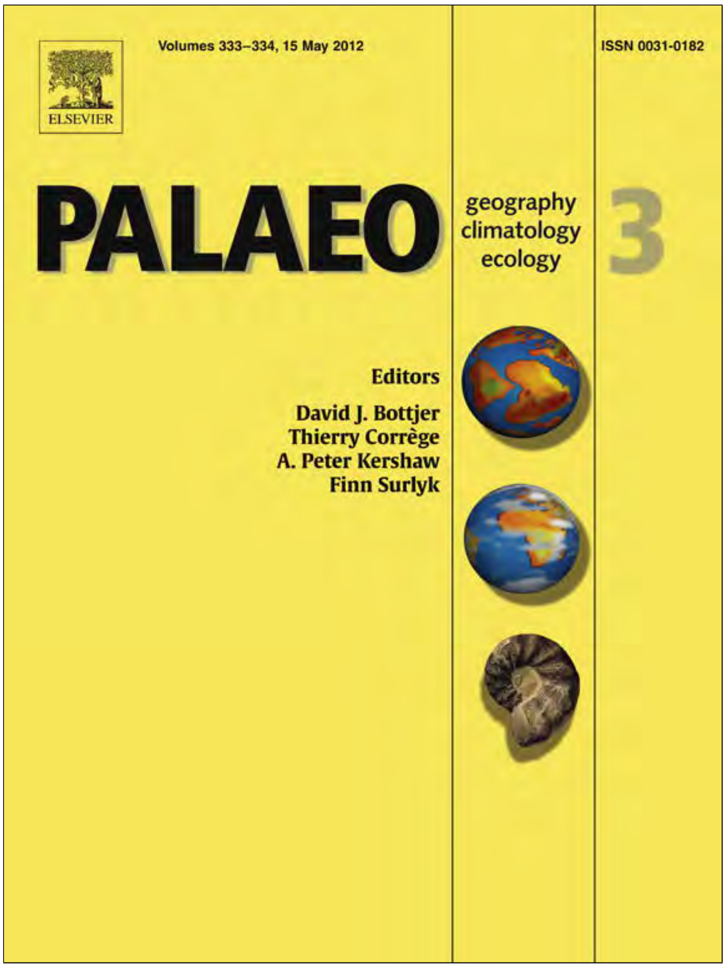

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A late Paleozoic fossil forest from the southern Andes, Argentina

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ABSTRACT

An anatomical and ecological study of a Late Pennsylvanian–early Permian assemblage of silicified trunks from the San Ignacio Formation of southern Andean Cordillera is detailed. This stratigraphic unit has been divided in three facies associations. The silicified trunks are abundant in the middle part of the facies association C (limestones, shales and volcanics) forming a persistent forested stratigraphic level. Anatomical information integrated with sedimentological data, has allowed reconstruction of a plant community that grew on the westernmost margin of Gondwana. The paleoforest grew in wetland environments, where a taphocoenosis of only permineralized trunks and stumps has been preserved. Based on characters of the stem and roots the trees are cordaitaleans, though distinct from other members of this group. Vascular traces exhibit tracheids arranged in circular patterns indicating auxin regulation of axial growth and probably the presence of epicormic shoots. These fossil trees also preserve anatomical evidence of plant–arthropod interactions and rootlets invading the decaying wood. Indistinct growth rings as well as additional indirect evidence indicate that this ecosystem experienced an overall humid, warm climatic regime.

1. Introduction

The locations that offer a rich fossil record of plants with preserved anatomy are uncommon in the upper Paleozoic of western Gondwana. Several studies of Permian pycnoxylic woods have been carried out in Argentina (Archangelsky, 1960; Herbst and Crisafulli, 1997; Crisafulli et al., 2000; Crisafulli, 2002) but only three Carboniferous species have been described, *Medullopitys menendezii* from the Mendoza Province (Petriella, 1982), *Abietopitys petriellae* and *Cuyoxylon multipunctatus* Pujana and Césari from the San Juan Province (Pujana, 2005). Permian deposits from Brazil, Uruguay and Paraguay contain more diverse assemblages including permineralized gymnosperms and ferns (Dohms, 1976; Mussa, 1978; Herbst, 1981, 1986, 1987; Crisafulli and Lutz, 2000; Crisafulli and Herbst, 2009; Crisafulli et al., 2009).

Following deglaciation in the western margin of Gondwana during the Bashkirian, lycopsids, Equisetales, pteridosperms and Cordaitales characterized the *Nothorhacopteris–Botrychiopsis–Ginkgophyllum* Flora (Archangelsky et al., 1996; Césari et al., 2007). This flora, mainly composed of herbaceous and sub-arborescent species, prevailed during most of the Pennsylvanian and began to decline towards the Carboniferous–Permian boundary when ferns, conifers and glossopterids became important probably linked to more humid and temperate climates (Lopez Gamundi et al., 1992). It was in this time that some small forests flourished in the western basins of Argentina such as those found in the Solca Formation (Crisafulli and Herbst, 2008) along the eastern margin of the Paganzo Basin. However, little or nothing is known about forests in the Andean region, not only for the Carboniferous but also for the Permian.

In this paper is described a unique fossil assemblage, from the Andean Cordillera of the San Juan Province, Argentina. Apparently monospecific, more than a hundred specimens of silicified trunks were preserved in the upper section of the San Ignacio Formation (Late Pennsylvanian–Cisuralian). Three aspects are remarkable about the flora: 1) Its exceptional preservation and autochthonous setting (buried in the original habitat without any further transport), permit a detailed anatomical analysis, 2) The development of the forest was closely related to intense volcanic activity coupled with oscillating water-table level position, resulting in plant communities with specialized ecological strategies and 3) The paleoflora here

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described fills an important biostratigraphic gap between the underlying Carboniferous postglacial floras and the overlying Permo-Triassic volcanic rocks.

2. Stratigraphic setting

The sequence crops out in Ñipas and Las Ánimas creeks, along the Sierra de Castaño in the Andean Cordillera of the San Juan Province (western Argentina). The Sierra de Castaño forms one of the eastern branches of the Andean Cordillera and it comprises late Paleozoic sedimentary sequences and thick volcanic successions of Permo-Triassic age (Fig. 1).

Late Paleozoic units comprise the Cerro Agua Negra Formation (Polanski, 1970), San Ignacio Formation (Rodríguez Fernández et al., 1996) and volcanic rocks included in the Choiyoi Group (Fig. 1). The Cerro Agua Negra Formation was deposited during the Pennsylvanian and comprises sandstones, mudstones and very scarce conglomerates cropping out in the core of the anticline of the Sierra de Castaño. The base of this unit is unknown in the region here studied, but 120 km to the north it overlies Devonian sandstones and mudstones. Overall, the Cerro Agua Negra Formation was deposited in shallow marine environments including inner platform, nearshore and lagoon environments. Only at some locations thin intercalations of progradational fluvial deposits have been observed.

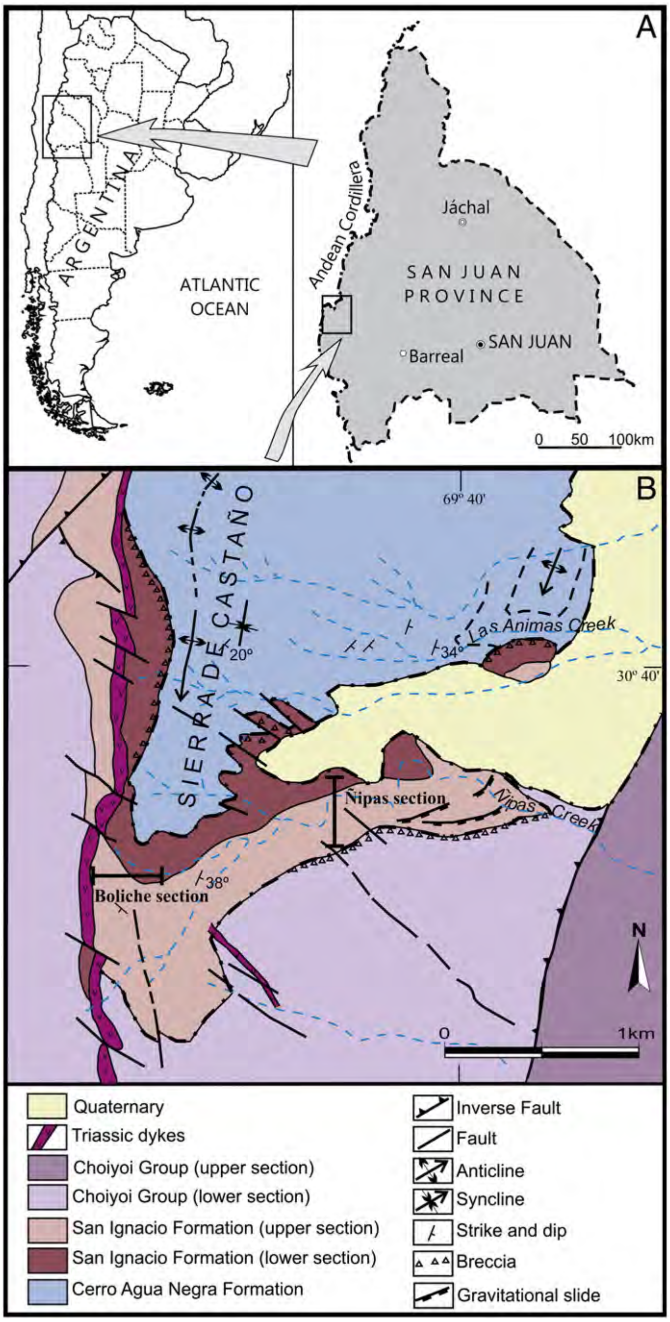


Fig. 1. Geological setting. A) Location of the Sierra de Castaño in the San Juan Province, Argentina. B) Geological map of the area, showing the main geological units and the location of the stratigraphic sections shown in Fig. 2.

The San Ignacio Formation, 185 m thick at the Ñipas section (Fig. 2), shows a complex lithological composition including conglomerates, breccias, coarse- to fine-grained sandstones, mudstones, limestones and volcanics (Busquets et al., 2007a, b). The unit unconformably overlies the Cerro Agua Negra Formation forming an irregular paleotopography filled by breccias and conglomerates belonging to the base of the San Ignacio Formation. Despite the fact that the age of these rocks was established as Late Pennsylvanian on the basis of scarce palynological remains (Busquets et al., 2005), the upper part of the San Ignacio may be early Permian according to regional correlations. Limestones from the nearby, and probably coeval, La Puerta Formation have yielded palynological assemblages (Ottone and Rossello, 1996) containing *Lueckisporites* that suggest a late Cisuralian age (Césari et al., 2011, Mori et al., 2012) in Argentina and Brazil.

