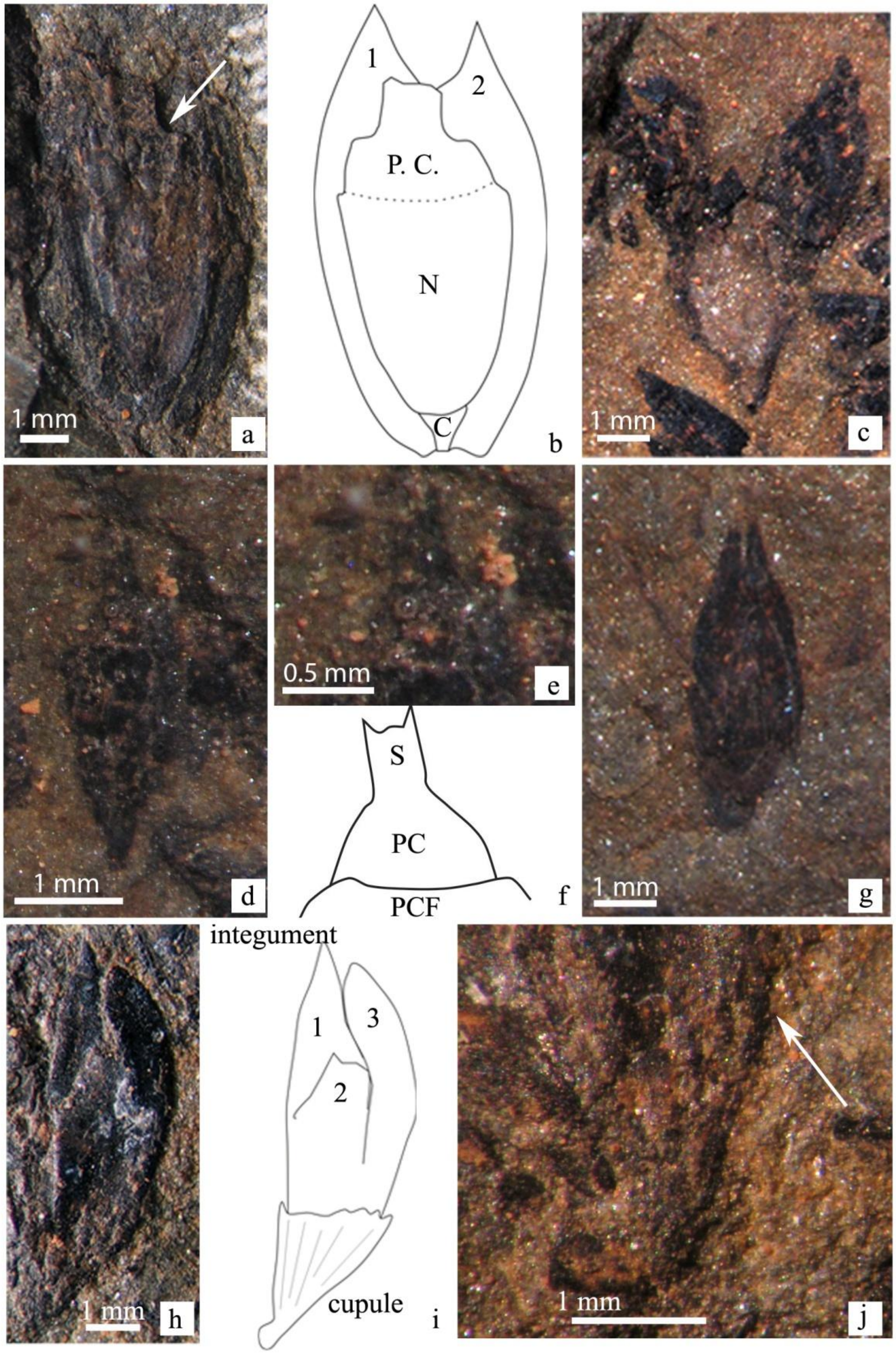

1 mm
a
1
2
P. C.
N
C
b
1 mm
c
1 mm
d
0.5 mm
e
S
PC
PCF
f
1 mm
g
integument
1
3
2
cupule
i
1 mm
h
1 mm
j

