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Porongodendron minitensis gen. nov. sp. nov. a new lycopsid from the Mississippian of Argentina with adaptations to tundra-like conditions

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ABSTRACT

The Mississippian is characterized worldwide by a general cooling of the environment and a climatic stratification of Earth. Argentina at that time was part of the megacontinent Gondwana. It occupied a position close to the South Pole around 60°S. Whereas paleoequatorial and paleotropical floras are relatively well known, higher latitude environments are still poorly understood. In this framework, a revision of Mississippian deposits is ongoing in Argentina. An extensive and detailed survey of the Sierra de las Minitas (La Rioja Province, western Argentina) involved drawing detailed sections and the systematic verification of all rock layers. Fossils were sampled and studied in the laboratory. We describe a new isoetalean lycopsid with a rare combination of characters. This plant presents an estimated low stature (approximately 30 cm), a branched rhizomorph, an inflated intermediary zone, a monocaulous growth form and evidence for cyclic fertility. These features are interpreted as representing specific adaptations to the harsher tundra conditions prevailing in the Lower Carboniferous Southern Polar environments.

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KEYWORDS

Fertile zones; Gondwana; periodicity; rhizomorph; *stigmara*; Tournaisian

Introduction

The Mississippian of Argentina has yielded many fossil plant remains (Menéndez 1965; Petriella and Arrondo 1978; Morel et al. 1993; Azcuy and Carrizo 1995; Carrizo and Azcuy 1998, 2006). They form low-diversity assemblages dominated by herbaceous or pseudoherbaceous lycophytes (*Archaeosigillaria* and *Frenquellia*), together with rare filicophytes and spermatophytes as secondary elements. Up to now mainly studied for biostratigraphical purposes, these assemblages are identified as characterizing the *Archaeosigillaria-Frenquellia* (AF) biozone, which is considered as Lower Carboniferous (likely Tournaisian) in age (Césari et al. 2011). Also known as the *Archaeosigillaria-Lepidodendropsis-Frenquellia* flora in Iannuzzi and Rösler (2000), it represents assemblages associated with cold climatic conditions that prevailed around the South Pole at that time.

Numerous relatively easily identified, but highly fragmented, lycophytic remains were discovered within this flora (Menéndez 1965; Petriella and Arrondo 1978; Morel et al. 1993; Azcuy and Carrizo 1995; Carrizo and Azcuy 1998, 2006). The generally small size of collected samples, as well as their preservation state, has until now discouraged valuable conceptual reconstruction of the original plants.

Nevertheless, the importance of establishing whole plant concepts has been repeatedly recognized (Bateman and Hilton 2009). It supersedes classical stratigraphic issues in order to address evolutionary and ecological questions.

In the course of a revision project of the Mississippian of Argentina, we explored a new section at the Sierra de las Minitas (La Rioja Province, Argentina). This Agua Quemada section yielded abundant fossil plant remains that included the early seed plants *Pseudosporogonites* cf. *hallei* Stockmans and *Warsteinia sancheziae* Prestianni et al. (Prestianni et al. 2015). Associated with these spermatophytes, we collected several specimens of what appears to be a new small monocaulous lycopsid. The goal of the present paper is to describe this new plant sufficiently well as to produce a whole plant concept, allowing us to address specific evolutionary and ecological questions.

Geographical and geological settings

The stratigraphic record surveyed in this contribution corresponds to the Mississippian filling of the Río Blanco Basin (Scalabrini Ortiz 1972), a high paleolatitude southern basin (>60° according to Isaacson et al. 2008) that forms part of a series of Late Paleozoic basins developed in southwestern Gondwana linked

to the functioning of an active tectonic margin (Limarino and Spalletti 2006). In addition, these Mississippian units contain many glacial features which, together with the paleogeographical position of the basin, and further evidence from other coeval regions of southwestern Gondwana, suggest a cold wet climate during this interval (Iannuzzi and Rösler 2000; Caputo et al. 2008; Isaacson et al. 2008; Prestianni et al. 2015; Ezpeleta et al. 2020).

The study unit is the Agua de Lucho Formation, cropping out at the Agua Quemada section (Ezpeleta et al. 2020) located at Sierra de Las Minitas, 30 km to the southwest of Jagüé town in La Rioja Province, western Argentina. The complete stratigraphic column at Agua Quemada is thicker than 1000 m; the detailed sedimentological and sequence stratigraphic analysis has been reported by Ezpeleta et al. (2020). The lower part of the Agua de Lucho Formation is characterized by the presence of glacially influenced sequences, whereas the upper part is dominated by sequences lacking direct glacial evidence (Ezpeleta et al. 2020). The Agua de Lucho Formation records a diverse fossil assemblage containing marine invertebrates and plant remains (Prestianni et al. 2015; Sterren et al. 2021). The marine fauna has been divided in five compositionally distinct assemblages (Sterren et al. 2021); the material studied in the present contribution occurred within the “fossiliferous interval 5” described by Sterren et al. (2021). More precisely, the fossils originated from the same plant bearing beds (levels AQ-365 and AQ-380) as those described by Prestianni et al. (2015), about 200 m above the last recorded glacial diamictite (see Ezpeleta et al. 2020 Supplementary material; Prestianni et al. 2015). These levels occur within sequence 10 as defined by Ezpeleta et al. (2020), which lacks evident proximal glacial influence. The succession represents a coarsening-upward interval, mainly composed of greenish to blackish green siltstones with relatively scarce interbedded fine-grained sandstones (for more stratigraphic details see Ezpeleta et al. 2020). Environmental interpretations based on lithofacies and faunal and floral fossil assemblages indicate that these fossiliferous levels represent shallow marine (shoreface) to deltaic settings (Ezpeleta et al. 2020).

The age of the plant-bearing deposit is considered Tournaisian, based on the record of the Gondwanan index miospore *Waltzispora lanzonii* Deamon 1974 (Playford and Melo 2010) immediately above the last registered glacial diamictite, nearly 150 m below plant level P2 of Prestianni et al. (2015). A more precise age of the studied levels as middle to upper Tournaisian is indicated by the presence of the regional index brachiopod *Azurduya chavelensis* (Amos), whose stratigraphic range is limited to sequence 10 of Ezpeleta

et al. (2020) at Agua Quemada (Sterren et al. 2021). The *Azurduya chavelensis* age has been constrained based on co-occurring ammonoid species in multiple localities (Sterren et al. 2021).

Material and methods

All specimens come from a single stratigraphic level (AQ-365 collecting site, 28° 48' 44.3" S/ 68° 45' 01.8" W) within a thick massive greenish-dark grey siltstone interval.

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. Plates were composed with Corel Draw X6. Transformations made to the images in Photoshop CS5 version 12.0 include cropping, rotation, and adjustment of contrast.

