



## *Alienopteris livingstonensis* gen. et sp. nov., enigmatic petrified tree fern stem (Cyatheaales) from the Aptian Cerro Negro Formation, Antarctica

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### ABSTRACT

A new genus and species of Mesozoic fern, *Alienopteris livingstonensis* gen. et sp. nov., is defined, based on permineralized stems recovered from the Aptian Cerro Negro Formation (Antarctica). This new taxon is characterized by the presence of Y-shaped meristeles in the stem, surrounding an heterogeneous pith, and the presence of complex petiole bases, consisting in abaxial and adaxial archs, similar to the ones present in the Cyatheaaceae s.l.. Since no living nor fossil filicalean fern possesses such mixture of features, and taking into account that no leaves and reproductive structures were found, phylogenetic relationships are not clear. Two independent cladistic analysis show clear placement of *Alienopteris livingstonensis* among the "core tree ferns."

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### 1. Introduction

The Cerro Negro Formation (Antarctica) is a volcanoclastic non-marine succession that crops out at President Head (Snow Island) and the Byers Peninsula (Livingston Island), with an age estimated in  $120.3 \pm 2.2$  My,  $119.4 \pm 0.6$  My and  $119.1 \pm 0.8$  My using the  $^{40}\text{Ar}/^{39}\text{Ar}$  method (Hathway, 1997; Hathway et al., 1999). It contains an abundant and diverse palaeoflora, including representatives of the Bryophyta (Cantrill, 2000), Hepatophyta (Césari et al., 1999; Cantrill, 2000), Equisetales (Césari et al., 1999), Filicales (Césari et al., 1999, 2001; Cantrill, 2000; Césari, 2006; Vera, 2007), Corystospermales (Hernández and Azcárate, 1971; Césari et al., 1999), Caytoniales (Césari et al., 1999; Cantrill, 2000), Bennettitales (Hernández and Azcárate, 1971; Torres et al., 1997; Césari et al., 1999; Cantrill, 2000; Falcon-Lang and Cantrill, 2001), Cycadales (Hernández and Azcárate, 1971; Césari et al., 1999), Pentoxylales (Césari et al., 1998; Cantrill, 2000), and Coniferales (Hernández and Azcárate, 1971; Césari et al., 1999; Cantrill, 2000; Falcon-Lang and Cantrill, 2001), among others. Permineralized and compression/impression specimens reveal that the filicalean ferns were one of the most abundant components of this flora, with representatives of the Cyatheaaceae, Lophosoriaceae, Osmundaceae, Dennstaedtiaceae and Gleicheniaceae (Cantrill, 2000; Césari et al., 1999, 2001; Césari, 2006; Vera, 2007). According to the modern representatives of these families (some of which are restricted to tropical or subtropical forests), this particular abundance of ferns in the

fossil record may be the result of frost-free climate for this Antarctic sector during the Aptian (Césari et al., 2001). Furthermore, Cantrill (1998) proposed minimum annual temperatures of eight degrees or more in the Southern High latitudes. Finally, Falcon-Lang and Cantrill (2002) suggested that the abundance of ferns may represent a post-eruption pioneer vegetation.

Several organ genera are known only from Antarctica, particularly from the Triassic period, including the fern *Soloropteris*, the cycadalean *Antarcticycas*, the petrified stem *Kikloxyton* (bearer of *Dicroidium* leaves) and the enigmatic petrified stem *Hapsydoxyton terpsichorum*, with a complex vascular arrangement superficially similar to some Devonian-Carboniferous Cladoxylales (Smoot et al., 1985; Millay and Taylor, 1990; Meyer-Berthaud et al., 1993; McManus et al., 2002). In this contribution, a new genus and species of filicalean fern, collected in the Cerro Negro Formation outcrops, is described in detail. The anatomy of the axis superficially resembles some representatives of the Cladoxylales, such as *Cladoxyton* and *Pietzschia*, with radial xylem arms surrounding a pith. On the other hand, the modified omega-shaped trace of the attached petioles can be compared with the one found in the dennstaedtioid or cyatheoid ferns. Two independent cladistic analysis are made, using different data matrices obtained from the literature (Rothwell, 1999; Pryer et al., 2001).

### 2. Materials and methods

Specimens were collected in the Aptian Cerro Negro Formation outcrops of Byers Peninsula, South Shetland Islands, Antarctica, at the West of the Rotch Dome ( $62^{\circ}38'41''\text{S}$  –  $60^{\circ}58'12''\text{W}$ , Párica et al.,

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2007) (Fig. 1). The peel technique (generally used for obtaining serial transverse sections of a petrified stem) gave poor results, and anatomical thin sections were prepared and mounted on microscope slides. Preservation quality of the specimens is variable, although in most cases it is good enough to study cellular details, or at least tissue position. Photographs were taken with a Nikon Coolpix 995 adapted to an Olympus BX-51 or a Nikon SMZ-2 t Microscope. Morphological data matrices were obtained from Pryer et al. (2001, including the new characters proposed by Rothwell and Nixon (2006)) and Rothwell (1999). Phylogenetic analysis were made using equal weighted maximum parsimony (TNT, Goloboff et al., 2000), to generate the most parsimonious trees (heuristic search, TBR swapping algorithm, 100 replicates, saving 10 trees per replication). All characters were unweighted, unpolarized, and multistate characters were unordered. Character coding for *Alienopteris* for both matrices is given in the appendix. Equally parsimonious trees were summarized using strict consensus tree. Trees were rooted through *Anthoceros* (Pryer et al., 2001) and *Aglaophyton* (Rothwell, 1999). The specimens are housed in the collection of the Museo Argentino de Ciencias Naturales “Bernardino R. Rivadavia,” División Paleobotánica, under BA Pb (hand specimens) and BA Pb Pm (microscope slides) numbers.

### 3. Systematic paleontology

Cyatheales A.B. Frank, 1877

“Core Tree Ferns” sensu Korall et al., 2006

Genus *Alienopteris* gen. nov.

Type species. *Alienopteris livingstonensis* (this work)

*Derivation of generic name.* Derived from the Latin word *alienus* (strange, different), because of the strange anatomy of the vascular cylinder; and *pteris* (fern).

*Generic diagnosis.* Stem upright, enclosed by two-layered sclerotic hypodermis, covered by petiole bases and dense indument of root traces and trichomes; cauline vasculature an amphiphloic dictyostele; meristemes surrounded by sclerenchyma sheath, Y-shaped when not involved in the production of leaf traces; adjacent meristemes fuse their proximal arms to initiate the production of a leaf trace; medullary and cortical bundles absent.

*Alienopteris livingstonensis* sp. nov.

Figs. 2–6.

*Derivation of specific name.* After Livingston Island, Antarctica, where the specimens were found.

*Types.* Holotype: BA Pb 14950 (BA Pb Pm 548, 549, 550), Paratype: BA Pb 14953 (BA Pb Pm 552).

*Additional specimens.* BA Pb 14951, BA Pb 14952 (BA Pb Pm 551), BA Pb 14954 (BA Pb Pm 553), BA Pb 14955 (BA Pb Pm 554, 555), BA Pb 14956 (BA Pb Pm 556), BA Pb 14957, BA Pb 14958, BA Pb 14959, BA Pb 14960, BA Pb 14961, BA Pb 14962, BA Pb 14963, BA Pb 14964, BA Pb 14965, BA Pb 14966, BA Pb 14967 (BA Pb Pm 557), BA Pb 14968 (BA Pb Pm 558), BA Pb 14969 (BA Pb Pm 559), BA Pb 14970, BA Pb 14971, BA Pb 14972, BA Pb 14973 (BA Pb Pm 560), BA Pb 14974, BA Pb 14975, BA Pb 14976.

*Type locality and stratigraphic horizon.* West of the Rotch Dome, at 62°38'41"S – 60°58'12"W, Byers Peninsula, Livingston Island, South Shetland Islands; Lower Cretaceous (Aptian) Cerro Negro Formation.