The top of the San Ignacio Formation corresponds to an important regional unconformity that marks the base of the Permo-Triassic Choiyoi Group. This unconformity produced a high relief surface marking the erosion of the whole of the San Ignacio Formation in many places of the Andean Cordillera. For this reason the volcanic series of the Choiyoi Group are more frequently found resting on the Agua Negra Formation.

The Choiyoi Group marks the most important volcanic activity along the western margin of Gondwana where more than 5000 m of volcanics from the Cisuralian to the earliest Triassic (Llambías, 1999) were accumulated. Traditionally, the Choiyoi Group has been divided in two sections differing in composition of the volcanic deposits and in age. The so-called lower Choiyoi (spanning from to 281 to 261 Ma, Rocha-Campos et al., 2011) is composed of ignimbrites, volcanic breccias, andesites and dacites forming a calc-alkaline volcanic association (Llambías, 1999). This succession is interpreted as formed during the latest stages of a late Paleozoic volcanic arch developed along the present day Andean Cordillera. In contrast, the upper Choiyoi is dominated by rhyolites, dacites, acid ignimbrites and different types of pyroclastic rocks, all of them included in the silicic volcanic association. According to Llambías (1999) the upper Choiyoi formed during the transition from subduction to intraplate volcanism, probably related in an extensional regime.

3. Facies associations of the San Ignacio Formation

As mentioned above, the Sierra de Castaño area is one of the scarce locations in the Andean Cordillera where the unconformity at the base of the Choiyoi Group did not eliminate the whole of the San Ignacio Formation sequence. Consequently, though forests presumably were fossilized in different areas of the basin, they have not survived and this locality provides an exceptional opportunity for the study of the latest Carboniferous–early Permian Andean trees. Indirect evidence of forest development in the region is given by the presence of large reworked trunks found in volcanic agglomerates and breccias of the lowermost levels of the overlying Choiyoi Group in different locations.

The San Ignacio Formation was studied in detail at the Ñipas and Boliche sections (Fig. 2) where three facies associations were recognized: 1. Breccias and coarse-grained sandstones (facies association A), 2. Conglomerates, sandstones and mudstones (facies association B) and 3. Limestones, shales and volcanics (facies association C).

Though the largest number of trunks appears in facies association C, some good specimens of stumps in life position also were found in facies association B (Figs. 3A, C).

3.1. Facies association of breccias and coarse-grained sandstones (facies association A)

This facies association is composed of clast-supported breccias, conglomerates, coarse- to medium-grained sandstones and very scarce levels of mudstones forming the base of the San Ignacio Formation. No remains of trunks were found in this facies association. The shifting thickness of this facies association (between 10 and 40 m) reflects the filling of the irregular topography produced as a result of the tectonic movements that originated the unconformity that separates the Cerro Agua Negra and San Ignacio formations.

It is likely that the lower part of this facies association was deposited as talus, small alluvial fans, or poorly organized proximal braided rivers flowing along an irregular topography. The local provenance of clasts indicates a scarce integration of the fluvial network with channels dominated by rapid avulsion with absent or extremely low lateral migration. Towards the middle and upper parts of the facies association talus appears to have disappeared and the prevailing depositional environment switched to braided alluvial plains.

3.2. Facies association of conglomerates, sandstones and mudstones (facies association B)

This facies association, 55 m thick, is composed of conglomerates, sandstones and mudstones grouped in fining-upward cycles ranging from 2 to 4 m in thickness. The lowermost part of each cycle comprises clast-supported polymictic orthoconglomerates showing rounded clasts up to 10 cm in maximum diameter. These rocks are commonly overlain by fine-grained sandstones with horizontal lamination or current ripple cross-laminated sets which in turn are covered by laminated mudstones.

The fining-upward arrangement, the presence of tabular beds and the existence of lateral-accretion surfaces suggest that fluvial channels were stable and migrated laterally. Moreover, very fine-grained sandstones and mudstones at the top of the cycles very probably represent flood-basin deposits. Trunks have been sporadically found in flood basin successions of this facies association.

3.3. Facies association of limestones, shales and volcanics (facies association C)

Facies association C forms the upper half of the San Ignacio Formation reaching a minimum thickness of 95 m. The characteristic feature of this facies is the presence of several levels of volcanics intercalated in interbedded mudstone–limestone sequences. Thin levels of tuffs and some beds of lithic arenites also occur within the association.

Limestones form tabular to irregular beds up to 200 cm thick. They are mostly microbial carbonates consisting of thrombolites and stromatolites (microbialites, sensu Burne and Moore, 1987). These limestones show evidence of extensive pedogenic processes. The microbial carbonates are arranged in sequences (0.1 to 9 m thick), generally incomplete, consisting, from bottom to top, of the following subfacies: thrombolites, stromatolites and paleosols; in some cases sub-aerial exposure is in evidence from mud-cracks. An additional feature of these paleosols is the development of secondary porosity, partially occluded by sparite, some of which is interpreted as the product of decomposition of higher plant roots.

Commonly, the carbonate sequences rest on volcanic rocks that show a progressive increase of carbonate content upwards. The most common volcanic facies are volcaniclastic deposits including pyroclastic fall and flow successions and resedimented volcaniclastic deposits. These volcaniclastic rocks have been subjected to different post-volcanic processes (devitrification, hydration, diagenetic compaction, and diagenetic/hydrothermal alteration) making awkward their correct classification and interpretation. Pyroclastic flow deposits correspond to welded ignimbrites, showing, in some cases, embedded silicified log remains (Busquets et al., 2007a).

Busquets et al. (2007a, b) interpreted the upper half of the San Ignacio Formation to have been deposited in a shallow water body subject to contemporary volcanism and repeated events of flooding and desiccation. The presence of stromatolites and thrombolites indicate subaqueous conditions, periods of stillstand and shallow water stability along the line coast and shallow and clear waters. In contrast, during periods of subaerial exposition, stromatolites and thrombolites were exposed and weathered, leading to soil formation.

4. Materials and methods

The studied specimens appear with different orientations in the embedding matrix the shorter stumps were found standing (Fig. 3A, D), whereas the longest cylindrical trunks were found in horizontal position (Fig. 3B). The departure of basal roots was seen occasionally, spreading laterally from the enlarged bases of stumps.

Approximately 55 different specimens were selected for this study. The anatomy of the stems was studied using thin sections. Transverse, tangential and radial thin sections of all specimens were prepared. Energy-dispersive X-ray spectroscopy (EDS or EDX) analysis shows that the main component of the samples is silica, occurring both in cell walls and lumina.

All the collected samples are housed at the Paleobotanical Collection of the San Juan Museum, University of San Juan under the label PBSJ.

5. Stems

Cuyoxylon Pujana and Césari, 2008
Type species: *Cuyoxylon multipunctatus* Pujana and Césari, 2008
Cuyoxylon sp. (Figs. 4 and 5).

5.1. Description

Although there are some variations among the specimens studied, they are interpreted as belonging to the same species. Diameter of many specimens is approximately 0.50 m and the estimated tree heights calculated on the basis of regression equations (Niklas, 1994) reach 28 m. The pith is poorly preserved but apparently consists of a homogeneous parenchyma (Fig. 4D). These cells range from 80 to 100 μm in diameter and 100 to 250 μm in height. The eustele comprises a number of discrete primary xylem strands (Fig. 4B) with the tracheids of the xylem showing spiral and scalariform thickening (Fig. 4E) finally succeeded by bordered pitting. Secondary xylem tracheids are usually small, ranging from 10 to 50 μm in diameter both in radial and tangential dimensions; they have up to six seriate pitting on radial walls only (Figs. 4F, H). Bordered pits (5 μm in diameter) have oblique, elliptical, crossed apertures. The pits are polygonal contiguous, rarely spaced. Rays are small, uniseriate (rarely biseriate) and 1–10 (commonly 2–3) cells high (Fig. 4G). They are composed of parenchyma cells without any evidence of ray tracheids. Cross-field areas show up to 26 simple to bordered pits (Fig. 4I). Secondary xylem is homogeneous; there is no evidence of distinctive growth rings (Fig. 4A) but there is some irregular zonation (Fig. 4C) that is interpreted as not reflective of annual growth periods. Cells show a subtle decreasing in diameter but have no thickening of the walls. “False rings”, consist of narrow (two to six cells wide), discontinuous rings of small (10–20 μm) diameter tracheids. One branch scar has been observed in the specimen illustrated in Fig. 3E (at the left). A tangential section of the