Figure 4

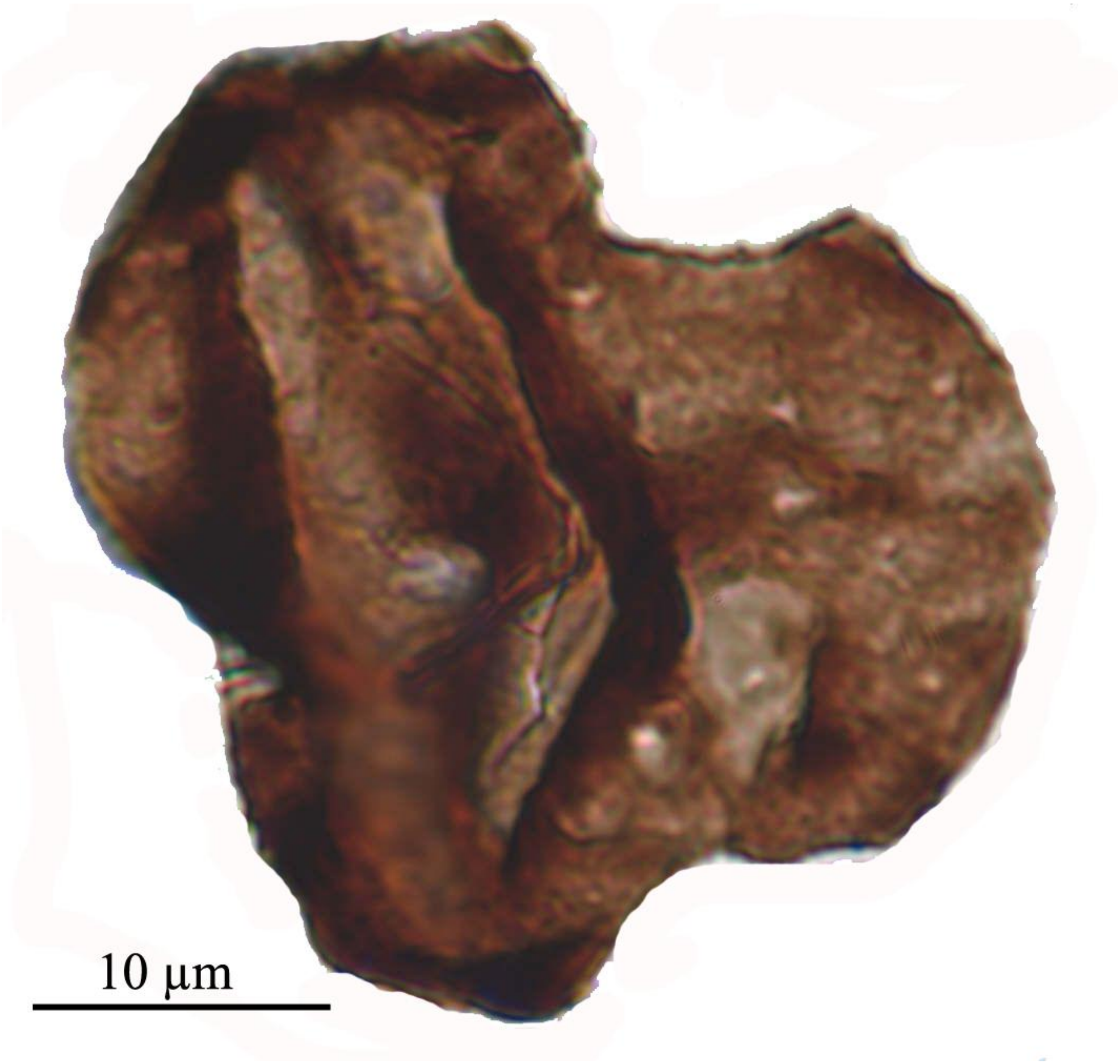
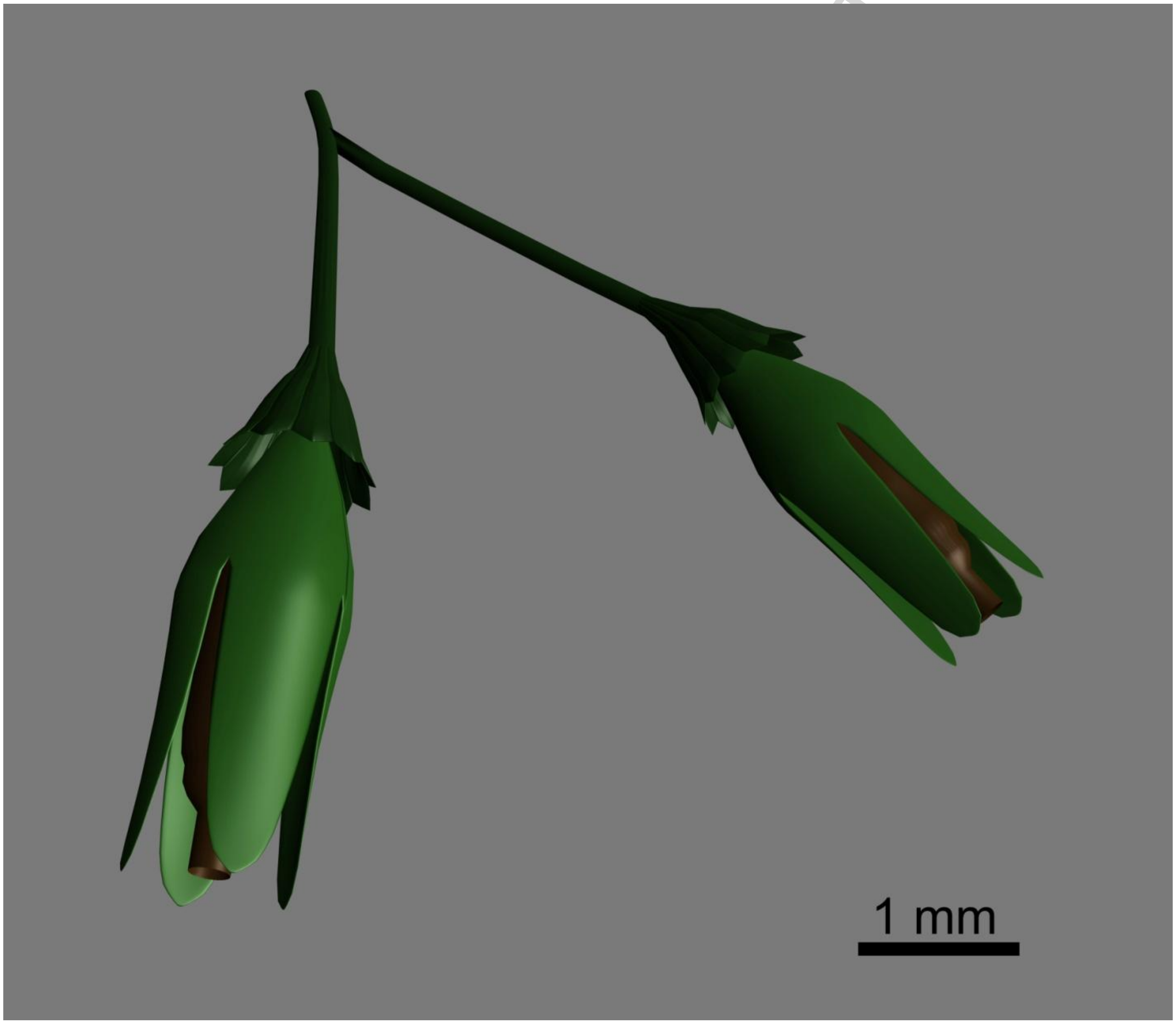


Figure 5



Graphical abstract

Research highlights

- We here document the earliest occurrence of spermatophytes on western Gondwana.
- We confirm (near) contact between Laurussia and Gondwana in the Tournaisian.
- We show delayed taxa occurrences between the Laurussia Dev. and Gondwana Tourn.