*Specific diagnosis.* Stem pith sclerenchymatous at the center and parenchymatous at the periphery; stele of the petiole bases composed by an adaxial arch formed by five small meristemes, central W-shaped and lateral V-shaped; abaxial arch composed of two bilaterally symmetrical units, each one composed of an adaxial meristeme, highly corrugated, and with the tips pointing inwards, and a smaller meristeme J-shaped, perpendicular to the symmetry axis; latter two meristemes can be fused; ground tissue with scattered sclerotic nests and secretory cavities.

*Description.* Specimens are 12–14 cm high and 6.5–13 cm wide, comprising a stem (3–6 cm wide) surrounded by helically distributed persistent petiole bases (Fig. 2A, C, E) and adventitious roots. Internally, the stem consists of a pith 5–20 mm wide, surrounded by Y-shaped meristemes, with the “base” of the Y of each meristeme pointing inwards (Fig. 2A, B). Surrounding this structure is located the cortical tissue, enclosed by a two layered hypodermis. Externally, a dense indument of trichomes originates from the endodermis (Fig. 3A).

The pith is composed by at least two different tissues. Internally, a big mass of sclerenchyma 5–11 mm in diameter, composed by

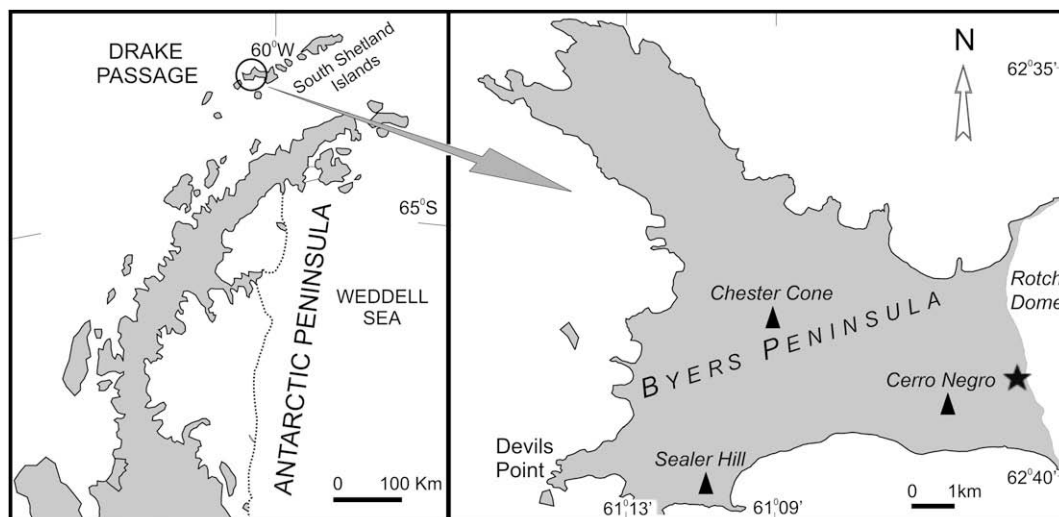
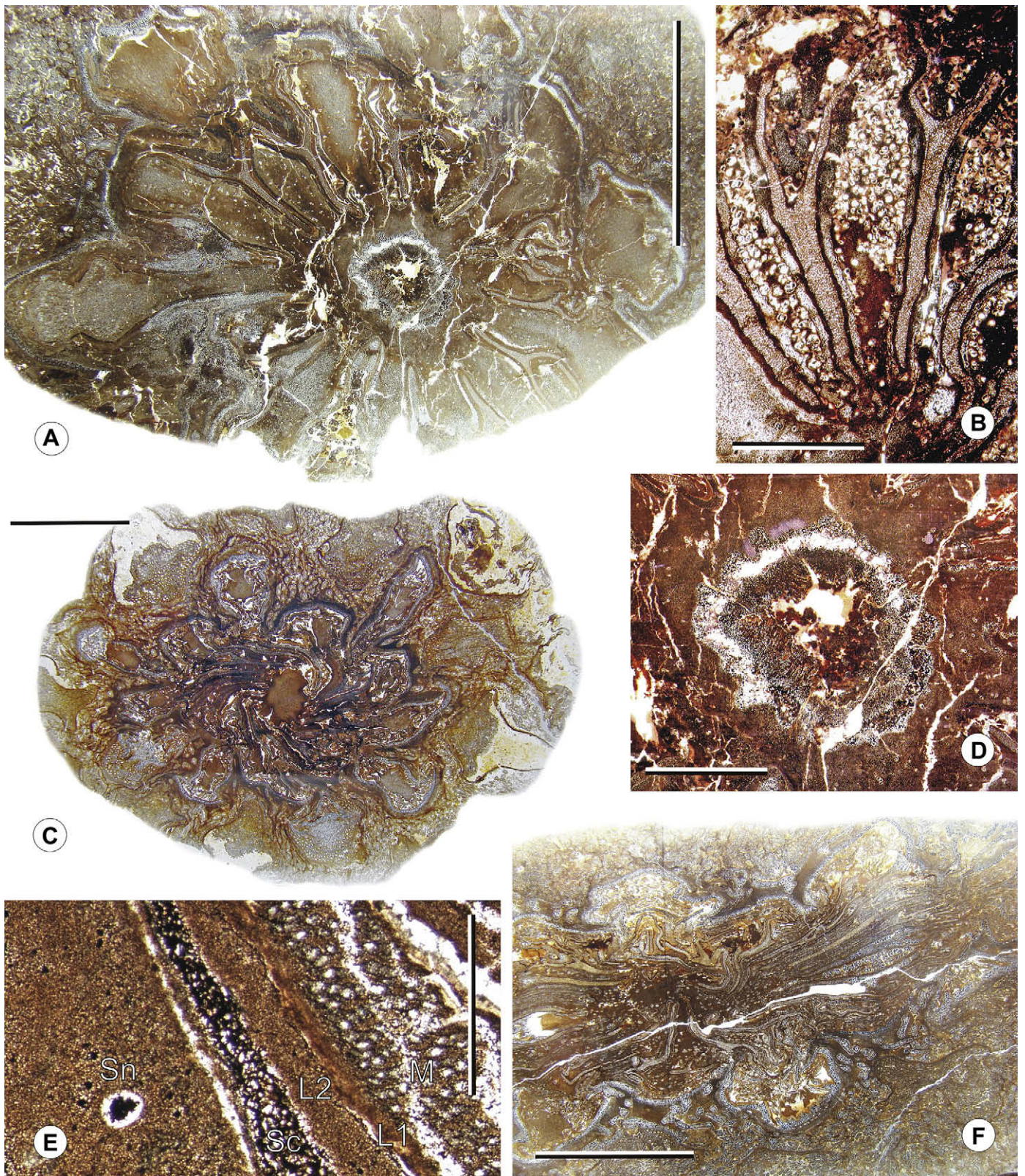


Fig. 1. Location map of Livingston Island, showing the place where the fossils of *Alienopteris livingstonensis* gen. et sp. nov. were found (star). (Modified from Césari et al., 1999, and Párica et al., 2007).





**Fig. 2.** *Alienopteris livingstonensis* gen. et sp. nov. Anatomy of the stem in transverse section. A, stem with attached petiole bases (BA Pb 14950, BA Pb Pm 549). B, detail of the stele, showing Y-shaped meristemes (BA Pb 14954, BA Pb Pm 554). C, cross section of a stem with meristemes having circular orientation (BA Pb 14953, BA Pb Pm 552). D, detail of the pith (BA Pb 14950, BA Pb Pm 549). E, detail of a meristeme, showing metaxylem tracheids and intercalary parenchyma (M), L1 and L2 layers, and sclerenchyma surrounding the structure (Sc). Notice the presence of a sclerotic nest (Sn) in the parenchymatic tissue (BA Pb 14950, BA Pb Pm 550). F, laterally crushed stem, showing the deformation of the stele (BA Pb 14956, BA Pm Pm 556). Scale bars represent 2 cm in A, C and F, 5 mm in B and D, and 1 mm in E.



cells 60–100  $\mu\text{m}$  wide, is located, surrounded by parenchymatic ground tissue (1–3 mm wide), which is poorly preserved, without cellular details (Fig. 2D).