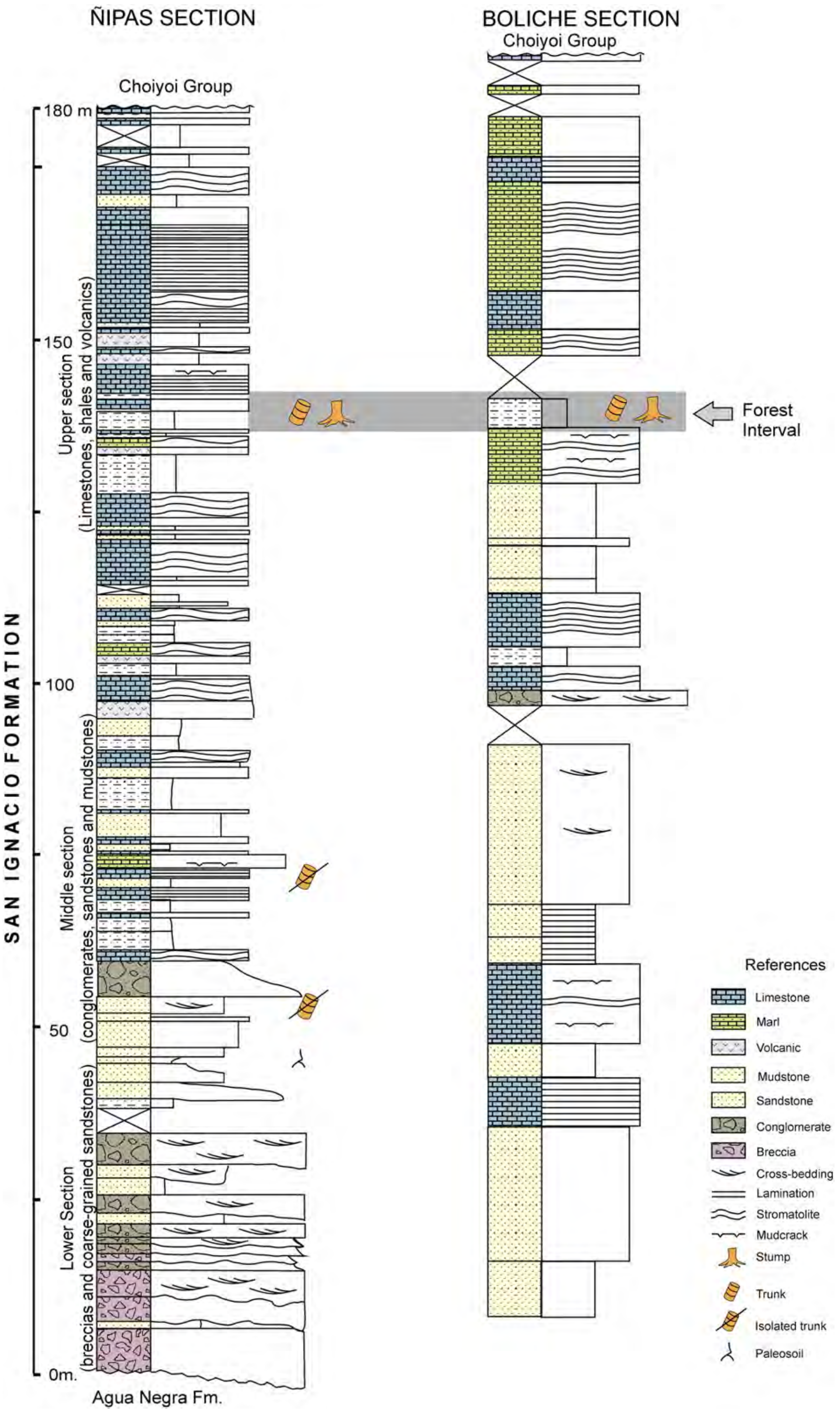


Fig. 2. Stratigraphic sections of the San Ignacio Formation.

stem, distal to the emergence of the branch trace, exhibits a pith cylinder and secondary xylem continuous with xylem of the stem (Figs. 5D, G).

5.1.1. Vascular traces

Several trunks, some found in upright position, externally display in the basal part a large number of vascular traces that appear as small oval scars (Figs. 3D, F). Vascular traces are apparently helically arranged (Fig. 5A) and internally ranged in diameter from about 1.5 mm to 2 mm. Tangential thin sections of the wood reveal transverse sections of the vascular traces showing a central pith of parenchyma cells (Figs. 5B, C, E, G). Circular patterns of tracheids are not only positioned distal to the vascular trace (Figs. 5C, E) but also they protrude the central part of the trace (Figs. 5B, E, F, H). A longitudinal section of the vascular trace is illustrated in Fig. 5G, showing a central column of parenchyma cells.

Tangential section of the secondary xylem of the stem (probably in the interface cambium-xylem zone), surrounding the vascular traces, exhibits mainly uniseriate and rare biseriate rays. Cells between the rays have the inner walls with thin spiral-reticulate thickenings and sometimes small pits aligned in discontinuous rows (Fig. 5I, J). As in extant conifers, these wall thickenings can represent a step of secondary xylem differentiation. Several changes can be observed in the thin-walled precursor cambial cells, including secondary cell-wall deposition, bordered pit formation and lignification (Savidge, 2001).

Similar small vascular traces were described by Creber and Ash (2004) in specimens referred to *Woodworthia arizonica* Jeffrey from the Triassic of Arizona and the Permian Iratí Formation (Brazil). They interpreted these vascular traces as related to preventitious buds. Recently, Creber and Collinson (2006) inferred that those small scars correspond to horizontal vascular traces traversing the secondary xylem from the center of the axis to the exterior. Likely, the specimen from the Iratí Formation coincides with some of the material described earlier, from the same unit, by Mussa (1978) as *Tordoxylon* Krausel, *Paratordoxylon* Mussa and *Myelontordoxylon* Mussa, who illustrated adventitious root- and branch-traces identical to those figured by Creber and Collinson (2006).

Preventitious buds are formed today deeply embedded in the bark of trunks, where they remain dormant for many years. When auxin flow is much reduced or stopped due to severe damage, the preventitious buds develop rapidly into new lateral branch systems or epicormic shoots, usually near the base of the plant. According to Creber and Collinson (2006) this type of shoot, emerging in large numbers from the trunk, functions as a valuable source of rapidly developing foliage to replace that lost in events such as forest fires.

Decombeix et al. (2010) noted that the oldest evidence of epicormic branching is that found in Late Devonian trunks of *Archaeopteris* (Trivett, 1993; Meyer-Berthaud et al., 2000). Other reports in Paleozoic gymnosperms include the cones of *Cordaixylon*, which can be borne as epicormic organs on proximal portions of stems (Rothwell, 1993), and clusters of epicormic shoots described from the late Permian of Antarctica (Decombeix et al., 2010).

Our traces are apparently not branched, suggesting that the possible epicormic shoots were not produced in clusters like those in the specimens from Antarctica. Evidence from the specimens indicates that these traces appear at least in the basal portion of trunks. In extant trees, collar sprouts have the potential to become independent from the parent tree under normal conditions (Del Tredici, 2001). Root sprouting is extremely rare among gymnosperms, having only been recognized in few tropical species. The close association of all the traces with the secondary xylem of the trunk in our specimens likely indicates an adventitious origin.

Moreover, the abundance of tracheids arranged in circular patterns indicates regulation of cambial activity. Rothwell et al. (2008) noted that anatomical evidence for the regulation of secondary xylem production by axial polar auxin flow is present in all three major clades of vascular plants that have produced abundant wood. Evidence of this vascular differentiation is present in the extinct progymnosperms, living species of both conifers and dicotyledonous flowering plants, as regions of distorted tracheids, branched tracheids, and circular patterns of cells associated with leaf trace divergences or branch junctions. Zimmermann (1983) described the xylem at a branch junction or at the base of a leaf as a water transport bottleneck that gives priority in water supply to the main stem over the lateral appendages. One of the structural changes recognized in those regions is the hydraulic control through circular patterns of tracheids or vessels at branch junctions (Lev-Yadun and Aloni, 1990). These authors found changes in vascular orientation at the zone of bifurcation. Also, circular vessels are found in roots (Fink, 1982), around or above suppressed, dormant (Aloni and Wolf, 1984) or developing buds.

6. Roots

Specimens regarded as roots were collected closely associated with big logs, mainly from volcaniclastic deposits. The specimens collected are up to 5 cm in diameter, some of which are bifurcated portions of bigger specimens (Figs. 3E and 6A). They are diarch, triarch (Figs. 6C, F) and tetrarch (Figs. 6E, G). The secondary xylem lacks growth rings (Figs. 6A, D) or has an irregular zonation (Fig. 6C). Pitting of the tracheids and cross-fields is the same as that of the stems. Primary branch roots are observed in some specimens (Fig. 6E). Transverse sections show them as persistent horizontal vascular traces attached to protoxylem poles traversing the axis from the center to the exterior (Figs. 6G, H). The root consists of an inner column of tracheary elements of primary xylem. Tracheary elements have reticulate pitting on the walls (Fig. 6 H).

Other vascular traces are similar to adventitious branch roots (Fig. 6J). These traces appear to have initiated after some thickness of secondary xylem of the parental axis have developed and promptly broadened. The formation of adventitious branch roots on root axes has been analyzed by Paolillo and Bassuk (2005). These authors studied the points of origin of branch roots formed within established woody parental root axes. Primary branch roots have connections with the primary xylem of the parental axis, while adventitious branch roots are initiated within the secondary body of the parental root axis.

Roots are similar to those of *Amyelon* Williamson emend. Cridland. This genus includes roots bearing rootlets, protostelic to eustelic with exarch primary xylem and with cambium, phloem and periderm preserved.

Like *Amyelon taiyuanense* Wang and Tian described by Wang et al. (2003) from the early Permian of China, our roots are di- to tetrarch, with the inner cortex aerenchymatous and exodermis surrounding the cortex. The roots of *Cordaixylon dumusum* have a parenchymatous primary cortex usually composed of closely spaced parenchyma cells and at proximal levels, the roots exhibit secondary tissue development (Rothwell and Warner, 1984).

7. Rootlets

Several specimens, mainly recovered from volcanic deposits below stromatolite beds that in some cases show mud-cracks (indicating subaerial exposure), are distinguished by the presence of many small rootlets invading the secondary xylem and pith (Figs. 7 and 8). Césari et al. (2010) interpreted them as tiny rootlets of seedlings developed on decaying logs that acted as nurse logs. They are very well preserved showing anatomical details in transverse and longitudinal sections (Figs. 7J, K, M). The rootlets invade the tissues from all the directions, but mainly vertically, and many of them show tiny lateral branches (Figs. 7D, G, N). A branched rootlet attached to a larger one is shown in Fig. 7D. Four cell layers of the outer cortex are well defined in the main rootlet whereas the inner cortex is poorly preserved; perhaps it was aerenchymatic tissue. The branching rootlet exhibits the vascular cylinder and three layers of parenchyma cells of the inner cortex and four layers of the most outer cortex. Another example of a lateral rootlet is observed emerging from a root that invaded longitudinally secondary xylem (Fig. 7N). In this case, the lateral rootlet runs perpendicularly to the tracheids.

Thin tangential sections of secondary xylem have allowed us to observe the vertical rootlets in longitudinal section (Figs. 7H, I, J). Specimen illustrated in Fig. 7H preserves the primary strands with annular to scalariform pitting (Fig. 7J) and parenchyma of the cortex. Tangential sections also exhibit rootlets invading the wood horizontally (Fig. 7L) and like in other cases only three or four cell layers of the outermost cortex are preserved.

Among the rootlets preserved inside what was the hollow center of a log is possible to observe some specimens that could correspond to cross-sections of seedlings at level of the hypocotyl (Figs. 7E, K).