Illustrated plant specimens have been numbered with the prefix PULR-B. They are housed in the palaeontological collections of the Museo de Ciencias Antropológicas y Naturales at Universidad Nacional de La Rioja, La Rioja, Argentina.

Systematic paleontology

Class–Lycopsida

Order–Isoetales Meyen 1987

Family–Incertae sedis

Genus–Porongodendron *gen. nov.*

Type species–Porongodendron minitensis *sp. nov.*

Generic diagnosis

Small, unbranched upright plant with complex branched rhizomorph. Transition zone present at the base of the stem. Leaf bases rounded with rounded leaf scar. Sporophylls occurring in fertile zones alternating with vegetative zones. Microphylls helically arranged, slender, present towards the apex of the plant. Microphylls deciduous.

Specific diagnosis

Stem 0.5–1 cm wide; helically arranged, rounded to slightly elongated leaf traces \approx 1 mm in diameter. Leaf trace density variable. Abruptly alternating vegetative and fertile zones. When microphylls are absent, alternating zones with widely spaced leaf bases (vegetative) and densely spaced leaf bases (fertile) are present. Microphylls 2–2.5 cm long, filiform, helically arranged and attached to axis at a 60° angle. Microsporophylls 1–1.5 cm long, filiform, helically arranged and attached to axis at a 60° angle. Sporangia ovate in shape, 1 mm long and 0.5 mm wide, on the adaxial face of the microsporophyll.

Derivation of the name

Porongo- is the Argentinian vernacular name of a gourd cup used for drinking the local infusion called mate, the shape of which resembles this plant. – *den-dron* is the Greek name for tree. *Minitensis* refers to the Sierra de la Minitas where the fossils were collected.

Material: PULR-B 001–025

Holotype. PULR-B 004 (Figure 1C)

Epitypes. PULR-B 001 (Figure 1A–B), PULR-B 010 (Figure 2H)

Paratypes. PULR-B 002 (Figure 1E), 003 (Figure 2C), 005–009, 011–025.

Repository. Palaeontology collections of the La Rioja University PULR- (Argentina, La Rioja Province).

Type locality. Sierra de Las Minitas, La Rioja Province, Argentina; Agua de Lucho Formation; Tournaisian.

Age. Middle to Late Tournaisian.

Description

Up to 100 specimens have been studied. They are preserved as compressions and impressions. They are represented by rhizomorphs, stems, microphylls and fertile parts.

Rhizomorph

Four representative specimens are described here in detail (Figure 1). One is preserved with rhizomorph parallel to the bedding plane (Figure 1A–B) and the other three are compressed following the long axis of the plant. All four specimens consist of the basal portion of the plant with stems and rhizomorphs in organic connection (Figure 1C–F). Only small specimens (juveniles?) have been found with the rooting system attached. These specimens range from 3.0 to 4.5 cm in length. Figure 1A, B shows the rooting system to consist of four main rooting axes departing from a single point. In this specimen the main rooting axes measures 2 mm in width. All four are broken after 0.4–0.9 mm. They seem to branch dichotomously shortly after divergence. Each axis is covered by either slender (up to 2.7 mm long and 0.1 mm wide) roots or by smaller (0.1 mm wide) root scars. Those specimens that compressed following the long axis of the plant (Figure 1D–F) show the “roots” arising from the stem base after a small constriction (arrowed on Figure 1D). They are 3–6 mm wide and abruptly spread away from the trunk base, dipping slightly by forming an angle of approximately 100° with the stem. Their surface is irregular; small, spirally arranged root scars were observed on the best-preserved specimens (Figure 1E). Slender roots up to 6 mm long are present on some specimens (arrowed on Figure 1 B and E) but a definite rhizotaxy is difficult to assess. Roots are always broken so their full length cannot be assessed

reliably. The specimen PULR-B 002 (Figure 1E) is as well preserved, with the long axis parallel to the bedding plane. It is 14.3 mm long and its stem is 3 mm wide. In this specimen, a casual cross section through the rhizomorph axis showed them to be filled with sediment, suggesting that they were originally hollow or filled with parenchyma that failed to preserve (Figure 1E). Each hollow root measures on this specimen 1.9 mm in diameter.

Intermediate zone

We interpret a smooth zone between the rhizomorph and the first row of leaf bases (Figure 1 C, E and F) as a transition zone. Only small specimens have been found with the transition zone preserved. When present, it ranges from 2.0 to 2.5 cm long and from 0.6 to 1.0 cm wide. This zone is slightly inflated in the middle and presents no discernible ornamentation (Figure 1F). Some specimens give the impression of rough longitudinal grooves that suggest shrinkage of this part of the plant, contrasting with the more rigid aspect presented by the stem.

Stems

All stems have the same general appearance. The largest available specimens are up to 13 cm long (Figure 2A). They consist of slender stem fragments ranging from 0.5 to 1 cm wide for most of their length (tab. 1). Slight narrowing from base to top is not considered significant, given the limited size of preserved plant fragments. At the base, close to the intermediate zone, the stem is marked by a constriction and measures ≈ 0.5 cm wide (Figure 1C and Figure 1F) and rapidly broadens upwards over 1 centimeter and then remains relatively constant as described above. Stems occur in several decortication stages (Figure 2A–C). No dichotomies have been observed. Leaf base morphology is visible on most specimens and constitutes a unifying feature for all stem remains (fig. 1C, 2A–E). Preservation has a strong influence on the general aspect of leaf bases. In some specimens they appear as a succession of depressions and protrusions, suggesting that both sides of the stem are visible (Figure 2A–B), but in others they rather appear as clear protrusions (Figure 2C–E). They are helically arranged and mainly rounded, measuring ≈ 0.5 mm in diameter. Leaf bases are raised on the surface of the axis (Figure 2 C–E, Figure 3 A–C). In side view, they present a characteristic truncated conical shape and measure ≈ 1 mm in height (Figure 2E). In perpendicular view they vary from nearly rounded in shape up to slightly decurrent downwards. Some of them are extended vertically by narrow ribs (Figure 2 D and E, Figure 3 A). The