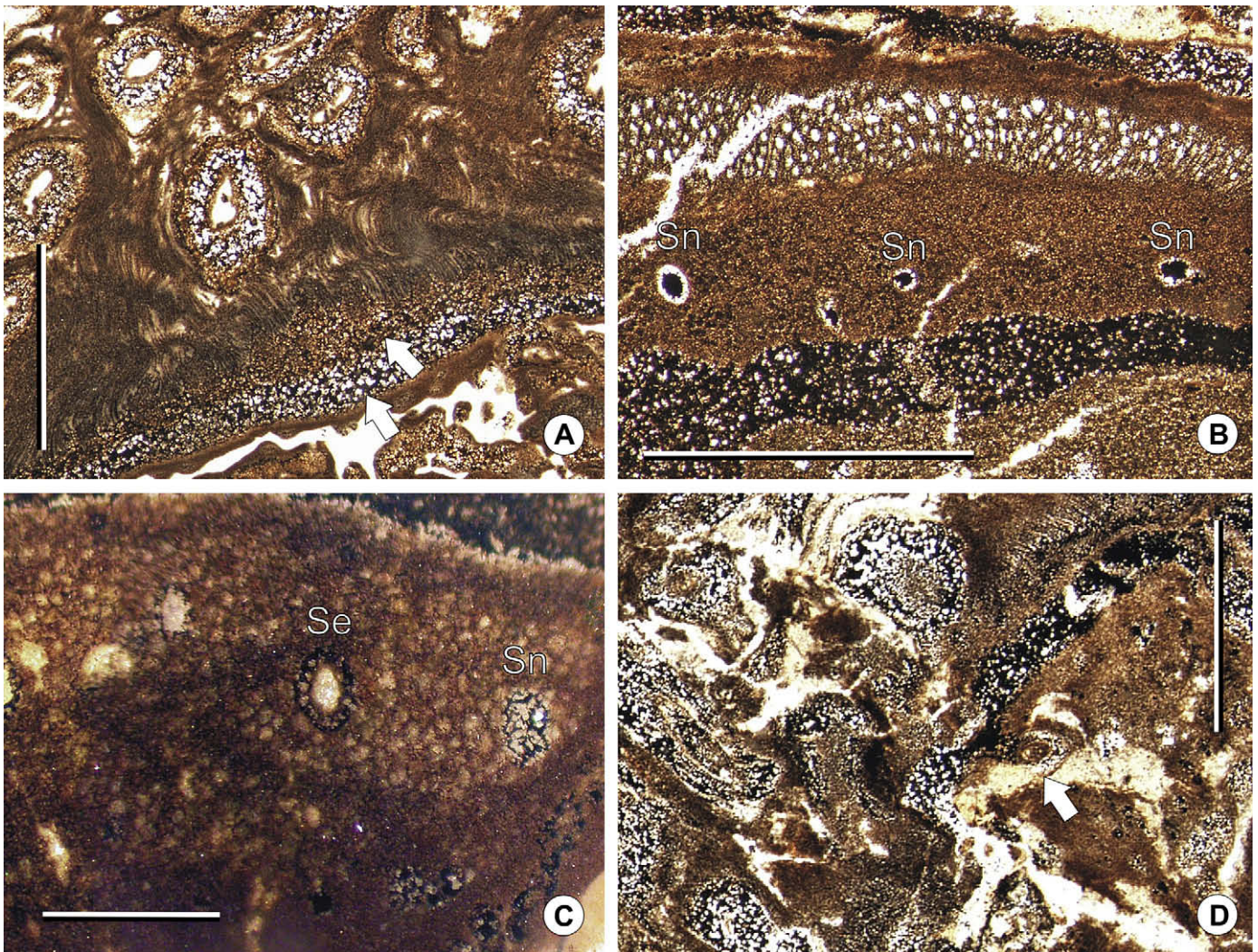
Surrounding the pith is located the vascular system, composed by 12–22 Y-shaped meristeles, forked in the distal half. In most of the studied specimens, the meristeles are placed parallel to the stem radii (Fig. 2A). However, other specimens display all the meristeles curved in one direction (Fig. 2C), and BA Pb 14955 has both arrangements depending where the cut was made. Finally, some stems are laterally crushed, which results in a compression of the vascular ring (Fig. 2F).

Meristele width is 0.95–2.6 mm in the adaxial “arm”, and 0.47–1.6 mm in the abaxial “arms”, although bifurcation region is wider (1.6–3.5 mm). Adaxial “arm” of each meristele is 6–12 mm long, whereas the abaxial “arms” are generally shorter (5–8 mm long) (Figs. 2A, F, 3B).

Each meristele is composed by several tissues. Internally, primary xylem (with metaxylem tracheids 40–100  $\mu\text{m}$  in diameter) intercalated with abundant small parenchymatic cells (totally obliterated) forms a structure of 250–600  $\mu\text{m}$  wide (5–12 tracheids thick). Cauline protoxylem was not observed. In the bigger specimens, a narrow (100–200  $\mu\text{m}$ ) poorly preserved layer of cells (L1) can be seen

surrounding this structure (interpreted as the phloem), surrounded by a wider zone (220–1100  $\mu\text{m}$ ) of parenchyma-looking cells (L2) (in some parts of the specimens, this “parenchyma” layer can be divided in two “sublayers”, but this division is only based in the different aspect and color of the layers, not in cellular characteristics). L2 presumably includes the pericycle, endodermis and a parenchyma sheath (although the degree of preservation precludes the final assignment of these tissues). Smaller specimens present a narrower (100–200  $\mu\text{m}$ ) L2. Finally, these tissues are surrounded by a 110–600  $\mu\text{m}$  wide sclerenchyma sheath (Fig. 2E). Externally, cubical cells were not observed, but this fact can be related to a deficient preservation, and not to a biological feature (Fig. 2E).

Stem cortex consists of an inner parenchymatic zone, with cells 45–70  $\mu\text{m}$  in diameter, surrounded by a two layered sclerotic hypodermis, and an epidermis bearing a dense indument of trichomes 0.5–1.5 mm long (Fig. 3A). Inner parenchymatic cortical region is similar and continuous with the pith parenchyma. Although preservation is not good, sclerotic layers of the hypodermis can be differentiated (Fig. 3A). Sclerotic hypodermis is also present in the petiole bases. Small sclerenchyma strands (sclerotic nests) 130–250  $\mu\text{m}$  wide (Figs. 2E, 3C) and secretory cavities 220–250  $\mu\text{m}$  wide (Fig. 3C) are present in the parenchymatic ground



**Fig. 3.** *Alienopteris livingstonensis* gen. et sp. nov. Anatomy of the stem in transverse section. A, detail of the two layered hypodermis (arrows) and the adventitious roots (BA Pb 14953, BA Pb Pm 552). B, sclerotic nests (Sn) enclosed by the sclerenchyma sheath of the cauline meristeles (BA Pb 14950, BA Pb Pm 550). C, Detail of a sclerotic nest (Sn) and a secretory cavity (Se) (BA Pb 14950, BA Pb Pm 550). D, adventitious roots (left) and developing trace (right), showing the presence of a root trace near the hypodermis (arrow) (BA Pb 14950, BA Pb Pm 550). Scale bars represent 2 mm in A, B and D, and 500  $\mu\text{m}$  in C.



tissue of the pith, leaf gaps and cortex, and also in the parenchyma of the meristemes (Fig. 3B).