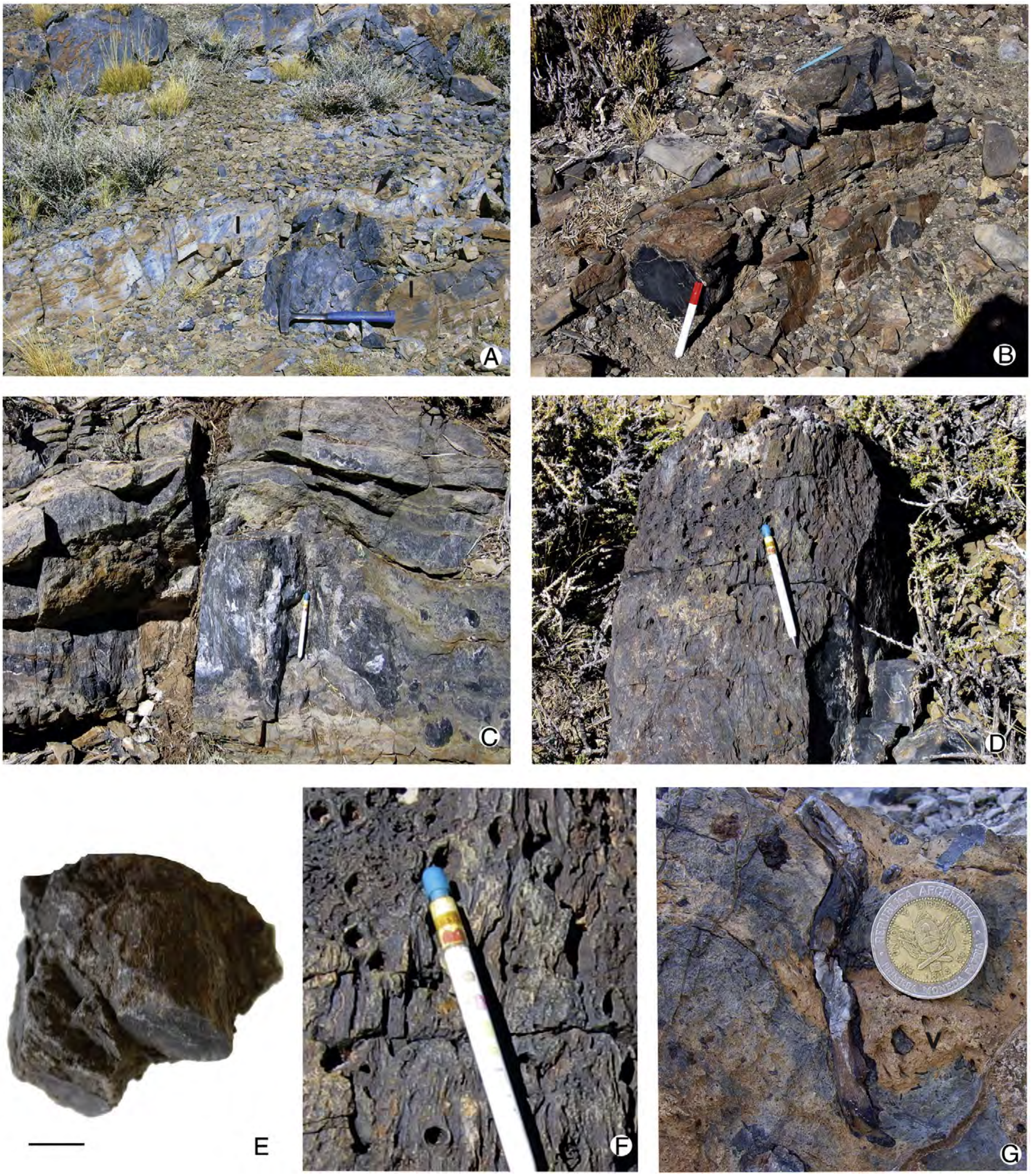


Fig. 3. A. Stump (t) embedded in limestones (l); B. Long trunk in horizontal position, parallel to the stratification; C: Standing stump draped by a limestone bed; D: Stump with densely packed scars of vascular traces in the surface; E: Branched root; F: Detail of scars in D; G: Small root in volcanic horizon (v).

The vascular cylinder is elongate, diarch and encircled by the endodermis and may have preserved the phi-thickenings (arrow Figs. 7E, K and 8G). The mesophyll consists of characteristic parenchyma cells of many gymnosperms that display folds that project like vertical ridges into the lumen of the cell. The hypodermis is up to 5–6 layers in thickness.

Some of the rootlets with diameters of 1–1.5 mm are diarch to polyarch and developed up to 15 layers of secondary xylem (Figs. 7A, B, C). Secondary xylem consists of radially arranged tracheids, square or rectangular in cross section. Another rootlets display only the vascular cylinder and the cortex divided into two zones, an outer and inner zone (Figs. 8C, D, K, M). Specimen PBSJ 459

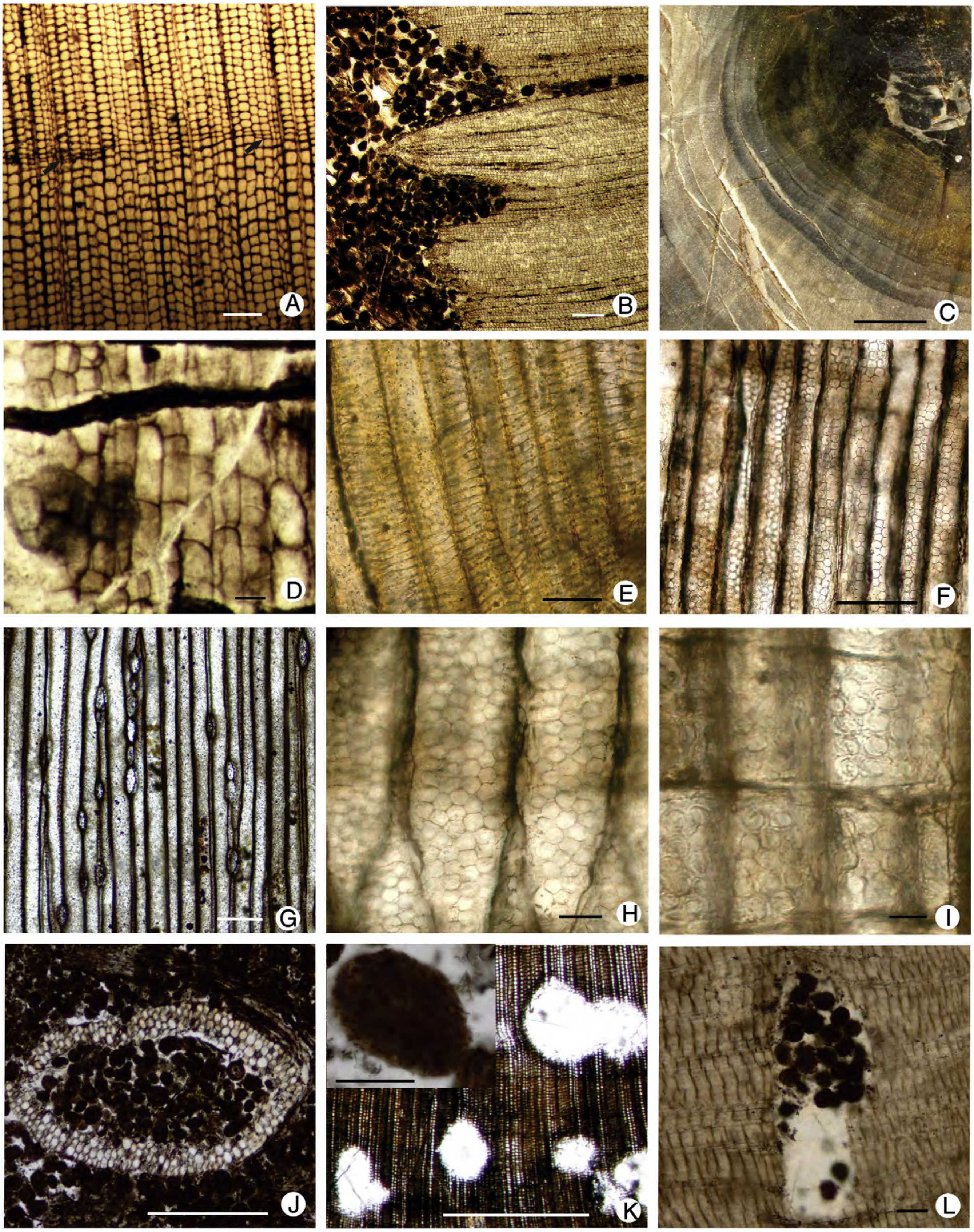


Fig. 4. A. Cross section of wood showing discontinuous and subtle changes in diameter of tracheids (arrows), PBSJ 461a; B: Cross section of secondary xylem protruding the pith cavity filled by fecal pellets, PBSJ 461a; C. General view of stem in transverse section, showing parenchymatous pith and secondary xylem with irregular zonation, PBSJ 461; D: parenchyma cells in pith, tangential section, PBSJ 461c; E: Primary xylem with scalariform thickening, PBSJ 461c; F: tracheids with multiseriate bordered pitting in the secondary xylem, PBSJ 461e; G: tracheids and uniseriate rays in the secondary xylem, tangential section, PBSJ 459e; H: Detail of pitting in tracheids, tangential section, PBSJ 461e, I: Araucarioid cross-field pitting, radial section, PBSJ 461e; J: fecal pellets in cross section of rootlet, PBSJ 462; K: Transverse section of wood with empty subcircular cross-sections of galleries probably excavated by mites, PBSJ 467; Enlargement showing the shape and composition of coprolite, PBSJ 462; L. Longitudinal section of tunnel containing microcoprolites in tangential oblique section of secondary xylem, PBSJ 462. Scale: A = 100 μm; B, I, H = 10 μm; C = 1 cm; D, F, G; L = 100 μm; E = 50 μm; J = 500 μm; K = 1 mm.

(Fig. 8A) shows in transverse section a rootlet, approximately 2 mm in diameter, occupying the space of the pith. At this level, a triarch stele is well defined (Fig. 8E). The cortex appears slightly divided in two zones, being the inner poorly preserved but showing some air spaces (Fig. 8D). The outer layer of cells of the cortex possesses a suberized strip on the radial wall. Other thin section of the same specimen (PBSJ 459) shows this rootlet with two well defined zones in the cortex (Fig. 8B). The outer zone consists of five layers of parenchyma cells and a thickened zone interpreted as the exodermis is clearly defined in the most outer layer (Fig. 8F). The inner zone consists of aerenchyma that comprises many large air chambers arranged radially (Fig. 8C). Some small rootlets show better defined the endodermis, and surrounding this single cell layer, are preserved in peculiar way the thickened radial walls of the first cells of the cortex (Fig. 8G). These phi-thickenings are in radial arrangement (Fig. 8G, H, I, J), as observed in Carboniferous *Radiculites*-type rootlets (Strullu-Derrien et al., 2009), Triassic Antarctic roots (Millay et al., 1987) and in extant material. Probably, the strong impregnation with lignin favored their preservation in our fossils, in the same way that enzymes or acids do not digest them in living roots.

The probable origin of the air spaces may be interpreted in the rootlet illustrated in Fig. 8K. This rootlet, 3 mm in diameter, displays two distinctive zones in the cortex. The inner cortex exhibits both well-defined air spaces and those in lysigenous process of development (Fig. 8L). Like in young roots of maize or rice (Justin and Amstrong, 1987), aerenchyma seems to have formed by the death of cells in the mid cortex. Lysigeny later spreads radially and longitudinally to form air spaces separated by radial bridges of cells.