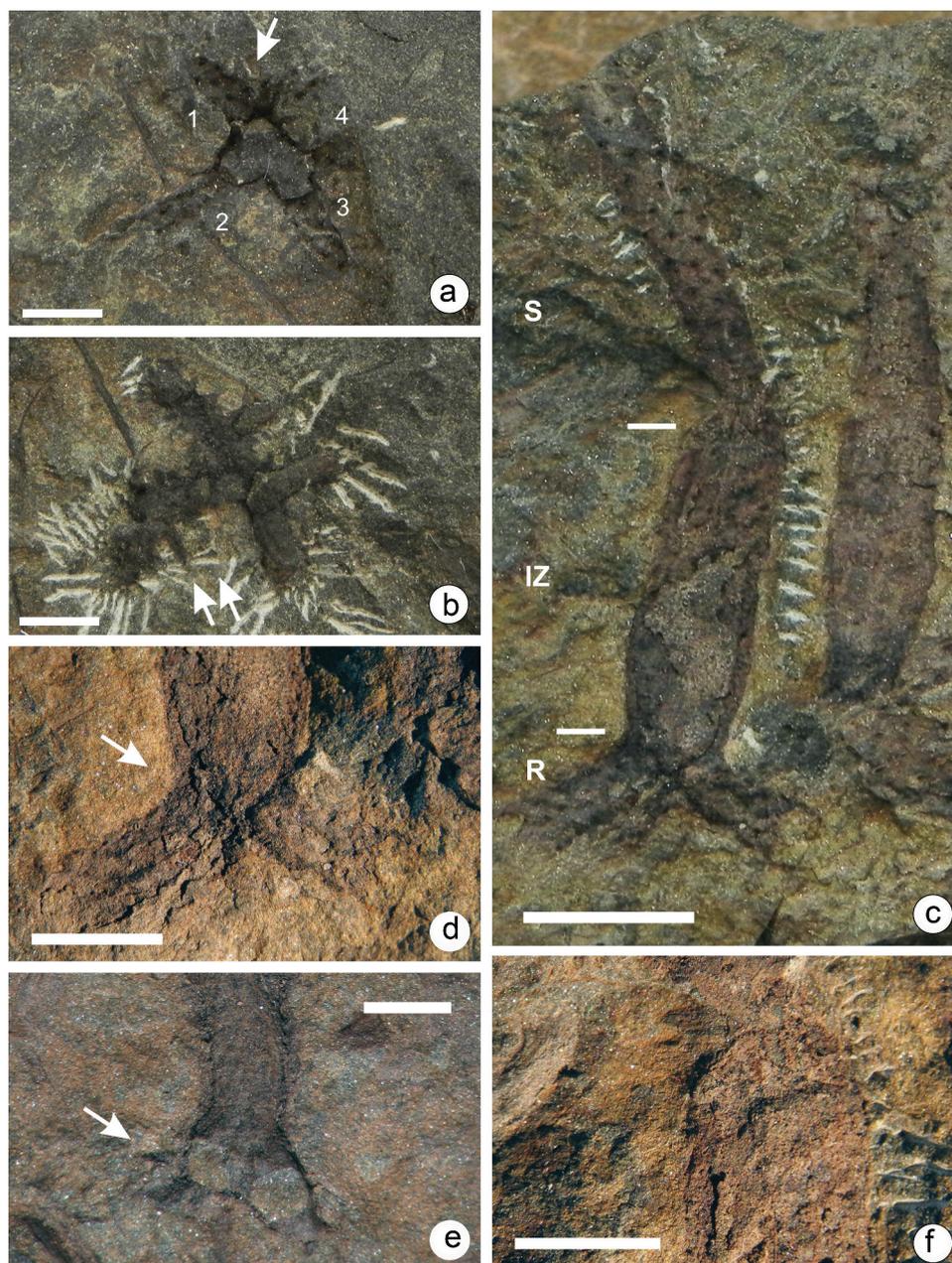


Figure 1. A) Specimen preserved with the main axis perpendicular to the bedding plane. The rhizomorph is seen in normal growth position. Four main roots are marked from 1–4. Note the presence of small rootlets and rootlet scars. PULR-B 001 a (Epitype). Scale = 0.5 cm. B) Counterpart of specimen Figure 1A. This specimen has been prepared by “dégagement”. PULR-B 001 b. Scale = 0.5 cm. C) Specimen preserved with the main axis in the same plane as the bedding. It shows the base of the plant with rhizomorph (R), intermediary zone (IZ) and stem (S). The rhizomorph shows two main roots departing from a central point. They are covered by small rootlet scars. Intermediary zone is smooth and links the rhizomorph to the stem, which is covered by small leaf scars. PULR-B 004 (Holotype). Scale = 1 cm. D) Detail of the specimen figure C. It shows the constriction at the base of the intermediary zone (arrowed) and the departure of two main roots from a central point. Scale = 0.5 cm. E) Specimen preserved with the main axis in the same plane as the bedding plane. It shows the base of two main roots presenting short and slender rootlets (arrowed). PULR 002. Scale = 0.3 cm. F) Detail of the specimen in figure C, showing the base of the stem. PULR-B 004 (Holotype). Scale = 0.5 cm.

angles that leaf scar parastichies form with the longitudinal axis of the stem ranges from 30 to 45°. The vertical distance between successive parastichies (i.e. the orthostichy) ranges from 2 to 4 mm and leaf scars are horizontally separated by 1 to 2.5 mm. There seems not to be a clear relationship between distances separating leaf scars and the size of the stems. The density of leaf scars at the surface of the stems is indeed highly variable,

even on the same stem. When preserved stem fragments are sufficiently long, they clearly show an alternation of densely and loosely arranged leaf bases. The specimen illustrated in Figure 2A is 11 cm long and clearly shows two zones where leaf bases are more loosely organized (GZ in Figure 2A). Looser zones are 3 to 4 cm in length whereas the alternating denser zones are only 1 to 1.5 cm in length.