Roots are 500–800  $\mu\text{m}$  in transverse section, and all run parallel to the stem (Fig. 3A, D). Individually, each root trace is composed by a small oval xylem strand, which probably was surrounded laterally by phloem in the living plant, and enclosed by parenchymatous-like cells (probably representing pericycle, endodermis and parenchyma sheath). Surrounding this structure is located a sclerotic layer, derived from the stem meristelar sclerenchyma. Cortical fleshy parenchyma and a narrow (hypodermal?) sclerenchyma layer surround the structure (Fig. 3A, D). Since preservation of these structures is deficient, most of observed root traces lack the tissues internal to the meristelar sclerenchyma. Furthermore, in some of them the fleshy parenchyma cannot be differentiated from the meristelar sclerenchyma nor the hypodermis. Root trace origin was impossible to determine, since all of the observed adventitious roots were located outside the stem. Although that, in one developing leaf trace, a root trace was observed, adjacent to the internal hypodermal layer. Thus, the origin of the root traces from the leaf trace when it is developing is suggested (Fig. 3D).

Leaf traces originate after the fusion of the closest “arms” of two adjacent meristemes. First, they fuse producing a continuity along the meristemes (Fig. 4A). After that, this part of the stele enlarges abaxially, developing a loop (Fig. 4B). This loop continues its enlargement, resulting in the morphology of the petiolar vasculature (Fig. 4C). Finally, the trace is released from the meristemes, which appear with their fused arms (as in the beginning of the process) (Fig. 4D). The final step is the separation of both adjacent meristemes. At the same time, the leaf trace traverses through the cortex, and separates from the stem.

Petiole bases are rhomboidal to circular, 1.5–2 mm high and 1.5–2.3 mm wide (Figs. 5A, 6), and diverge from the stem in an angle of approximately 30–40 degrees relative to the stem axis. Internally, the petiolar trace is similar to the cauline meristemes. It is formed by a layer of metaxylem tracheids, mixed with parenchyma cells, surrounded by a poorly preserved tissue, which probably includes phloem, pericycle, endodermis and a parenchyma sheath. This structure, as the cauline meristemes, is surrounded by a layer of sclerenchyma. Externally, it is immersed in cortical parenchyma, a two layered hypodermis, and an endodermis where a dense indument of trichomes originates (Fig. 5A).

The petiole trace configuration can be described as a modified omega-shaped structure. The abaxial arc is composed by five meristemes (Figs. 5A, 6). The central meristeme is W-shaped, whereas the rest are V-shaped (Figs. 5A, B, 6). Adaxial arch is formed by two bilaterally symmetrical units, each one composed by two meristemes. The most adaxial is larger and highly corrugated, gently convex (in reference to the petiolar pith), and with the tips pointing inwards. The second meristeme of this unit is smaller and less corrugated, J-shaped, with its long arm placed perpendicular to the symmetry axis, and adaxially oriented, and the concavity of the structure pointing to the center of the petiole (Fig. 5A, C). In some petioles, the latter two meristemes are fused, and each unit of the adaxial arch is composed by only one meristeme.

## 4. Discussion

### 4.1. Phylogenetic relationship of *Alienopteris livingstonensis*

The described specimens have a mixture of characters present in some species included in the fern families Cyatheaceae and Dennstaedtiaceae. Among them, the presence of a heterogeneous pith with a big central sclerotic region, similar to *Rickwoodopteris hirsuta* (Stockey and Rothwell, 2004) and *Microlepia marginata* (Ogura, 1972), meristemes completely surrounded by sclerenchyma,

dense indument of trichomes and two layered hypodermis. Furthermore, the modified omega-shaped morphology of the traces present in the petiole bases of *Alienopteris livingstonensis* closely resembles the one found in these families. However, cauline stelar anatomy of *A. livingstonensis* is strikingly different from the one present in these groups of plants.

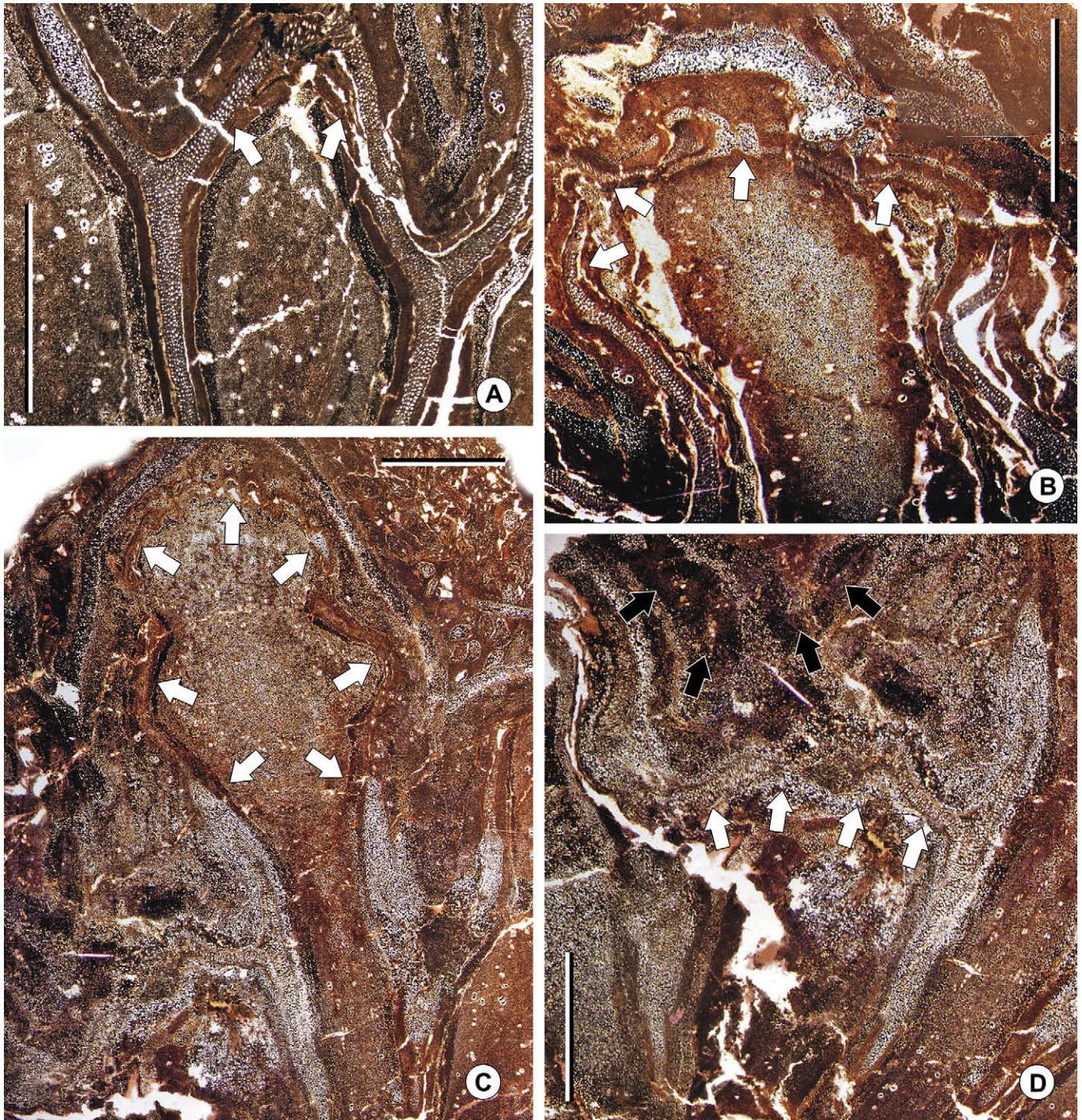
Tissues present in the cauline meristemes of *Alienopteris livingstonensis* are similar to the ones found in several ferns, such as *Acrostichum*, *Dicksonia* (Pteridaceae sensu Ogura, 1972), and the Cyatheae tribe of the Cyatheaceae family (sensu Ogura, 1972), with thick bands of sclerenchyma surrounding each meristelar band. Unfortunately, the degree of preservation of the stems here studied doesn't allow the observation of cubical cells. On the other hand, the absence of medullary bundles in *Alienopteris livingstonensis* is shared with the species found in the Pteridaceae and the Protocyatheeae tribe of the Cyatheaceae (as well as with other taxa without major similarities with the studied specimens), but excludes it from the Cyatheae tribe (sensu Ogura, 1972).