One large rootlet, 6.2 mm wide (Fig. 8M) shows the pith and four exarch primary xylem poles in transverse section of the central vascular cylinder (Fig. 8N). Rounded and thin walled pith cells are clearly distinguishable from the thickened primary xylem cells (up to 50 μm in diameter). The cortex exhibits large air spaces and is encircled by the exodermis (Fig. 8M). At one end of the cortex, penetrating the parenchyma cells, another small rootlet is preserved in cross section. Probably this small rootlet is a branching of the parent root, running obliquely.

Some examples of Upper Paleozoic roots with well-developed air spaces include the cordaitalean *Amyelon* (Cridland, 1964; Costanza, 1985; Wang et al., 2003) and the associated rootlets, illustrated by those authors and by Raymond et al. (2010). According to Wang et al. (2003), *A. taiyuanense* includes rootlets less than 4 mm in diameter and large roots greater than 4 mm in diameter. The rootlets greater than 0.5 mm in diameter display two zones in the cortex, being aerenchymatous the inner. Roots have secondary xylem with four to six pits on radial walls of the tracheids.

Daugherty (1963) described small roots within large fragments of a hollow log from the Triassic of Arizona. This author defined a new genus and species *Araucariorhiza joae* for these roots with a diarch stele and secondary xylem consisting of 1 or 2 cuneate groups.

8. Affinities with Cordaites

The wood of the specimens shares anatomical characters with some form-genera like *Agathoxylon* Hartig and *Araucarioxylon* Kraus, widely used for fossil woods with secondary-xylem anatomy similar to the extant Araucariaceae (Philippe, 1995; Bamford and Philippe, 2001). However, several views regarding the validity of these genera have been published elsewhere. Philippe (2010) proposed including in *Agathoxylon* the species already proposed for *Araucarioxylon* and, because this wood type displays few characteristic features, only one species should be retained. According to the original diagnosis and the later interpretation of Philippe (1995, 2010), *Agathoxylon* is considered a morphotaxon characterized only by the main features of secondary xylem. Therefore, we prefer to refer our specimens showing characters of the pith and primary xylem, to *Cuyoxylon* Pujana and Césari (2008) previously recorded in this Gondwanic region. Pujana and Césari (2008) defined this Carboniferous genus for stems with mesarch primary xylem, centrifugal secondary xylem, bi-multiseriate crowded pitting on the radial walls of the tracheids, uniseriate homogenous rays, and cross-fields with numerous bordered small pits. *Cuyoxylon* as well as our specimens are similar to the wood of *Cordaites* and especially to *Mesoxylon* Scott and Maslen. This latter Euramerican morphogenus of cordaitalean whole plant lacks distinctive sympodia and its primary vascular system typically consists of double mesarch leaf traces located at the margin of the pith (Trivett and Rothwell, 1985). The Argentinian specimens also differ from *Mesoxylon* in having numerous crossfield pits. The other cordaitalean morphogenus *Cordaixylon* usually has septate pith, apparently absent in our specimens and always has endarch protoxylem, sympodial vasculature and secondary xylem similar to *Mesoxylon*.

Some rootlets, found inside the wood, have anatomical characters that coincide with those of the roots attached to the trunks; therefore we consider that they belong to the same taxon. The close resemblance between our roots and rootlets and those referred to Cordaitean species confirms the similarity with this plant group. Nevertheless, the presence of true *Cordaites* in Gondwana has been an unresolved question. Many Gondwanic Upper Paleozoic assemblages contain abundant imprints of spatulate leaves and dispersed seeds similar to the northern *Cordaites*, but no fertile shoots have been described confirming the worldwide distribution of these gymnosperms.

9. Evidence of plant–arthropod interactions

Evidence of plant–arthropod interactions, in the form of coprolites and tunnels in wood and other tissues, was found in some specimens. Kellogg and Taylor (2004) noted that the majority of the cells in woody tissue (i.e., secondary xylem) are dead at maturity, so wood-boring activity in the fossil record can rarely be conclusively designated as detritivory or herbivory. Coprolites are abundant in the central cavity that occupied the pith (Fig. 4B), they are small round bodies about 0·010 and 0·1 mm in diameter. Their diameters are within the size range of coprolites reported from permineralized floras attributed to oribatid mites (Baxendale, 1979; Scott and Taylor, 1983; Goth and Wilde, 1992). Moreover, they possess the characteristic ovoidal, elliptical shape and contain many minute fragments of plant tissues (Fig. 4K). The secondary tissue exhibits tunnel-like areas (Figs. 4K, L) with irregular borders but having subcircular shape in transverse view. The presence of coprolites within the central part of rootlets (Fig. 4J) is evidence of the activity of arthropods at a later stage of rootlet development inside of the decayed wood. However, probably the arthropods began to invade the wood at the same time that the stumps functioned as nurse logs.

Labandeira et al. (1997) proposed that oribatid mites, particularly the superfamilies Euphthiracaroidea, Phthiracaroidea, Hermannielloidea, Carabodoidea and Liacaroidea, were the arthropod clades responsible for the extensive borings found in a diversity of Pennsylvanian plant hosts and plant tissues. Today, oribatid mites are necessary to the decomposition of plant tissues in modern temperate forests, helping in the production of the soil organic matter. Oribatid mites are chelicerate arthropods usually not larger than 1.0 mm that produce somewhat fewer than one to eight fecal pellets per day. These pellets are chemically similar to their parent plant tissues. A diverse oribatid mite fauna is usually found in decaying wood, including xylophages and probably fungivorouss types. Upper Paleozoic evidence of oribatid mite tunnels and coprolites has been documented from lycopsids, sphenopsids, ferns, pteridosperms, cordaites (Cichan and Taylor, 1982; Scott and Taylor, 1983; Rolfe, 1985), and conifers. These oribatid mites produced spheroidal and

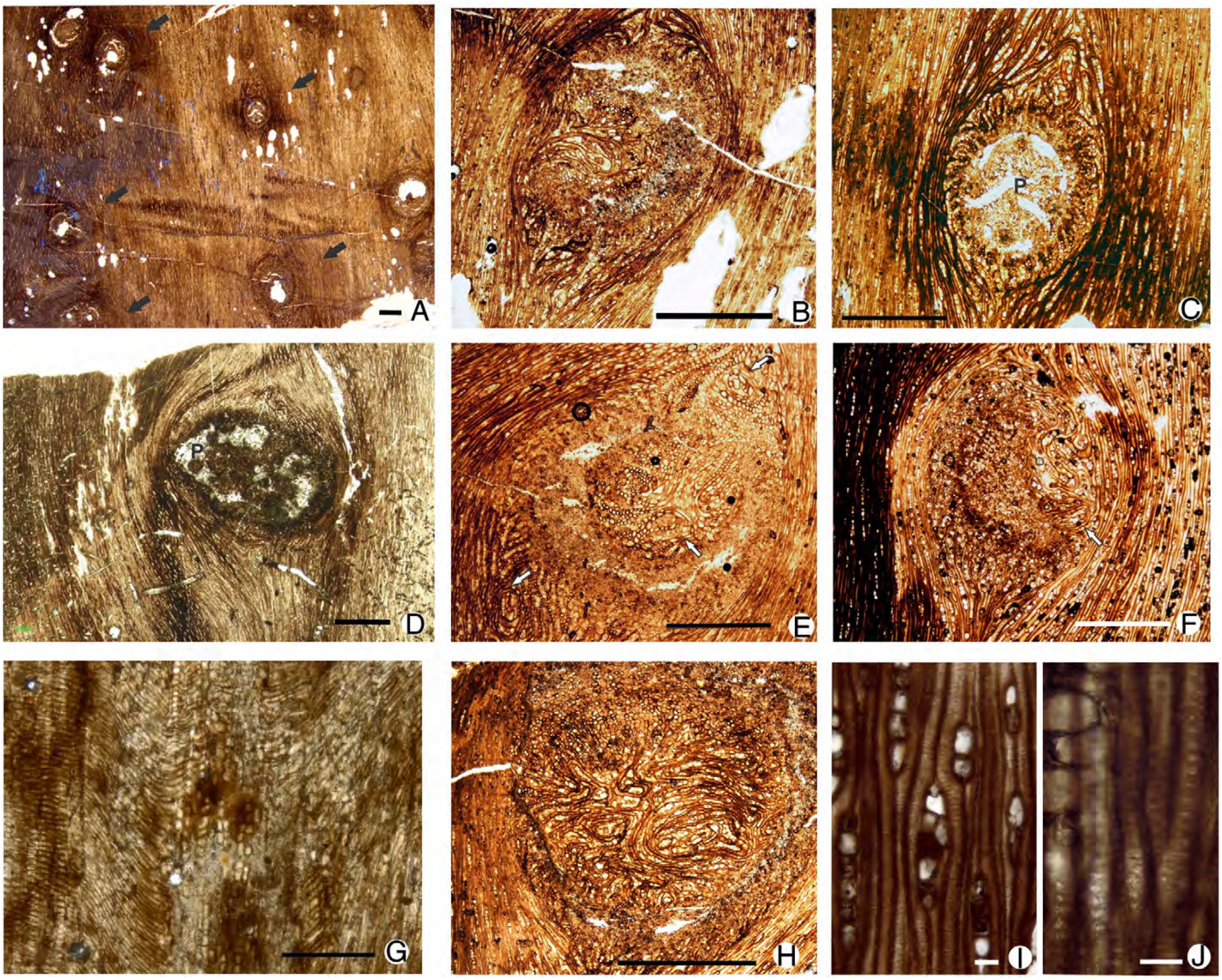


Fig. 5. A. Tangential section of secondary xylem with vascular traces (arrows), PBSJ 463; B. Cross section of vascular trace showing disordered wood pattern with swirls and circular patterns of cells, PBSJ 463; C: Cross section of vascular trace with pith (P), PBSJ 463; D: Cross section of branch trace, showing a central cylinder of pith (P) in tangential section of wood, PBSJ 464. E, F. Vascular traces with circular tracheids (arrows) and curved tracheids, PBSJ 463; G: Longitudinal section of vascular trace, PBSJ 463; H: Cross section of vascular trace I, PBSJ 463; J: Tracheids in tangential section showing spiral-reticulate thickenings, PBSJ 463. Scale: A-F = 1 mm; G = 500 μm; H = 1 mm, I-J = 50 μm.