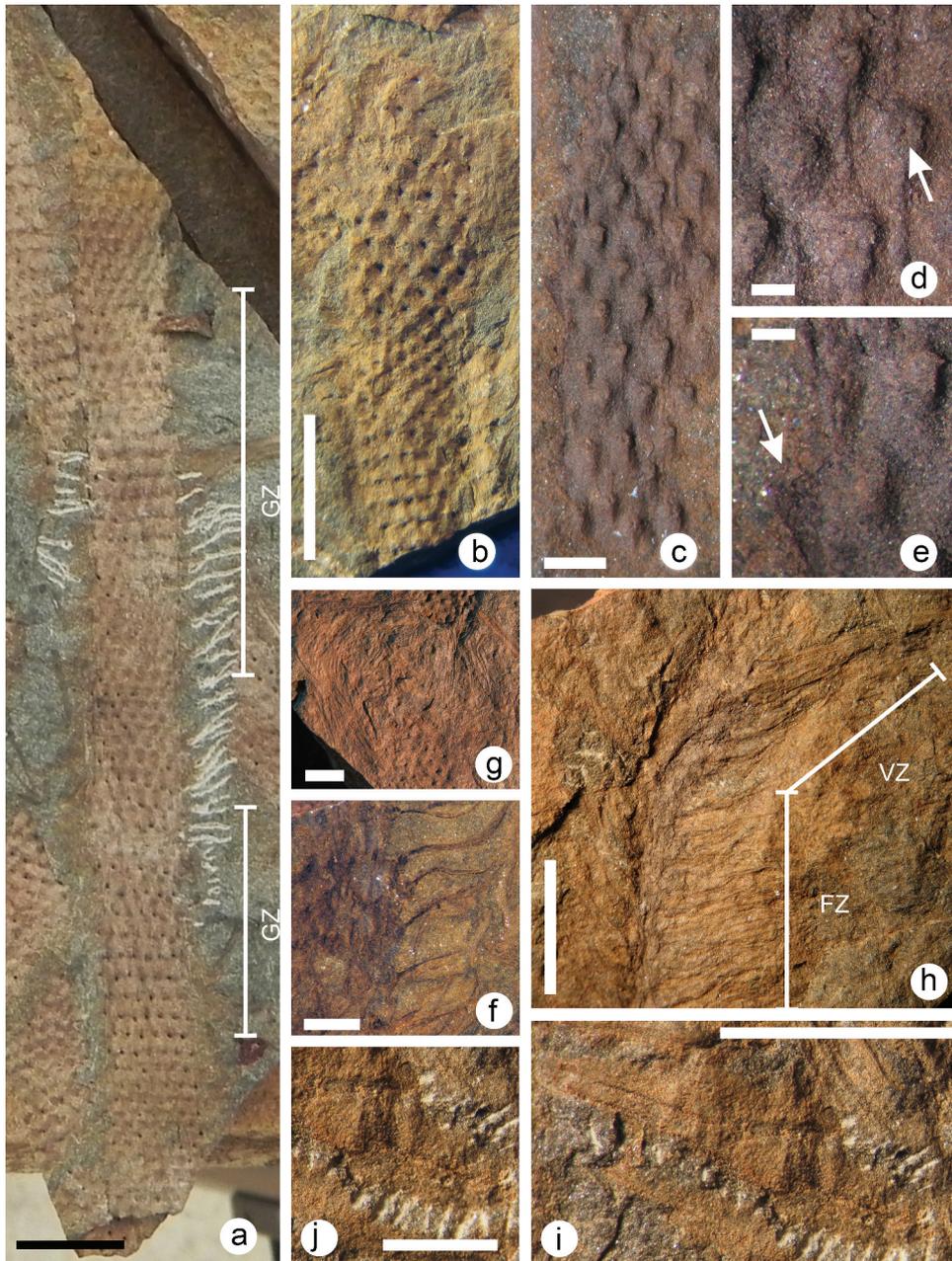


Figure 2. A) Specimen showing the succession between loosely spaced leaf bases and more densely organized ones. PULR-B 006. Scale = 1 cm. B) Specimen showing the succession between loosely spaced leaf bases and more densely organized ones. PULR-B 007. Scale = 1 cm. C) Particularly well-preserved non-decorticated specimens showing details of the external organization of the stem. Leaf bases are three dimensionally preserved. PULR-B 003. Scale = 2 mm. D) Detail of specimen figure C showing details of a leaf base with a scar corresponding to the vascular bundle. Scale = 0.5 mm. E) Detail of specimen figure C showing the right side of the stem where leaf scars are seen in profile view (arrow). Scale = 0.5 mm. F) Specimen showing a stem covered with leaves. PULR-B 008. Scale = 0.5 cm. G) Photographed under water, this specimen shows the shape of the leaves and their attachment on the stem surface. PULR-B 09. Scale = 0.5 cm. H) Small stem fragment showing a fertile zone (FZ) immediately followed by a vegetative zone (VZ). PULR-B 010. Scale = 1 cm. I) Detail of a fertile microphyll. It shows the elongate ovate shape of the sporangium. PULR-B 011. Scale = 1 mm. J) Detail of specimen in Figure 2I showing the sporangium. Scale = 0.5 mm.

Microphylls

Vegetative leaves (microphylls) are present in a few specimens (Figure 2F-G). The base of vegetative microphylls is conical in shape (Figure 2G, Figure 3 B-C). Microphylls are filiform and 0.2 mm broad at the base. They are up to 2–2.5 cm long and narrow distally to a pointed tip. Together they form a loose

cover around the stem. The large number of naked stems, however, suggests that they are deciduous. There are some indications of vascular traces in one particularly well-preserved specimen (Figure 2D-E). The vascular trace in this specimen is situated in the center of the leaf scar. It is circular in shape and measures 0.1 mm wide.

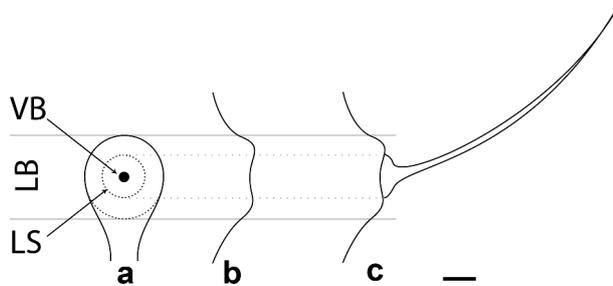


Figure 3. Schematic drawing of the leaf bases: in face view (A), side view without leaf (B) and side view with leaf attached (C). LB = Leaf base; LS = Leaf scar; VB = Vascular bundle. Scale = 0.1 cm.

Fertile zone

Ten compact fertile zones have been recovered (Figure 2H–J). They are always found dispersed. These fertile zones are consistently found in relatively narrow stems, suggesting that they were located at the apex of the plant when functional. They range from 0.5 to 1 cm wide basally and progressively taper distally. As they are always broken, their length is difficult to assess reliably, but they never seem to exceed 2 cm in length. The sporophylls are arranged helically and in a denser pattern than the microphylls of the vegetative parts (Figure 2H). They are inserted at an angle of $\approx 60^\circ$ on the stem (Figure 2H–I). The sporophylls are between 1.5 cm long basally, shortening to 1.0 cm toward the presumed stem apex, and have entire margins (Figure 2I). The sporangia, although difficult to observe due to preservation state, are ovate in shape and adaxially borne (Figure 2I–J). They are approximately 1 mm long and 0.5 mm wide. Their attachment mode on the microsporophyll is difficult to assess reliably, considering the coarse grain of the sediment (Figure 2J). Consequently, any evidence of a ligule would not be preserved.

The specimen illustrated Figure 2H is particularly interesting. It is 3.2 cm long and shows the apical part of the plant. The width of the stem is difficult to assess reliably as it is covered by microphylls for its entire length. Two types of microphylls are present. Fertile sporophylls cover the first 1.7 cm of the stem fragment (FZ on Figure 2H) whereas vegetative microphylls cover the 1.5 cm long apical most part of the specimen (VZ on Figure 2H). The fertile zone is characterized by a denser cone-like organization with individual sporophylls difficult to identify, whereas the distalmost part presents a looser organization with individual sporophylls clearly identifiable. No spores were observed.