Petiole bases of *Alienopteris livingstonensis* fairly resemble the ones present in the Cyatheaceae s.l. (sensu Lantz et al., 1999) and Dennstaedtiaceae, which present greater structural complexity than that of the rest of the extant ferns (Keating, 1968). They can be described as omega-shaped, or horseshoe shaped, with several modifications depending on the species. Keating (1968) suggested that independent origins of this structure in these ferns is difficult to conceive, and probably these different groups are phylogenetically close. Despite that, phylogenetic relationship among the “tree ferns” and the Dennstaedtiaceae are not clear, and more recent studies place the latter group as more primitive than the cyatheoids (Rothwell, 1999), basal to the polypodeaceous ferns (Smith, 1995) or even deep inside this group (Pryer et al., 2004).

Features of *Alienopteris livingstonensis* were added to the morphological data matrices of Rothwell (1999) and Pryer et al. (2001), including in the latter the new characters proposed by Rothwell and Nixon (2006). The addition of *Alienopteris* produces a matrix of 153 characters and 36 taxa (in Pryer et al. (2001) matrix), and 101 characters and 53 taxa (in Rothwell (1999) matrix), and gives a general idea of the systematic position of *Alienopteris* within the monilophytes. The analysis yielded 13 equally parsimonious trees of 391 steps (Pryer et al. (2001) matrix), and 16 equally parsimonious trees of 435 steps (Rothwell (1999) matrix). The strict consensus of both analyses has basically the same topology of the cladogram obtained excluding *Alienopteris*. Although only 18% of the characters were codified for *Alienopteris* in Pryer et al. (2001) and 51% in Rothwell (1999) matrices, the results of the analysis reveal that it is more close related with the tree ferns (i.e. *Cyathea* and *Dicksonia*) than to the Dennstaedtiaceae (represented in the analysis by the genera *Pteridium* and *Dennstaedtia*), or to any other fern group (Fig. 7A, B).

Kubitzky (1990) recognized seven families among the tree fern clade (Cyatheaceae, Dicksoniaceae, Hymenophyllopsidaceae, Lophosoriaceae, Loxomataceae, Metaxyaceae, and Plagiogyriaceae), whereas Smith et al. (2006) also recognize Cibotiaceae and Culcitaceae as families, and included Hymenophyllopsidaceae in the Cyatheaceae, and Lophosoriaceae among Dicksoniaceae. Korall et al. (2006) performed a phylogenetic study of the tree ferns based on molecular data. Their results revealed the presence of an internal clade among the tree ferns, named by the authors “core tree ferns”, which included, (following Smith et al. (2006) classification) the Cyatheaceae, Dicksoniaceae, Metaxyaceae, and Cibotiaceae, excluding the Thyrsopteridaceae, Loxomataceae, Culcitaceae, and Plagiogyriaceae. The results of the phylogenetic analysis performed with Pryer et al. (2001) dataset (Fig. 7A), when compared with the phylogenetic tree obtained by Korall et al. (2006) reveal that *Alienopteris livingstonensis* is more closely related





**Fig. 4.** *Alienopteris livingstonensis* gen. et sp. nov. A–D, progressive development of the leaf trace (white arrows point to the stem vascular trace) (BA Pb 14950, BA Pb Pm 549). A, fusion of adjacent meristeles. B, C, progressive development of the leaf trace. D, released leaf trace (black arrows) and resulting fused meristeles. Scale bars represent 5 mm.

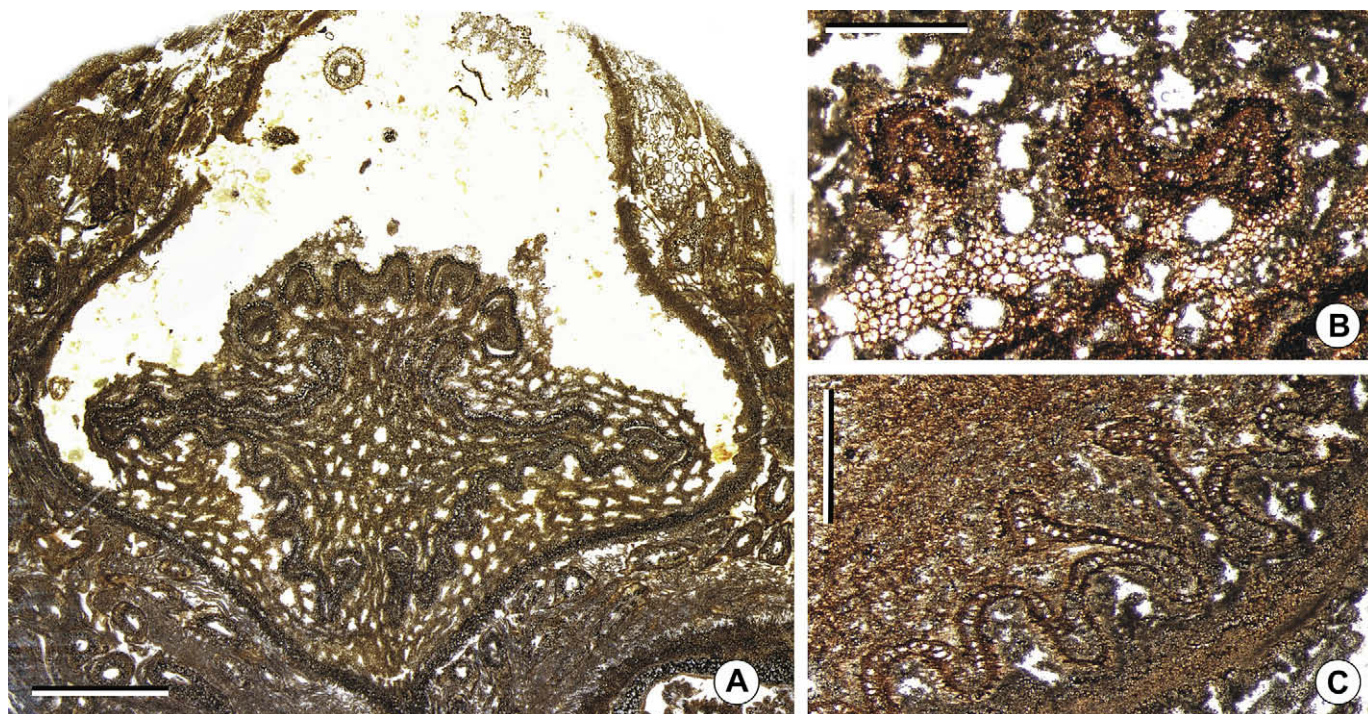
with the “core tree ferns” than to the rest of the tree fern clade. Furthermore, [Korall et al. \(2006\)](#) pointed out that polystelic petiolar bases are generally present in the “core tree ferns”, but absent in the rest of the tree ferns, as well as in the outgroups. The presence of polystelic petiolar bases in *Alienopteris livingstonensis* supports its placement among the “core tree ferns” clade.

Among the “core tree ferns”, Metaxyaceae includes a single genus with dorsiventral and solenostelic stems, different from *Alienopteris*. Living species included in the Cyatheaceae possess medullary bundles ([Lantz et al., 1999](#)), a feature absent in *Alienopteris livingstonensis*. The petiole bases of the Cibotiaceae, as

defined by [Smith et al. \(2006\)](#), contain three corrugated vascular strands arranged in a modified omega-shape, different from the generally nine strands found in the petiole bases of *Alienopteris livingstonensis*. Finally, Dicksoniaceae sensu [Smith et al. \(2006\)](#) contains three living genera (*Dicksonia*, *Lophosoria*, and *Calochlaena*). Taxa included in this family typically present a continuous vascular bundle in the petiole bases, whereas nine bundles are found in *Alienopteris livingstonensis*.