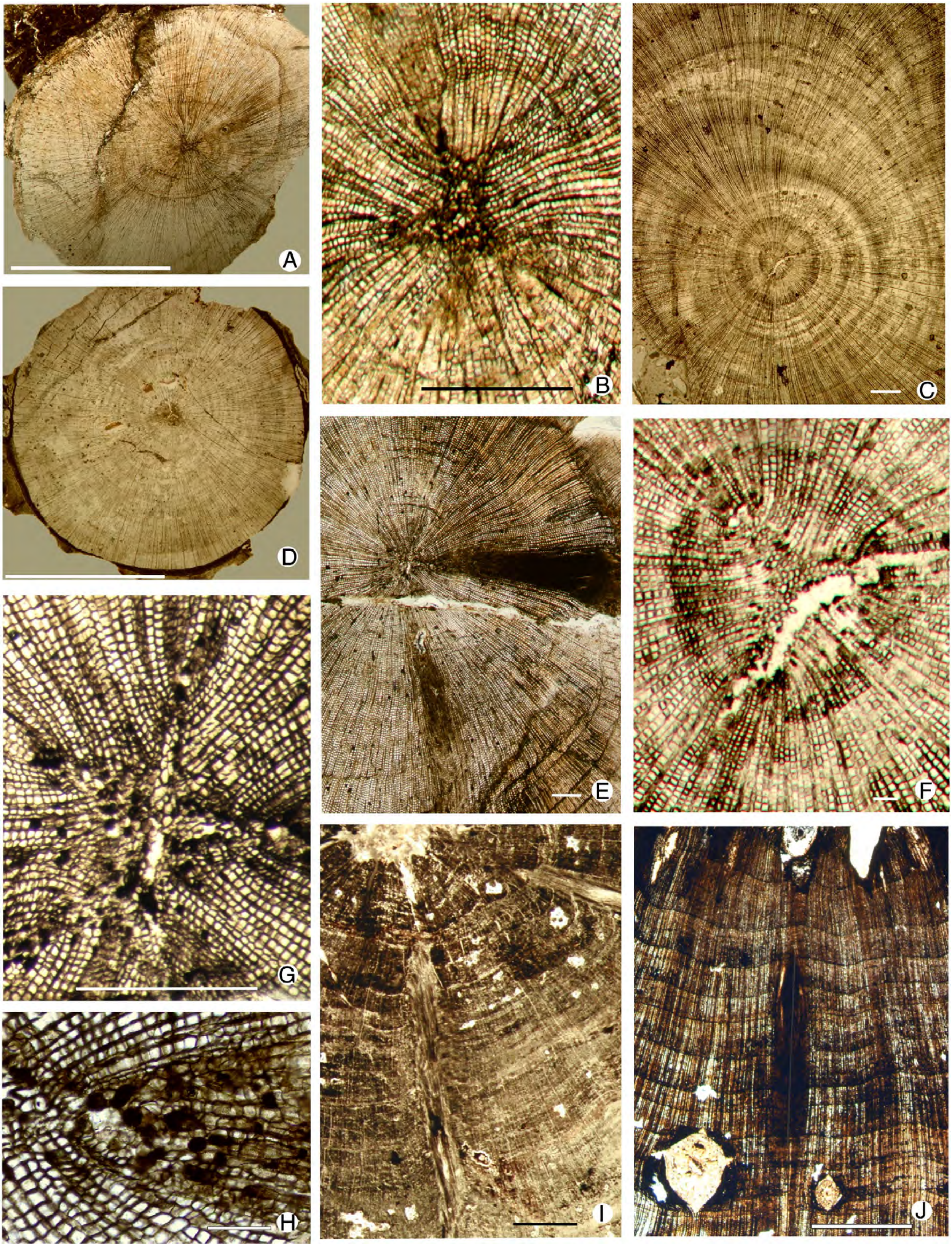
ovoidal to cylindrical coprolites ranging from 45 μm to 110 μm in size, and tunnels within plant tissues.

10. Paleoenvironmental considerations

An autochthonous origin of the trees studied here is inferred based on the upright position of some stumps with their bases penetrating the underlying beds together with abundant "fallen" logs in horizontal or sub-horizontal position. The burial deposits are interpreted as formed in low energy environments without evidence of significant transport of the logs, which probably represent trees from the original vegetation that fell on the forest floor. It is important to highlight the lack of channels, the absence of alignment of trunks and anomalous accumulations of logs, indicating that they were kept in the original soils. Assemblages like the one described here, where some upright stumps are preserved together with abundant "fallen" logs evidencing no or minimal transport cannot be considered allochthonous or parautocthonous, i.e., specimens entombed by processes able to transport them, either outside or within their original habitat. In contrast, fossil forests buried in growth position in a geological instant (T^0 assemblages) differ in having all or almost all specimens rooted in their original soils (Dimichele and Falcon-Lang, 2011). The Andean trees may be not considered a complete "snapshot" of the vegetation but certainly represent part of a natural forest and their anatomical characteristics reflect the environmental conditions. However, they not provide information about structure of the canopy, tree density or ecological gradients of ancient vegetation.

The studied fossiliferous succession consists of carbonate microbialites intercalated with thin detritic horizons and volcanoclastic rocks. Microbialites are formed of non-laminated facies (thrombolites) in the lower parts, and laminated facies (stromatolites) in the upper parts. These sequences are capped by paleosol facies showing abundant silicified trunks including, in some cases, tree stumps in life position. Sedimentology indicates that standing water and saturated soils were present.

Trees of this Upper Paleozoic Andean forest were rooted in a volcanic weathered substrate and micritic muds. Many stumps are


A
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preserved to a height of 0.45–0.50 m, projecting into carbonate muds that on some bedding surfaces exhibit mud-cracks indicating periodic desiccation of shallow water bodies. Therefore, volcanism and episodic flooding and desiccations were the most important events that affected the vegetation (Fig. 9). López and Kursar (2007) suggested that relatively few species have the specific suite of traits needed to disperse and establish in an alternating flood–drought regime. They compare the seasonally flooded forests in eastern Amazonia, which lack a severe dry season and appear much more diverse than those in northern South and Central America that experience drought. This assumption may be useful to explain the low diversity of the assemblage studied.

Sedimentological evidence suggests that vegetation lived under intermittent flooded conditions similar to mangroves, but the identification of mangroves should only rely on evidence of flooding by marine waters contemporaneous with the life of the tree (Plaziat et al., 2001). Although the San Ignacio Formation has not provided marine fossils yet, it may be correlated with the Early Permian Huentelauquen Formation in the nearby region of Chile (Charrier et al., 2007) which is also composed of limestones, shales and sandstones that bear remains of marine invertebrates. Therefore, the flooding sequences in the outcrops studied here could represent fluctuations in sea level position within a coastal lagoon (probably inland mangrove) environment (Fig. 9). These forests appear isolated from the sea, but influenced by groundwater exchange occurring at the land-margin zone. All these features are consistent with those reported by DiMichele and Falcon-Lang (2011) as the most favorable for the preservation of Paleozoic autochthonous assemblages (wetland settings at, or close to, sea level and environments proximal to volcanic centers)

10.1. Absence of distinctive growth rings

Three quantitative aspects of woods have been used for many years to interpret ancient climates: 1) mean growth ring width was analyzed as an indicator of favorable growing conditions; 2) mean sensitivity was a marker of environmental variability and 3) the percentage latewood was interpreted to indicate the existence of climatic seasonality or favorable conditions toward the end of the growing season. These parameters were analyzed at a global scale by Falcon-Lang (2005) who recommended that quantitative percentage latewood data and mean ring width data no longer be used as paleoclimatic indicators. However, he proposed that qualitative characters such as the presence or absence of growth rings or growth interruptions, and the occurrence of traumatic rings or false rings provide important qualitative paleoclimatic data.

Brison et al. (2001) studied woods from Jurassic–Cretaceous interval and suggested that *Agathoxylon* never has thick latewood, and its growth rings should be interpreted with caution. They pointed out that extant Araucariaceae with *Agathoxylon*-type wood never display marked latewood even when growing in clearly seasonal climates. The wood of the fossil trunks studied here are of the *Agathoxylon*-type and, according to the rule, lacks distinctive growth rings. Cordaitalean wood of dryland settings lacks growth rings although weak growth rings are present in branches, probably because they are more susceptible to environmental fluctuations (Falcon-Lang, 2007). On the other hand, Falcon-Lang (2000) found that the greater the leaf longevity, the more weakly developed are the growth rings in the wood.

The faint growth changes observed in the wood of the studied specimens can be interpreted as response to local stress conditions rather than to climatic fluctuations.

10.2. Adaptations to flooding

The roots studied here are comparable to *Cordaites* rooting organs. Cridland (1964) compared the cordaite roots (*Amyelon iowense*) with the aerial roots of modern mangroves (i.e. *Rhizophora mangle*, *Langucularia racemosa*, *Avicennia tomentosa*). However, Raymond et al. (2010) considered that most of the morphological features attributed by Cridland (1964) to mangroves also exist in freshwater wetland trees. Therefore, these authors proposed that the morphology of cordaites roots growing in mires suggests the presence of water-logged soils, independent of salinity. According to Tomlinson (1986) modern mangroves and freshwater wetland trees do not have different root anatomy. The proposal that cordaites grew in seasonal climates on well-drained occasionally flooded peats, was presented by DiMichele and Philips (1994). Falcon-Lang and Bashforth (2005) proposed that cordaitalean plants in paleotropical Euramerica, include forms that grew in lagoons, peat mires, coastal plains, alluvial fans, and in mountainous terrains.

According to Kozlowski (1997) the way in which flood-tolerant plants survive waterlogging includes morphological, anatomical and physiological adaptations. Increase in the diffusion of O_2 in the stems and roots is one of the most important adaptations. The efficient transport of O_2 through the plant to the roots is favored by aerenchyma tissues, lenticels and adventitious roots. We lack evidence of aerenchyma preserved in the roots attached to the trunks, but this tissue is present in the rootlets growing inside the wood. Transverse sections of such rootlets show the typical aerenchymatic spaces that today develop in plants living in waterlogged soils (Justin and Amstrong, 1987; Kozlowski, 1997). As it was discussed, the air spaces probably originated via lysigeny. Lysigenous air-space development arises from programmed death of targeted cells in a process that is mediated by ethylene increase under low O_2 concentration (Jackson and Armstrong, 1999). If we believe that the rootlets are young equivalents of the mature roots, we can argue that the latter also may have developed aerenchyma as an ecological response to the environment. Moreover, it must be considered that living mangrove seedlings have lacunae in the ground tissue that allow them to maintain aerobic metabolism during periods of flooding.

The occurrence of adventitious roots can be interpreted as an adaptation to flooding. Kozlowski (1997) pointed out that they are commonly produced by flooded plants and described four lines of evidence indicating that they help in the loss of decayed portions of the original roots following flooding.