Discussion

Comparison

The fossil record of the Late Devonian/Early Carboniferous contains many reports of lycopytic remains (e.g. Chaloner and Boureau 1967). However, in

many cases they are highly fragmented with only the stem preserved in a more or less advanced decortication state. In addition to the whole-plant concept here proposed for *Porongodendron*, it is equally important to identify the organ-taxa that constitute this species concept.

These elements allow new insights into the taxonomic puzzle surrounding the so-called “dwarf” lycophyte taxa from the Mississippian of Southwestern Gondwana (Frenguelli 1951, 1952; Menéndez 1965; Arrondo et al. 1991; Gutiérrez and Arrondo 1994). The main sources of confusion regarding taxonomy based exclusively on stem characters is that it may either encourage an over-split taxonomy that fails to consider the natural ontogenetic (and taphonomic) variations within a species or, on the other hand, to inclusion of several contrasting forms within the same name. Indeed, similar stem morphologies can correspond to several plants, leading to important and undesirable imprecision, notably in biostratigraphic interpretations. The risk for confusion increases considerably when dealing with relatively simple organs (e.g. *Hostimella*). The lycophyte stems compared here are very simple in construction. The present comparison is thus conducted with care and with conscience of the limited utility of such taxonomic comparisons. Moreover, we opted to limit the comparison to regionally important taxa, to avoid as much as possible taxonomic confusion.

The presence of reliably unbranched axes bearing spirally arranged, slightly raised rounded leaf bases is characteristic of either *Haplostigma* Seward, *Malanzania* Archangelsky et al. and/or *Malimanium* Carrizo and Azcuy (Seward 1932; Archangelsky et al. 1981; Carrizo and Azcuy 2015). All three genera have been described from Gondwana. They are mainly differentiated on the shape and organisation of the leaf bases. Additional differentiating characters are the size of the stems, the shape of the leaf bases and the presence/absence of ribbing. In turn, each taxon seems to have a specific stratigraphic range (Devonian for *Haplostigma*, Mississippian for *Malimanium* and Pennsylvanian for *Malanzania*). It appears particularly difficult to differentiate these genera, as morphological differences are very tenuous and could sometimes be linked to ontogenetic and/or diagenetic processes.

Haplostigma irregularis Seward (1932) is the type species of the genus, originally named *Bothrodendron irregulare* (Schwarz 1906). The validity of this genus has been questioned several times (e.g. Chaloner and Boureau 1967; Moisan et al. 2011). However, Moisan et al. (2011) suggested to use it as a morphogenus “for unbranched herbaceous Palaeozoic lycopod stems lacking vascular traces (*nb* better said with indistinct vascular traces)”. The recent publication of new abundant material from Brazil included a discussion of the genus (Matsumura et al. 2015). This work, as well as a revision conducted by CP, allowed the identification of several

important features of the genus. The stems in *Haplostigma* present enlarged spine-like leaf cushions that form rounded to subhexagonal patterns and follow a pseudosigillarioid to sigillarioid phyllotaxy. In *Porongodendron* the stems are similarly covered by spine-like rounded leaf bases, but they present a more lepidodendroid phyllotaxy. By contrast with *Haplostigma*, the leaf bases in this plant do not form clear vertical ridges. Naked stems of *Porongodendron* cannot in consequence be assigned to the genus *Haplostigma*.

Malanzania was originally erected for herbaceous stem remains from the Bashkirian Malanzán Formation, Argentina (Archangelsky et al. 1981). Four species have thus far been recognised within the genus: *M. nana* Archangelsky et al., *M. Antigua* Archangelsky, *M. ottonei* Carrizo and Azcuy, and *M. starckii* Di Pasquo. *Malanzania nana* is the basionym of the genus and is early Bashkirian in age (Archangelsky et al. 1981). It is characterized by unbranched stems up to 13 mm wide bearing subcircular to subrhombic 1 mm wide leaf bases and following a lepidodendroid phyllotaxy. They form up to 1 mm long spiny structures. *Porongodendron* and *M. nana* differ in stem organisation, which is simpler in the latter, lacking the characteristic cyclic growth and presenting smaller and more widely spaced leaf bases.

Malanzania Antigua corresponds to Middle Devonian remains from the Malvinas Islands (Archangelsky 1983). First reported by Seward and Walton (1923), the species is based on a few specimens representing up to 3 cm wide stems covered by helically arranged 1–1.5 mm wide dome-shaped leaf bases (Archangelsky 1983; Gutiérrez 1996). *Malanzania Antigua* shares many features with *Haplostigma irregularis* and *H. furquei* to which it has repeatedly been assigned (Frenguelli 1951, 1952; Menéndez 1967). *Porongodendron* does not compare favourably with stems of these other taxa.

Interestingly, *Malanzania ottonei* has been collected from lower Mississippian deposits here interpreted as closely related to the Agua Quemada section (Carrizo and Azcuy 1998, M. Ezpeleta, pers. comm. December 2015). This species corresponds to plants presenting a growth habit very similar to that of *M. nana* but with typically smaller features. The stems are up to 5 mm wide and covered by 0.5 to 1 mm wide subcircular leaf bases, which follow a lepidodendroid phyllotaxy with rows at 40° to 50° from the vertical. These characteristics are similar to those observed in smaller stems of *Porongodendron*. We consider that *Malanzania ottonei* corresponds with an early ontogenic stage of the stem of *Porongodendron*.

Malimanium lillum Carrizo and Azcuy is a lower Mississippian plant also presenting similar characteristics. Stems are up to 30 mm wide and covered by up to 2 mm wide leaf bases forming an angle of about 45°

with the vertical axis. Despite differences in respective sizes of the stems and leaf bases, this plant presents many characteristics in common with the bigger stems of *Porongodendron*. Indeed, one specimen (Figure 2C) has been partially three dimensionally preserved. It shows feature very similar, if not identical, to *Malimanium lillum*. *Malimanium* is, however, a form genus that only refers to stem fragments representing a specific ontogenic stage.

It is clear from this comparison that dispersed stems of *Porongodendron* could either be attributed to *Malanzania* and/or to *Malimanium*. Therefore, both *Malanzania* and *Malimanium* should be considered fossil-genera, and could indeed represent different ontogenic stages of the same plant. However, unbranched stem fragments with simple leaf bases are relatively common in the fossil record and it is impossible in most cases to ascertain the natural species they represent. We suggest that *Malanzania* and *Malimanium* should be kept as fossil-genera that accommodate isolated stem fragments of which it is impossible to associate a whole plant reconstruction.