In sum, the combination of features present in *Alienopteris livingstonensis* (e.g. Y-shaped cauline meristeles, absence of medullary bundles, polystelic petiole bases with 9 meristeles) makes





**Fig. 5.** *Alienopteris livingstonensis* gen. et sp. nov. Petiole bases in transverse section. A, general view of a petiole base, showing the disposition of the vascular bundles (BA Pb 14953, BA Pb Pm 552). B, detail of the V and W shaped meristemes of the abaxial arc (BA Pb 14952, BA Pb Pm 551). C, detail of the curved ends of the adaxial arc (BA Pb 14952, BA Pb Pm 551). Scale bars represent 3 mm in A, and 1 mm in B and C.

impossible to refer it to recognized families among the “core tree fern” clade (sensu Korall et al., 2006).

#### 4.2. Comparison with fossil tree fern taxa

Fossil tree fern stems have been previously described for Mesozoic and Tertiary strata.

*Alsophilocalis calveloi* Menéndez (1961), *Dendropteridium cyatheoides* Bancroft (1932), *Paracyathocalis ogurae* Nishida (1989), *Cibotiocalis tateiwai* Ogura emend. Nishida (1989), and the species included in the Early Cretaceous genus *Cyathocalis* Ogura emend. Nishida (1989) (*C. naktongensis* Ogura (1927), *C. yabei* Ogura (1941), *C. nihei-takagii* Nishida and Nishida (1983), and *C. yezopteroides* Nishida (1989)) are generally included in the Cyatheaceae, and can

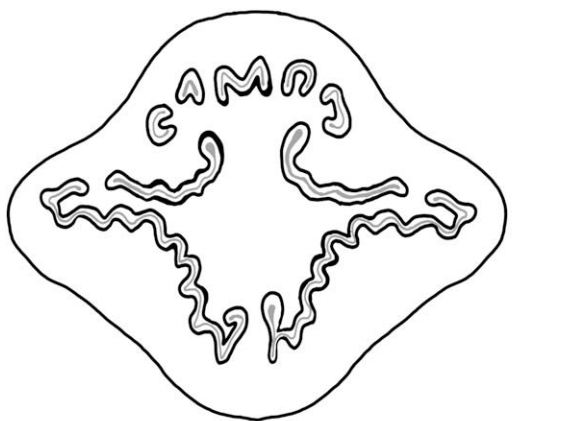
be differentiated from *Alienopteris livingstonensis* by the absence of medullary bundles in the latter taxon. Furthermore, *A. livingstonensis* possess nine vascular strands in the petiole bases, a small number when compared with these taxa (Lantz et al., 1999). Only *Rickwoodopteris hirsuta* has been previously described as presenting more than three meristemes in the petiole bases, but not reaching the high number of traces observed in the Cyatheaceae. However, *R. hirsuta* can be differentiated from *Alienopteris livingstonensis* by the number and distribution of petiolar meristemes, and the morphology of the stem vascular bundles (Stockey and Rothwell, 2004).

Some genera of tree ferns present a three-parted trace in the petiole bases, including *Lophosoria*, *Thyrsopteris*, and the fossil stem species *Conantiopteris schuchmanii* Lantz Rothwell and Stockey (Lantz et al., 1999), different from the nine-parted trace found in the petiole bases of *Alienopteris livingstonensis*.

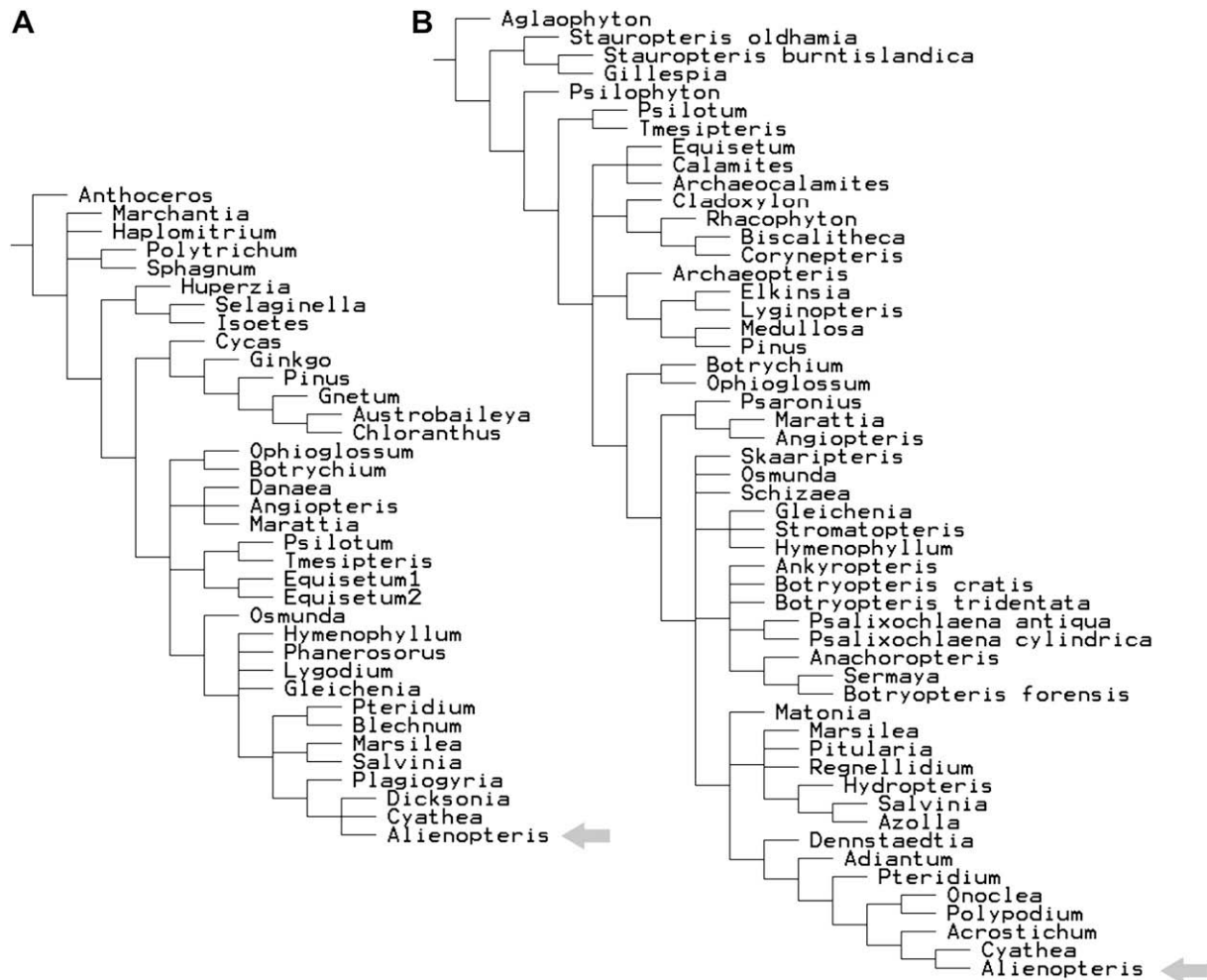
Unlike *Alienopteris livingstonensis*, *Lophosoria japonica* Nishida 1982, as well as *Protopteris microrhiza* Corda (1845), *Protopteris cottai* Corda (1845), *Protopteris witteana* Schenk (1871), *Protopteris fibrosa* Stenzel (1887), *Protopteris sternbergii* Corda (1845), and *Dicksonia buvigiera* (Brongniart) Renault (1883) have one undivided meristeme in the petiole bases (Lantz et al., 1999).

Sclerenchyma surrounding the vascular strands of the stem and petiole bases is generally present in the tree ferns, as well as in *Alienopteris livingstonensis*, but is absent in the species of the genus *Cibotium*, including the fossil taxa *Cibotium tasmanense* Gould (1972), *Cibotium oregonense* Barrington (1983), and *Cibotium iwataense* Ogura (1933), as well as in *Nishidacaulis burgii* Tidwell and Nishida (Tidwell and Nishida, 1993).