Hose et al. (2001) consider the exodermis a barrier to the flow of water to internal root cells and conducting elements. They pointed out that in wetland plants the exodermis is a barrier for oxygen diffusion out of the aerenchyma into the surroundings.

Phi thickenings were first described in the nineteenth century and consist of nitrocellulose wall deposits that are impregnated with lignin. They usually form on the walls of certain cell layers in the root cortex of some gymnosperms (Haas et al., 1976) and a few families

Fig. 6. A–J: Transverse sections of roots. A: One branch of the root shown in Fig. 3.E, with secondary xylem, PBSJ 471; B: enlargement of A, showing the tetrarch vascular cylinder; C: Triarch root with irregular zonation in secondary xylem, PBSJ 465; D: Triarch root, PBSJ 465; E: Tetrarch root with two vascular traces of primary branch roots, PBSJ 468; F: Enlargement of C showing the three vascular bundles; G: Enlargement of E showing vascular cylinder and branch root arising at the protoxylem pole; H: Enlargement of G, showing the inner column of tracheary elements of primary xylem of the branch root with reticulate pitting; I. Cross section of wood with two primary branch roots traversing the axis from the center to the exterior, PBSJ 469; J: Cross section of wood showing a probable adventitious branch root, PBSJ 458. Scale: A–D = 1 cm, B, C, I = 1 mm, E, G = 1 mm, F, H = 100 μm, J = 3 mm.

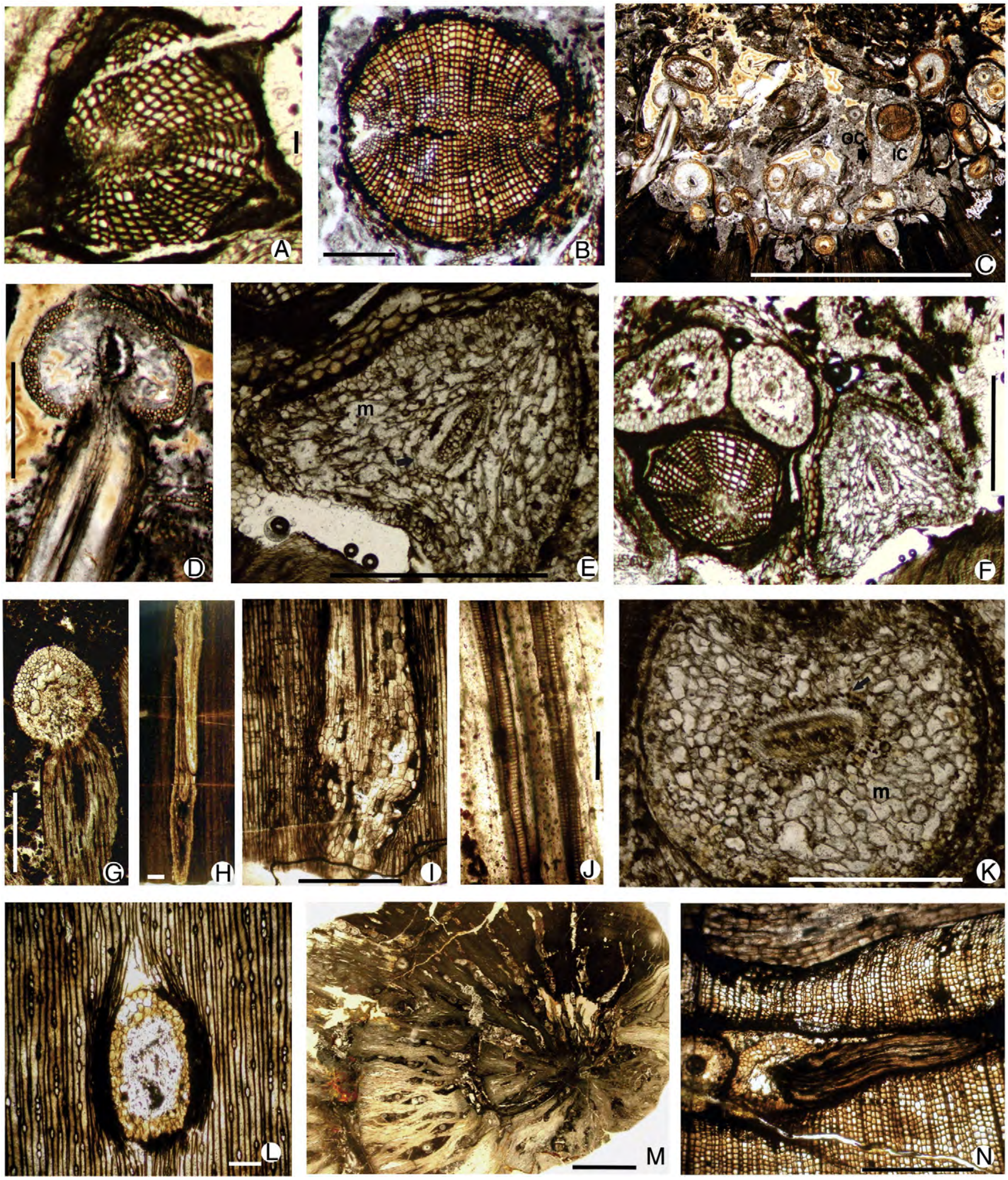

Fig. 7. A. Cross section of triarch rootlet with secondary xylem, PBSJ 460; B: Enlargement of diarch rootlet with secondary xylem shown in C (white arrow), PBSJ 458; C: general view of wood invades by rootlets, one of them showing the inner (IC) and outer cortex (OC, short arrow), black arrow marks rootlet shown in D, PBSJ 458; D: cross section of rootlet with lateral branching in longitudinal section; E: cross-sections of probable seedlings at level of the hypocotyl, showing parenchyma cells representing mesophyll (m) and the diarch vascular cylinder, PBSJ 460; F, Overview of four rootlets in different ontogenetic stages; G: young rootlet rising out from another rootlet, PBSJ 460; H: Tangential section of wood showing roots in longitudinal view, PBSJ 459e; I: Tangential section of wood showing longitudinal section of root with parenchyma cells and primary xylem, PBSJ 459 d; J: Enlargement of the primary xylem shown in I; K: Cross section of seedling showing the probable mesophyll (m) and phi thickenings (arrow), PBSJ 460; L: Tangential section of wood with rootlet en cross section, PBSJ 459e; M. Overview of stem with degraded wood invade by rootlets, PBSJ 470; N: Young root rising out from another root in cross section of wood, PBSJ 459a. Scale: A, E, K, L = 100 μm; B, J = 50 μm; C, M = 1 cm; D, F, G, H, I, N = 1 mm.

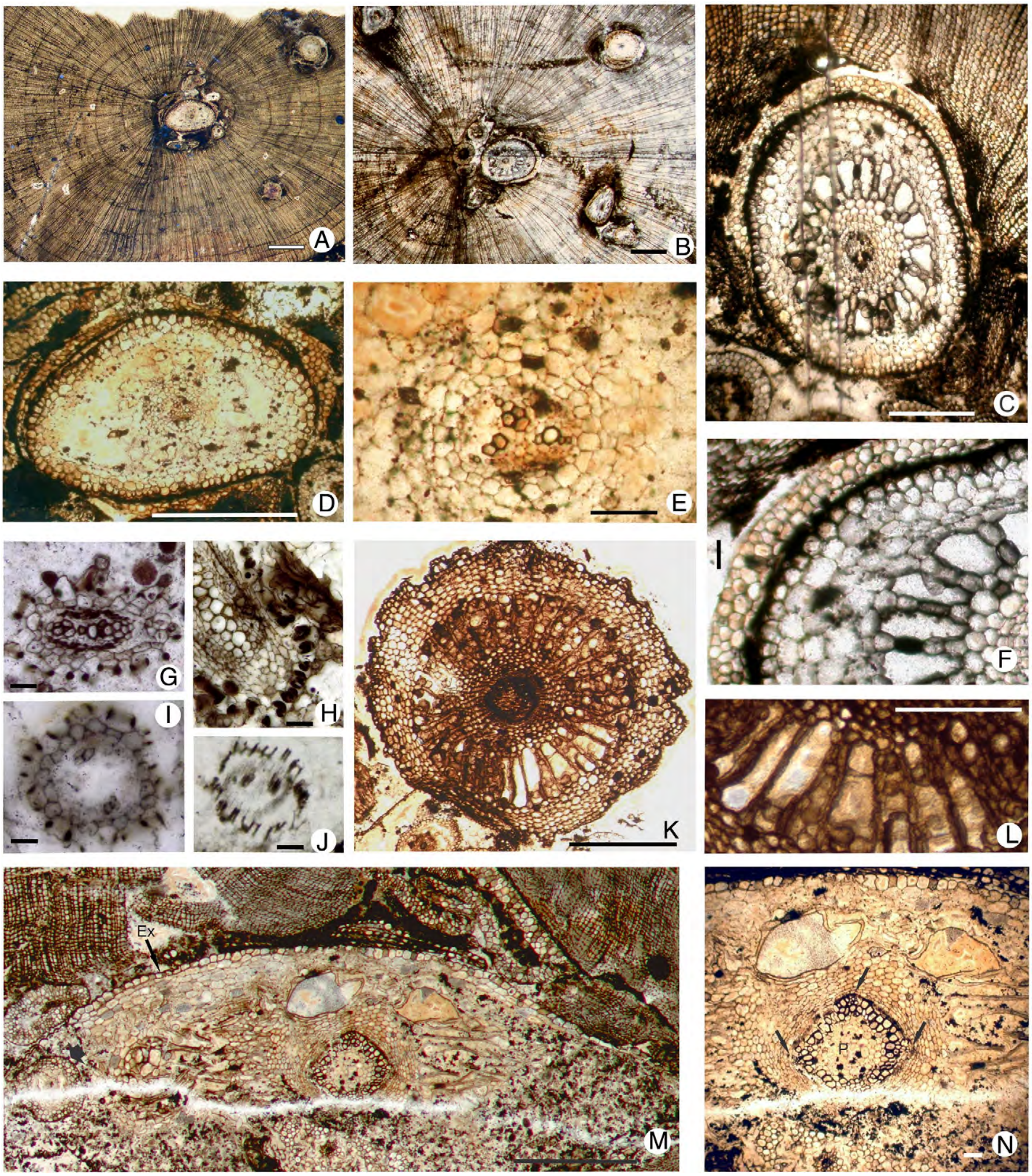

Fig. 8. A. Overview of stem with secondary xylem showing rootlets in cross section. At center a triarch rootlet, PBSJ 459b. B. Overview of another section of stem shown in A, with the central triarch rootlet exhibiting aerenchyma spaces, PBSJ 459a; C. Enlargement of B showing the inner cortex with radial aerenchyma spaces and thickened exodermis; D. Enlargement of A, showing the thickened exodermis, the poorly preserved inner cortex with some air spaces; E. Detail of the vascular cylinder of the rootlet shown in D. F. Detail of inner and outer cortex shown in C; G–J: Variability in the preservation of phi thickenings close to the vascular cylinder, PBSJ 460; K., cross section of rootlet with radial, large intercellular spaces in the inner cortex, PBSJ 458a; L: Enlargement of K showing the M: Cross section of tetrarch root showing inner, outer cortex and exodermis, PBSJ 459; N: Enlargement of M, showing the protoxylem poles (arrows), pith (P), compact inner cortex and air spaces in the outer cortex. Scale: A, B, C, D, K, M = 1 mm; E, F, N = 100 µm; G, H, I, J = 50 µm.

of angiosperms (Peterson et al., 1981; Praktikakis et al., 1998). The presence of phi thickenings is apparently not affected by waterlogging (Gerrath et al., 2005).