Whole plant reconstruction

Despite its fragmentary preservation state, a reconstruction of *Porongodendron* was made possible through the identification of stem features shared by specimens showing the roots and specimens showing the leaves (both fertile and vegetative) (Figure 4A). This allowed a reconstruction based on both organic connections and morphological similarity (*sensu* Bateman and Hilton 2009). The plant presents a branched rhizomorph with four main axes bearing slender roots (Figure 4B). The rhizomorph is immediately topped in the youngest ontogenic stages by a smooth intermediary zone that is slightly expanded in the middle. The stem is unbranched, naked basally and covered distally by slender and undivided long loosely organized microphylls. Leaf bases occur in a pattern with alternating densely and loosely organized zones. The fertile parts present shorter and densely organized sporophylls bearing ovate sporangia on the adaxial face. Both the microphylls and the sporophylls are deciduous leaving on the stem characteristic leaf scars. The leaf bases are ovate in shape and present a vascular trace in the center. A repeated pattern of dense and looser leaf bases is suggested to correspond to the alternation of fertile and vegetative zones. This suggests cyclic fertility periods. Unfortunately, no spores were preserved. It is however very likely that given that all known rhizomorphic lycopsids are heterosporous, *Porongodendron* as well was heterosporous. We estimate that the plant did not exceed 30 cm in height. A reconstruction is proposed on Figures 4 and 5.

Affinities of *Porongodendron*

As reconstructed here, *Porongodendron* presents a particular set of characters combining features of arborescent lycopsids such as the branched rhizomorph with the monocaulous growth habit of certain non-rhizomorphic early Paleozoic lycopsids (Pigg and Taylor 1985; Chitale and Pigg 1996; Pigg 2001). The reconstructed growth habit, as well as details of the structure of the stem and fertile zone(s) in *Porongodendron*, are strongly reminiscent of *Clevelandodendron ohioensis* from the Famennian Ohio shales (USA). This plant has a long, unbranched stem with a terminal fertile zone. The most striking difference between the two plants is the organization of the rooting system that does not show evidence of "stigmarian" branched rhizomorph and stigmarian roots. It rather consists of a rounded base with simple roots attached to it (Chitale and Pigg 1996). The stem is decorticated, however simpler elongated leaf bases can be observed. The stem is at least twice the diameter of *Porongodendron*. Preservation in both *Porongodendron* and *Clevelandodendron* however prevents further comparisons to be done. The absence of a transition zone and the presence of a dense terminal strobilus and the absence of periodicity in occurrence of fertile zones are other major differences between the two species.

Other unbranched monopodial lycopsids have also been found in several stratigraphically younger assemblages; these include the Pennsylvanian *Chaloneria* and *Sporangiostrobus* and the Mesozoic Pleuromeiales (Pigg and Rothwell 1983a; Pigg 1992, 2001).

The Chaloneriaceae are also comprised of several unbranched monopodial lycopsids such as *Polysporia* Newberry and *Chaloneria* Pigg and Rothwell (DiMichele et al. 1979; Pigg and Rothwell 1983a, 1983b; Bek et al. 2008). These two genera are very comparable in all aspects and could be synonymous, though the former is exclusively preserved in compression and the latter is exclusively anatomically preserved. They are free-sporing heterosporous unbranched sub-arborescent lycophytes with a cormose rooting structure and ligulate leaves. In addition to the cormose rooting structure, which constitutes an important difference with *Porongodendron*, they are very robust plants with stems up to 2 m tall and up to 10 cm in diameter (DiMichele et al. 1979; Pigg and Rothwell 1983a, 1983b; Bek et al. 2008). Even though they appear to be very different from *Porongodendron*, interestingly, they are comprised of both species with terminal strobili and species with cyclic fertile zones. *Chaloneria periodica* Pigg and Rothwell (1983b) has been found in Middle Pennsylvanian coal balls of Illinois, their anatomical preservation making comparison with our exclusively compressed material difficult. Nevertheless, this plant

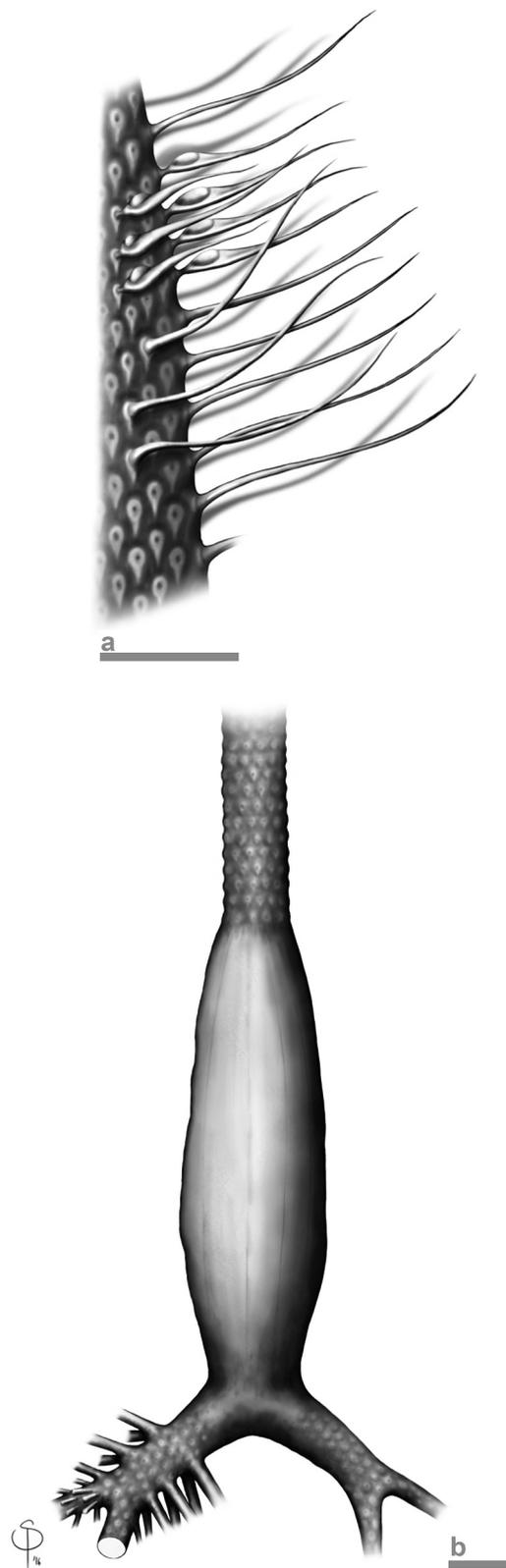


Figure 4. Reconstruction of selected parts of *Porongodendron minitensis*. Reconstruction showing the stem at the transition between a growth zone and a fertile part (A). Scale = 1 cm. Reconstruction of the base of the stem at an early growth stage (B). Scale = 0.5 cm.