The combination of characters seen in *Alienopteris livingstonensis* (Y-shaped meristemes, nine-parted trace on the petiole bases, sclerenchyma surrounding the vascular bundles of the stem and petiole bases) allows to differentiate between it and the rest of the petrified tree fern stems assigned to the Cyatheales.



**Fig. 6.** *Alienopteris livingstonensis* gen. et sp. nov. Sketch of a petiole base, showing disposition of the sclerenchyma (black) and vascular trace (grey). Scale bar represents 1 mm.



**Fig. 7.** Strict consensus trees obtained from the cladistic analysis performed for *Alienopteris*, for Pryer et al. (2001) (A) and Rothwell (1999) (B) matrices. Notice that in both cases the new taxon is placed as closely related with the “tree ferns.”

#### 4.3. The fossil record of tree ferns in the Cerro Negro Formation

Fossil tree fern stems recovered from the Cerro Negro Formation were illustrated and preliminarily assigned to the Cyatheaceae by Césari et al. (2001). An examination of these specimens, as well as others collected in the same locality, has shown that none of these show the mixture of features present in *Alienopteris livingstonensis* (i.e. Y-shaped cauline meristemes, absence of medullary bundles, nine-parted frond trace).

More extensive is the fossil record of fertile fronds assigned to the tree ferns. Cantrill (1998) described for the unit the fossil frond *Lophosoria cupulata* Cantrill, bearer of *Cyatheadites* spores which probably has affinities with the Lophosoriaceae (sensu Kubitzky, 1990). *Sergioa austrina* Césari, is another frond morphospecies with affinities with the Lophosoriaceae, different from *L. cupulata*, which included preserved sporangia with *Cyatheadites* type spores. Finally, the fertile frond *Eocyathea remesaliae* Césari (with preserved sporangia containing *Cyathidites* spores) was related to the Cyatheaceae (Césari, 2006). Furthermore, Cantrill (2000) suggested that many fossil specimens assigned to the Gleicheniaceae in the Southern Hemisphere may represent Lophosoriaceae foliage. However, none of these frond taxa can be adequately linked to *Alienopteris livingstonensis*, since no organic connection was found between stems of the new taxon and foliage.

Finally, disperse spores (genera *Cyathidites* and *Cyatheadites*) were also reported from the Cerro Negro Formation (Torres et al., 1997; Hathway et al. 1999).

#### 5. Conclusions

A new genus and species of filicalean fern, *Alienopteris livingstonensis*, is described in detail, based on several specimens collected from the Cerro Negro Formation, which is characterized by the presence of abundant fern remains (Césari et al., 2001; Cantrill, 1998, among others). The radial symmetry of the stele and leaf traces, as well as the fact that all the root traces run parallel to the major axis of the stem (since they are all cut transversally in transverse slides of the stem) suggest that *Alienopteris livingstonensis* was one of the erect plants that inhabited the Antarctic realm during the Early Cretaceous.

Developmental stages of the fossil ferns are difficult to study, and sometimes two fossil species may represent two ontogenetic stages of only one species (see Herbst (2001, 2006) for examples in the Osmundaceae). In this case, the meristellar morphology of *Alienopteris* may be interpreted as a result of the fossilization of basal or apical sections of cyatheoid stems, where it differs from the one found along the trunk. The rest of the tree fern stems recovered from the same locality (work in prep.) overlap with the range of sizes present in *Alienopteris livingstonensis*, but are clearly different in several traits (revealing that the latter is not conspecific with the rest of the flora collected at the moment). Thus, if *Alienopteris livingstonensis* were an immature section of a plant, this adult plant would have been not collected yet.

Since recent fern phylogenetic studies yielded conflicting results regarding relationships within this group, and with other major



groups (Rothwell and Nixon, 2006), two different data matrices were used for determining the possible affinities of *Alienopteris livingstonensis*. In both cases, its position was resolved without ambiguity among the tree ferns. It is true that both matrices give different topologies of the final consensus tree (see Rothwell and Nixon, 2006 for a detailed discussion about the most recent phylogenetic studies in ferns), but the fact that in both cases *Alienopteris* was placed in a similar position is used here as an evidence of the close relationship between it and the tree ferns. Furthermore, the analysis using Pryer et al (2001) dataset, and the presence of polystelic petiolar bases, support the placement of *Alienopteris livingstonensis* among the “core tree ferns” (sensu Korall et al. (2006)). However, the combination of features seen in this new taxon (e.g. Y-shaped cauline meristemes, absence of medullary bundles, polystelic petiole bases with 9 meristemes, among others) makes impossible to refer it to one of the four families (following Smith et al., 2006) recognized among the “core three ferns” (Cyatheaceae, Dicksoniaceae, Cibotiaceae and Metaxiaceae). Fossil tree ferns with unclear affinities have been previously reported (Lantz et al., 1999; Stockey and Rothwell, 2004). In reference with this fact, Stockey and Rothwell (2004) proposed and active diversification of the tree ferns during the Cretaceous, and Lantz et al. (1999) suggested the existence of common events of extinction and cladogenesis among the tree ferns during Mesozoic and Tertiary times.

The particular morphology of the new species reveal that the filiclean diversity during the Mesozoic was more important than previously thought. Copeland (1930) suggested an Antarctic origin for several fern lineages, with posterior northward migrations. The discovery of new specimens in Antarctica or the rest of the continents will reveal if *Alienopteris livingstonensis* is a representative of an extinct cyatheoid lineage of exclusive Antarctic distribution or it had a more worldwide distribution.