Mycorrhizae have not been observed in the numerous specimens studied. Probably, their absence in our material is due to their strongly aerobic character, being rare in waterlogged soils, although

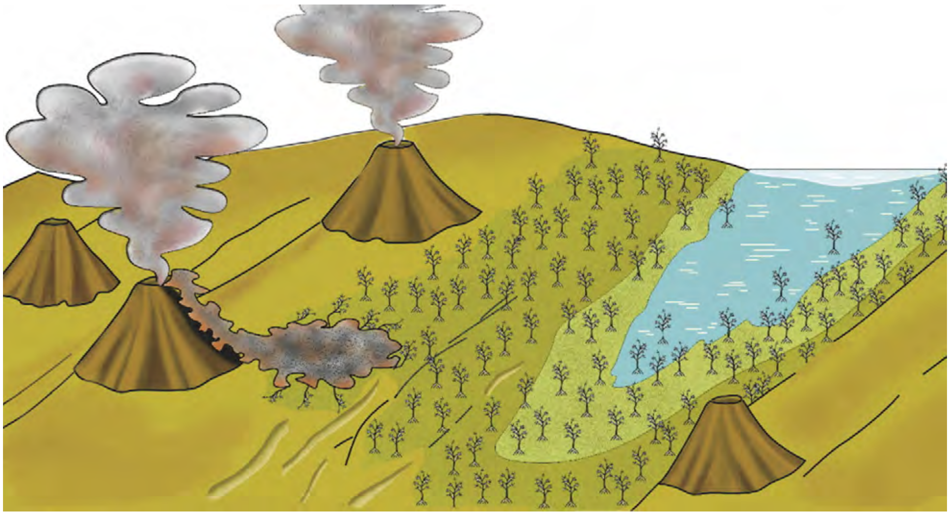

Fig. 9. Reconstruction of the paleoenvironment and the cordaite-dominated plant community.

arbuscural mycorrhizal fungi tolerate wetland conditions (Bohrer et al., 2004).

10.3. Regulation of cambial activity

The abundance of vascular traces exhibiting tracheids arranged in circular patterns is related to axial polar auxin flow. These patterns are seen in living plants in reaction to a disruption of axial polar auxin flow by the presence of buds on branches. Fossil evidence of these patterns was described by Rothwell and Lev-Yadun (2005) in *Archaeopteris* Dawson.

The capacity to produce opportunistic shoots was an important adaptation that provided the chance for the Andean trees to rapidly colonize new niches in the stressed environments of the area. According to Decombeix et al. (2010), in extant trees, epicormic branching can be part of the normal architectural development of the plant, or related to long-term changes in light conditions, or caused by a short-term environmental stress. They interpreted the epicormic shoots from Antarctica as the result of an architectural plasticity of the trees that allowed them to respond rapidly to short- or long-term environmental stresses. Cooper-Ellis et al. (1999) proposed that breakage of branches due to the fall of another tree, flooding events, snow, and strong winds represent causes for the formation of epicormic branching. *Sequoia sempervirens* (D. Don.) Endl. frequently regenerates through stump sprouts after cutting or fire (O'Hara and Berrill, 2009) or basal sprouts or root sprouts from uncut trees. These sprouts originate from a lignotuber near the base (Del Tredici, 1998), or dormant (preventitious, Fink, 1984) and adventitious buds on the tree trunk, and are generally assumed to be an adaptation to allow rapid replacement of lost foliage.

10.4. Nurse logs

Volcanism not only preserved forests but also affected periodically the vegetation opening different ways of recovering. Pyroclastic flows including incandescent mixtures of gas and solids produced by explosive eruptions covered the vegetation forming ignimbrite flows.

Del Moral and Grishin (1999) described volcanic disturbance regimes and their ecological consequences, especially how plants colonize newly created volcanic surfaces. According to Del Moral and Grishin (1999) lavas and pyroclastic flows are of such magnitude and severity that survival is rare in extant forests. Haruki and Tsuyuzaki (2001) evaluated woody plant seedling establishment in the early stages of volcanic plant succession. They concluded that ground surface texture is an important factor in determining seedling establishment in the early stages of volcanic plant succession, and nutrient status is unimportant. Coarse particles trap various sized, wind-blown seeds more effectively than other substrates and subsequently show higher seedling densities.

In a volcanically affected environment, where the vegetation studied here developed, one of the ecological strategies of recovery would have been the sprouting of seedlings in decaying logs. The presence of rootlets within the secondary xylem of the Argentinian stems was interpreted by Césari et al. (2010) as evidence of the "nurse logs" ecological strategy during the Upper Paleozoic. The occurrence of nurse logs in the Andean assemblage was recognized by DiMichele and Falcon-Lang (2011) as fossil evidence of real-time dynamics of the ancient vegetation. Today, nurse logs are found in many forests throughout North America, such as the *Picea sitchensis* zone of the Pacific Northwest (Harmon et al., 1986). According to Harmon and Franklin (1989) shading of herbs and mosses on the forest floor appears to be responsible for the unequal number of tree seedlings found on logs. Fallen logs represent safe sites where competition is low enough for tree seedling recruitment. In contrast, competition from understory plants did not appear to be the main factor determining the abundance of seedlings on logs in the Chilean rainforest, where seedlings of small-seeded species are common on fallen logs and stumps (Lusk, 1995).

11. Coeval vegetation in western Gondwana

Most studies of Carboniferous–Permian fossil plants in western Gondwana are based on floras from South Africa, Argentina and Brazil (e.g., Anderson and Anderson, 1985; Archangelsky et al., 1996; Césari et al., 2007; Iannuzzi et al., 2010). Studies of floras from Peru (Iannuzzi et al., 1998) and Chile (Breitkreuz et al., 1992) are less numerous and more recent. Although the *Nothorhacopteris* and *Glossopteris* leaf morphotypes were common in the Carboniferous and Permian respectively throughout Gondwana, diverse assemblages are found in the westernmost area. The stratigraphic position of the flora studied herein, proposes a first comparison with the Argentinian late Carboniferous Interval Biozone (Archangelsky and Cúneo, 1991) that succeeds the well-known *Nothorhacopteris–Botrychiopsis–Ginkgophyllum* (NBG) Biozone. The age of the NBG Biozone that flourished under glacial and postglacial conditions, was recently constrained to the late Serpukhovian–Moscovian by radiometric dating (Césari et al., 2011). The Interval flora is characterized by the first macrofloristic records of conifers and ferns in assemblages comprising the classical components of the NBG flora, i.e., pteridosperms, articulates, lycophytes and leaves of probable cordaitales. Ferns are represented by *Pecopteris* and *Asterotheca* fronds and conifers include *Paranocladus* and *Kraeuselcladus* leafy twigs. Late Carboniferous–early Cisuralian Argentinian deposits bearing permineralized woods are known from the Solca Formation where several different wood types are represented (Crisafulli and Herbst, 2008). The species *Agathoxylon kumarpurensis* (Bajpai and Singh) Crisafulli and Herbst, *Agathoxylon ningahense* (Maheshwari) Crisafulli and Herbst, *Podocarpoxylon indicum* (Bhardwaj) Bose and Maheshwari, *Chapmanoxylon jamuriense* Pant and Singh and *Chapmanoxylon oltaense* Crisafulli and Herbst were described by Crisafulli and Herbst (2008), but none of them is similar to the specimens from the San Ignacio Formation.

The northwestern Argentinian succeeding early Cisuralian flora is well represented in the classical localities of Bajo de Véliz and Arroyo de Totoral, where glossopterid and cordaitean leaves together with conifers are abundant. Anatomical preserved woods are scarce in the Permian of Argentina (Crisafulli et al., 2000). Permineralized plant stems are common in the South American late Cisuralian deposits of Paraguay (Crisafulli and Herbst, 2009), Brazil (Dohms, 1976; Mussa, 1978) and Uruguay (Crisafulli and Lutz, 1997; Crisafulli, 2001, 2002; Crisafulli et al., 2009). Probably, the specimens described from the Brazilian Irati Formation by Mussa (1978) are the more comparable with the here studied; however a detailed description of some anatomical characters (i.e., pitting of the tracheids, number of pits in cross-fields, etc.) would be necessary for a closer comparison. Palynological assemblages of the Irati Formation have been referred to the *Lueckisporites virkkiae* Zone that can be estimated between 281.4 ± 3.4 Ma and 278.4 ± 2.2 Ma (Mori et al., 2012).

12. Conclusions

The identification of a fossil forest interval developed and buried under a combination of environmental conditions that promoted its exceptional preservation has enabled the recognition of fine anatomical structures. These Argentinian fossils represent one example of an autochthonous assemblage of cordaitean trees preserved in the late Paleozoic of western Gondwana.

The available sedimentologic evidence suggests that the trees grew under unstable environmental conditions, affected by periodic flooding, drying and volcanism. Although there is no evidence of marine influence in the forest interval itself, probably flourished near the coast (inland mangrove), under brackish conditions with intermittent desiccation. According to biomechanical calculations based on the stump diameter the trees could reach up to 28 m in height. Anatomical evidence helps to reconstruct their habitat: 1) Discontinuous and subtle growth rings suggest cessation in growth due to stress, 2) Aerenchyma in rootlets allowed growth in anoxic, waterlogged soils, 3) Presence of adventitious roots can be interpreted as an adaptation to flooding, 4) Abundance of fecal pellets indicates periodic aerial exposition, 5) Possible epicormic branching provided the chance to rapidly overcome environmental stress, 6) Nurse log ecological strategy was developed for the recovery of the vegetation under adverse conditions. These data improve the Gondwanan late Paleozoic vegetation models and the knowledge about dynamics at community-scale ecology.

Acknowledgments

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