has been reconstructed as unbranched and up to 2 m tall (DiMichele et al. 1979; Pigg and Rothwell 1983b). It presents repeated fertile zones with a clear dimorphism between fertile and vegetative microphylls. This

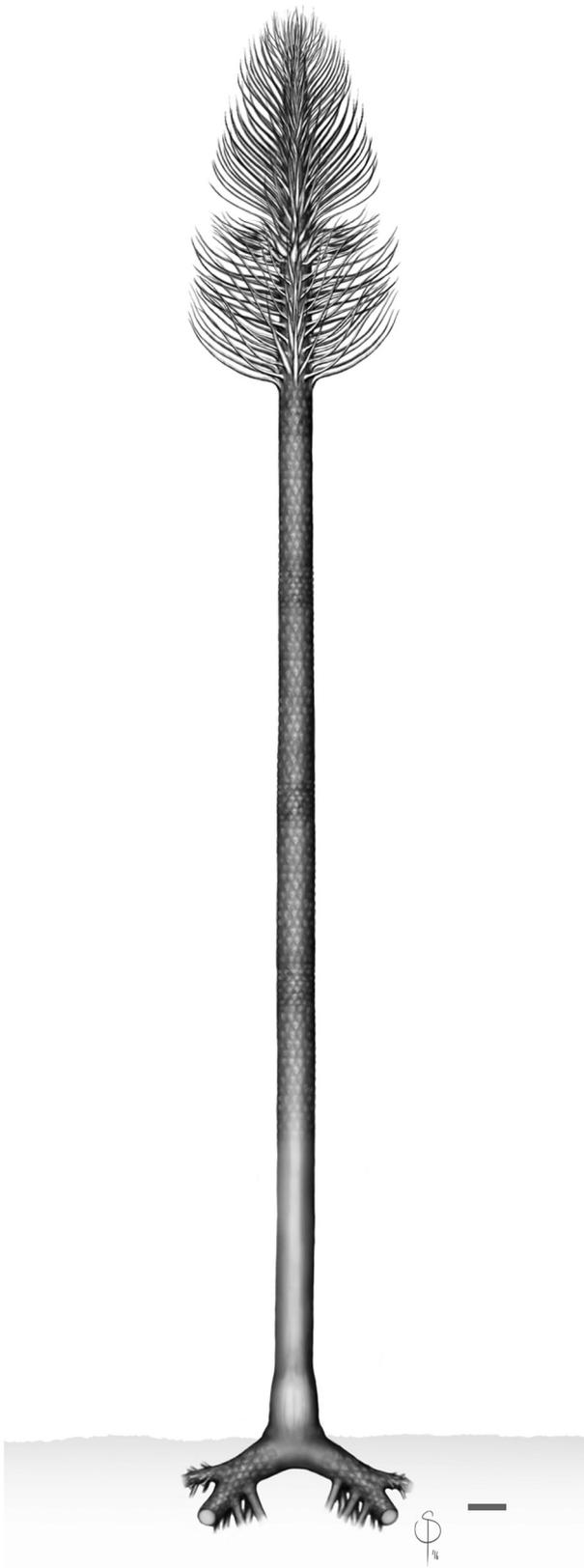


Figure 5. Reconstruction of a mature specimen of *Porongodendron minitensis*. Scale = 0.75 cm.

character is very similar to what is observed in *Porongodendron* although the two plants differ in many other respects.

Despite the lack of preserved spores, our reconstruction of *Porongodendron minitensis* is as close as we can get from a whole plant reconstruction. It is

therefore essential to consider it as such when discussing its affinities. Undoubtedly, this plant, because of the bipolar growth revealed by the branched rhizomorph, has to be included in the rhizomorphic clade (= Isoëtales) yet its affinities are difficult to establish accurately. The Isoëtales are comprised of a huge diversity of form ranging from the simple diminutive *Oxroadia* and *Paurodendron* to the large and complex Lepidodendraceae. The very simple general organization of the plant, and more precisely of the leaves and leaf bases, precludes for the moment a thorough discussion of its affinities. It is, however, noticeable that the literature contains several examples (notably in the lower Mississippian) of lycopsids presenting similar simple rounded leaf bases (Chaloner and Boureau 1967). They were in many cases attributed to various species of *Cyclostigma* and *Pinakodendron* (Chaloner and Boureau 1967). The review and the systematic comparison of these often severely disarticulated remains lies outside the scope of the present paper. Yet, the relatively simple organization of the fertile regions and the absence of strobilus could indicate a relatively basal position within the Isoëtales as these characters have been considered to represent ancestral morphologies (e.g. DiMichele and Bateman 1996). However, as recently stressed by Bonacorsi and Leslie (2019), functional diversity may have played an important role in the evolution of plant reproduction. As discussed in the next section, *Porongodendron minitensis* very likely lived under particularly harsh conditions that may have strongly influenced several of its morphological characters. Detailed discussion of its affinities is thus difficult in the absence of a detailed phylogenetic study however made difficult by the lack of anatomical preservation.

Ecological interpretation

Within the broader context of the Late Paleozoic Ice age (Montañez and Poulsen 2013), a rich stratigraphic record (namely from Brazil, Bolivia, Peru and Argentina) shows that the Mississippian of Southwestern Gondwana was under recurrent glacial conditions (Caputo et al. 2008; Isaacson et al. 2008). In addition to glacial tillites, the plant associations are the main evidence supporting these interpretations (Iannuzzi and Rösler 2000; Caputo et al. 2008; Pfefferkorn et al. 2014; Prestianni et al. 2015). During the Tournaisian, western Argentinian basins were situated within – or very close to – the South polar circle (Stampfli et al. 2013). The first evidence of undoubted climatic amelioration does not appear until the Serpukhovian (Balseiro et al. 2009). The ecological characteristics of the Tournaisian plant assemblages, linked to the stratigraphic record of

Porongodendron, agree with those reported from other coeval basins from southwestern Gondwana, thus suggesting a prevailing cold climate (Iannuzzi and Rösler 2000; Pfefferkorn et al. 2014). The remarkable occurrence of thick diamictite beds clearly of glacial origin in the successions surveyed reinforces this interpretation.

Taking into account these observations, as well as the general poverty of the autochthonous palynological assemblage, we suggest that the Agua Quemada plant record represents a tundra-like environment, which has been extensively developed along Southwestern Gondwana during the Tournaisian.

Tundra environments are treeless areas beyond the climatic limit for tree growth (Wielgolaski 1997a). Living conditions in such environments are particularly harsh, characterized by short growing seasons, strong winds and hydric stress (Wielgolaski 1997b). In modern-day tundra, plants present various adaptations either morphologically or physiologically (Bliss 1962; Wielgolaski 1997a, 1997b). These are notably reduced height of above ground parts and modifications to ratios between crowns and roots. The particular combination of morphological characters that constitutes *Porongodendron* could be interpreted in this framework.