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## References

- Bancroft, H., 1932. A fossil cyatheoid stem from Mount Elgon, East Africa. *New Phytologist* 31, 241–253.
- Barrington, D.S., 1983. *Cibotium oregonense*: an Eocene tree-fern stem and petioles with internal structure. *American Journal of Botany* 70, 1118–1124.
- Cantrill, D.J., 1998. Early Cretaceous fern foliage from President Head, Snow Island, Antarctica. *Alcheringa* 22, 241–258.
- Cantrill, D.J., 2000. A Cretaceous (Aptian) flora from President Head, Snow Island, Antarctica. *Palaeontographica Abteilung B* 253, 153–191.
- Césari, S.N., 2006. Aptian ferns with in situ spores from the South Shetland Islands, Antarctica. *Review of Palaeobotany and Palynology* 138, 227–238.
- Césari, S.N., Párica, C., Remesal, M., Salani, F., 1998. First evidence of Pentoxylales in Antarctica. *Cretaceous Research* 19, 733–743.
- Césari, S.N., Párica, C., Remesal, M., Salani, F., 1999. Paleoflora del Cretácico Inferior de península Byers. *Ameghiniana* 36, 3–22.
- Césari, S.N., Remesal, M., Párica, C., 2001. Ferns: a palaeoclimatic significant component of the Cretaceous flora from Livingston Island, Antarctica. *Asociación Paleontológica Argentina. Publicación Especial 7* (VII International Symposium on Mesozoic Terrestrial Ecosystems), pp 45–50.
- Copeland, E.B., 1930. Antarctica as the source of existing ferns. *Proceedings of the 6th Pacific Science Congress* 4, 625–627.
- Corda, A.J., 1845. *Flora Protogaea-Beitrage zur Flora der Vorwelt*. Calvary, Berlin.
- Falcon-Lang, H.J., Cantrill, D.J., 2001. Gymnosperm woods from the Cretaceous (mid-Aptian) Cerro Negro Formation, Byers Peninsula, Livingston Island, Antarctica: the arborescent vegetation of a volcanic arc. *Cretaceous Research* 22, 277–293.
- Falcon-Lang, H.J., Cantrill, D.J., 2002. Terrestrial Paleoeology of the Cretaceous (Early Aptian) Cerro Negro Formation, South Shetland Islands, Antarctica: a record of polar vegetation in a volcanic arc environment. *Palaios* 17, 491–506.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2000. T.N.T.: Tree Analysis Using New Technology. Program and documentation, available from the authors, and at [www.zmuc.dk/public/phylogeny](http://www.zmuc.dk/public/phylogeny).
- Gould, R.E., 1972. *Cibotium tasmanense* sp. nov., a fossil tree-fern from the Tertiary of Tasmania. *Australian Journal of Botany* 20, 119–126.
- Hathway, B., 1997. Nonmarine sedimentation in an Early Cretaceous extensional continental-margin arc, Byers Peninsula, Livingston Island, South Shetland Islands. *Journal of Sedimentary Research* 67, 686–697.
- Hathway, B., Duane, A.M., Cantrill, D.J., Kelley, S.P., 1999.  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology and palynology of the Cerro Negro Formation, South Shetland Islands, Antarctica: a new radiometric tie for Cretaceous terrestrial biostratigraphy in the Southern Hemisphere. *Australian Journal of Earth Sciences* 46, 593–606.
- Herbst, R., 2001. A revision of the anatomy of *Millerocaulis patagonica* (Archangelky and de la Sota) Tidwell (Filices, Osmundaceae), from the Middle Jurassic of Santa Cruz Province, Argentina. *Asociación Paleontológica Argentina. Publicación Especial 8* (XI Simposio Argentino de Paleobotánica y Palinología), pp 39–48.
- Herbst, R., 2006. *Millerocaulis* (Erasmus) ex Tidwell (Osmundales, Filices) de la Formación Carrizal (Triásico Superior) de Marayes, provincia de San Juan, Argentina. *Revista del Museo Argentino de Ciencias Naturales. Nueva Serie* 8, 185–193.
- Hernández, P.J., Azcárate, V., 1971. Estudio paleobotánico preliminar sobre restos de una tafoflora de la Península Byers (Cerro Negro), Isla Livingston: Islas Shetland del Sur. *Instituto Nacional Antártico Chileno. Serie Científica* 2, 15–50.
- Keating, R.C., 1968. Trends of specialization in the stipe anatomy of *Dennstaedtia* and related genera. *American Fern Journal* 58, 126–140.
- Korall, P., Pryer, K.M., Metzgar, J.S., Schneider, H., Conant, D.S., 2006. Tree ferns: monophyletic groups and their relationships as revealed by four protein-coding plastid loci. *Molecular Phylogenetics and Evolution* 39, 830–845.
- Kubitzky, K., 1990. The Families and Genera of vascular plants. In: Kramer, K.U., Green, P.S. (Eds.), *Pteridophytes and Gymnosperms*, vol. 1. Springer-Verlag, Berlin, Germany.
- Lantz, T.C., Rothwell, G.W., Stockey, R.A., 1999. *Conantiopteris schuchmanii*, gen. et sp. nov., and the role of fossils in resolving the phylogeny of Cyatheaceae s.l. *Journal of Plant Research* 112, 361–381.
- Menéndez, C.A., 1961. Estípites petrificados de una nueva Cyatheaceae del Terciario de Neuquén. *Boletín de la Sociedad Argentina de Botánica* 9, 331–358.
- McManus, H.A., Boucher, L., Taylor, E., Taylor, T.N., 2002. *Hapsidoxylon terpsichorum* gen. et sp. nov., a stem with unusual anatomy from the Triassic of Antarctica. *American Journal of Botany* 89, 1958–1966.
- Meyer-Berthaud, B., Taylor, T.N., Taylor, E.L., 1993. Petrified stems bearing *Dicroidium* leaves from the Triassic of Antarctica. *Palaeontology* 36, 337–356.
- Millay, M.A., Taylor, T.N., 1990. New fern stems from the Triassic of Antarctica. *Review of Palaeobotany and Palynology* 62, 41–64.
- Nishida, H., 1989. Structure and affinities of the petrified plants from the Cretaceous of Japan and Saghalien. V. Tree fern stems from Hokkaido, *Paracyathocaulis ogurae* gen. et comb. nov. and *Cyathocaulis yezopteroides* sp. nov. *Botanical Magazine* 102, 255–282.
- Nishida, H., Nishida, M., 1983. On some petrified plants from the Cretaceous of Choshi, Chiba Prefecture. VII. *Botanical Magazine* 96, 93–101.
- Ogura, Y., 1927. On the structure and affinities of some fossil tree-ferns from Japan. *Journal of the Faculty of Science, University of Tokyo. Section III Botany* 1, 350–380.
- Ogura, Y., 1933. On the structure of a fossil fern stem of *Cibotium* type from the Upper Cretaceous of Iwate. *Botanical Magazine* 47, 748–754.
- Ogura, Y., 1941. On the structure of a fossil Tree Fern stem from Mindoro, Philippine Islands, 241. *Jubilee Publication for Professor Yabe*. 911–917.
- Ogura, Y., 1972. Comparative Anatomy of Vegetative Organs of the Pteridophytes. In: *Handbuch der Pflanzenanatomie*, vol. 7. Borntraeger, Berlin. 502.
- Párica, C.A., Salani, F.M., Vera, E., Remesal, M., Césari, S.N., 2007. Geología de la Formación Cerro Negro (Cretácico) en Isla Livingston: aportes a su geocronología y contenido paleontológico. *Revista de la Asociación Geológica Argentina* 62 (4), 553–567.
- Pryer, K.M., Schneider, H., Smith, A.R., Cranfill, R., Wolf, P.G., Hunt, J.S., Sipes, S.D., 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* 409, 618–621.
- Pryer, K.M., Schuettpelz, E., Wolf, P.G., Schneider, H., Smith, A.R., Cranfill, R., 2004. Phylogeny and evolution of ferns (Monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany* 91, 1582–1598.
- Renault, M.B., 1883. *Cours de botanique fossile*, vol. 3. Librairie de l'Académie de Médecine, Paris.
- Rothwell, G.W., 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* 65, 188–218.
- Rothwell, G.W., Nixon, K.C., 2006. How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *International Journal of Plant Sciences* 167, 737–749.
- Schenk, A., 1871. Beiträge zur Flora der Vorwelt. Die Flora der nordwestdeutschen Wealdenformation. *Palaeontographica Abteilung B* 19, 203–262.
- Smith, A.R., 1995. Non-molecular phylogenetic hypotheses for ferns. *American Fern Journal* 85, 104–122.
- Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. *Taxon* 55, 705–731.



- Smoot, E.L., Taylor, T.N., Delevoryas, T., 1985. Structurally preserved fossil plants from Antarctica I. *Antarcticycas*, gen. nov., a Triassic cycad stem from the Beardmore Glacier area. *American Journal of Botany* 72, 1410–1423.
- Stenzel, C.G., 1887. Verkieselte farne von Kamenz in Sachsen. Mittheil Königsbrücker Mineralogie und Geologie Museum zu Dresden 13.
- Stockey, R.A., Rothwell, G.W., 2004. Cretaceous tree ferns of western North America: *Rickwoodopteris hirsuta* gen. et sp. nov. (Cyatheaaceae s.l.). *Review of Palaeobotany and Palynology* 132, 103–114.
- Tidwell, W.D., Nishida, H., 1993. A new fossilized tree fern stem, *Nishidacaulis burgii* gen. et sp. nov., from Nebraska-South Dakota, USA. *Review of Palaeobotany and Palynology* 78, 55–67.
- Torres, T., Barale, G., Méon, H., Plilippe, M., Thévenard, F., 1997. Cretaceous floras from Snow Island (South Shetland Islands, Antarctica) and their biostratigraphic significance. In: C.A. Ricci (Ed.) *The Antarctic region: geological evolution and processes*, 7th International Symposium on Antarctic Earth Sciences (1995), Proceedings, Terra Antarctica Publication. pp. 1023–1028.
- Vera, E.I., 2007. A new species of *Ashicaulis* Tidwell (Osmundaceae) from Aptian strata of Livingston Island, Antarctica. *Cretaceous Research* 28, 500–508.

## Appendix

### Character coding of *Alienopteris* for Pryer et al. (2001) morphological matrix

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### Character coding of *Alienopteris* for Rothwell (1999) matrix

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