As reconstructed here, *Porongodendron* is characterized by a generally low stature, and enlarged intermediate zone, deciduous microphylls and a branched rhizomorph (Figure 5). The small size of the above-ground parts in modern tundra plants is interpreted in the first place as an adaptation to the strong wind conditions prevailing in colder environments (Bliss 1962). The general poverty of soils as well as the limited amount of available energy is a common feature of all present-day cooler environments (Bliss 1962). This may in part explain the increase of the root/shoot ratio (see Wielgolaski (1997b) for more references). It seems to be more economic to store organic matter and nutrients closer to the growing point in order to limit translocation costs. This could explain the enlarged intermediate zone that would act as a storing organ close to the ground at the limit between the two parts of the plant. By many aspects of its organisation, *P. minitensis* is very similar to an arborescent lycopsid but presenting a much simpler aerial organisation and a generally smaller size.

Moreover, as discussed earlier, *Porongodendron minitensis* is characterized by a succession of fertile zones and vegetative zones showing a periodicity in plant growth. Despite being rarely observed among fossil and living lycopsids, this pattern has been discussed several times. Both Kerp et al. (2013) and Zhang et al. (2016) discussed similar cases respectively in the Lower Devonian *Asteroxylon mackiei* Kidston

and Lang and Late Devonian *Monilistrobus yixingiensis* Wang and Berry. They both inferred a phylogenetic signal to this condition, referring to the organisation of zosterophylls and earlier representatives of the lycopsid clade such as *Baragwanathia* Lang and Cookson and *Drepanophycus* Goeppert. However as further discussed by these authors, this pattern has been observed among various and seemingly unrelated plants including the Pennsylvanian *Chaloneria periodica* Pigg and Rothwell and the contemporaneous *Huperzia selago* (L.) Bernhardt ex Schrank & Martius (Bateman et al. 2007; Kerp et al. 2013; Zhang et al. 2016). DiMichele et al. (1979) also discussed this feature and gave a more ecological perspective to it. The repetition of the reproduction is interpreted as advantageous in stressful environments such as “the fluctuating marshlands and areas marginal to swamps”. This however applies to the tropical habitats.

By contrast, as already stated, *Porongodendron* is interpreted as living under cold conditions. In this case, we suspect that the observed periodicity more than bearing a strong phylogenetic signal could rather constitute an adaptation to the particular climatic conditions prevailing in “tundra” environments. A specific life history is the result of the compromise between different constraints (Begon et al. 2006). The above discussed monocaulous architecture is by itself a constraint. The limitation of the plant morphology to a single stem limits the possible range of its life histories. Only two options are possible: the first implies a long phase of vegetative growth preceding a unique terminal fertile burst; the second supposes several fertile periods interspaced by vegetative phases. The first option is linked to steady environments with low sources of mortality and is often associated with a greater investment in reproduction marked by larger propagules (Begon et al. 2006). It is observed in tropical to equatorial extant plants such as *Lobelia telekii* Schweinfurth and fossil *Clevelandodendron ohioensis* or *Pleuromeia* Corda.

The second option, which is more characteristic of difficult environments and high sources of mortality or reproductive constraints (short growth seasons), is almost always associated with small propagules. Despite the lack of preserved spores but considering the small size of the sporangia, this is consistent with the life history recorded in *Porongodendron minitensis*. A short time period of development between embryo and reproductive maturity would have limited the probability of dying before reproducing. By having several fertile cycles on the same plant and by producing propagules that limited the energetic and nutrient costs – important in poor environments – these plants had greater chances to reproduce favourably. Finally, in the framework of a hypothesized lack of dormancy and at the scale of the population, these plants were

each year producing massive bursts of spores that even if taken individually had limited chances to ever germinate or to develop into a mature organism were augmenting the probability of the whole population to reproduce reasonably. Population densities might moreover have been low, which could have proved advantageous in an environment with such limited resources. The observed fertile periodicity of *Porongodendron minitensis* could thus be the result of an optimisation of the plant life cycle under the constraints of its phylogenetic history (i.e. monocaulous stem, lack of dormancy) and those induced by the cold and strongly seasonal polar environments.

Although we have a reasonable understanding of the general climatic conditions in which *Porongodendron* was living, there is no direct evidence of the original soil type and vegetation cover. However, considering the paleogeographic position of the Agua Quemada section right on the polar circle, strong winds and thin soils could be hypothesized (Wielgolaski 1997b). Under these conditions, laterally extensive *Stigmalaria*-like anchoring structures could have been preferentially selected. The branched rhizomorph could be the only way to increase the stability of the plant. In other words, to strengthen its anchoring in the substrate it was necessary to enlarge the root-producing organ. Interestingly, Niklas (1998) discussed the relationship between root form and function in terms of biomechanical behaviour. His model showed that the base of the trunk at the air-soil interface acted as a pivot-point that necessarily must be stabilized. The soil conditions are critical to this stabilisation.

The sole living representative of the rhizomorphic clade is the genus *Isoetes*. *Isoetes* is a cosmopolitan genus of heterosporous more or less aquatic plants (Rørslett and Brettum 1989; Taylor and Hickey 1992). It is characterized by a very reduced stem that implies that a high fraction of the biomass is devoted to the rooting system (Rørslett and Brettum 1989). Biomass allocation is, one of the traits that allow the characterization of a plant strategy (Barrat-Segretain 2001). A low stem to root ratio has been linked to a stress-tolerant strategy for plants living in frequently disturbed environments (e.g. P'Yankov and Ivanov 2000; Barrat-Segretain 2001). The presence, in *Porongodendron*, of a relatively reduced stem and a branched rhizomorph means that a larger part of the biomass was located in the rooting system. This would suggest adaptation to stressful conditions and fits with the hypothesis of a plant living under harsh polar or peri-polar climates. The branched rhizomorph as well as the inflated intermediary zone would have functioned as storage organs that promoted resistance to disturbance events (e.g. the long polar winter).

Conclusions

Porongodendron minitensis is a new genus of small lycosid. In this paper we were able to reconstruct the plant and propose an almost whole plant concept for it. Interestingly, it presents a set of characters that differentiate it at a taxonomic level from all other lycosids. These characters such as a branched rhizomorph, an enlarged transitional zone and periodicity of reproductive zones are here interpreted as representing specific adaptations to the harsher tundra conditions prevailing in the Lower Carboniferous Southern Polar environments.

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Author contributions

The entire team carried out the field work and collecting of the material. Cyrille Prestianni prepared and studied the material. Juan José Rustán, Diego Balseiro and Emilio Vaccari ensured the logging and interpretation of the outcrop. They also wrote the geological context. Cyrille Prestianni interpreted the material and wrote the manuscript with inputs from the entire team.

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