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# *Millerocaulis tekelili* sp. nov., a new species of osmundalean fern from the Aptian Cerro Negro Formation (Antarctica)

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A new species of the osmundalean fossil morphogenus *Millerocaulis* Tidwell *emend.* Vera, *Millerocaulis tekelili* sp. nov. is defined, based on several permineralized stems recovered from exposures of the Lower Cretaceous Cerro Negro Formation on Livingston Island, South Shetland Islands, Antarctica. This new species is characterized by the presence of an ectophloic–dictyoxylic siphonostele, inner parenchymatic and outer sclerotic cortices, heterogeneous sclerotic ring in the petiole bases, absence of sclerenchyma associated with the petiolar xylem trace, petiolar inner cortex with sclerenchyma strands and stipular wings having a large sclerenchyma bundle and several smaller ones. The presence of non-homogeneous sclerotic rings in the petiole bases allows this new species to be clearly distinguished from other Antarctic *Millerocaulis*, and suggests that it may represent an intermediate form in the evolutionary lineage leading from *Millerocaulis* to subgenus *Claytosmunda* of *Osmunda*.

Key words: *Millerocaulis*, Pteridophyta, Cretaceous, Osmundaceae, Livingston Island, Byers Peninsula, Antarctica.



OSMUNDACEAE is a basal family of ferns, with approximately 21 living species grouped in the genera *Osmunda* L., *Todea* Willd. ex Bernh., *Leptopteris* C. Presl and the recently recognized *Osmundastrum* (C. Presl) C. Presl. Some taxa included in this family are very long-ranging, with *Osmunda* recorded from the Triassic Lashly Formation of Antarctica (Phipps *et al*. 1998), *Todea* present in Lower Cretaceous strata of Canada (Jud *et al*. 2008) and fossils assigned to the extant species *Osmundastrum cinnamomeum* (L.) C. Presl recovered from the Upper Cretaceous Horseshoe Canyon Formation of North America (Serbet & Rothwell 1999). Fossil axes are, when possible, referred to extant genera or, if impossible, to several fossil morphogenera. One such morphogenus, *Millerocaulis* Tidwell *emend*. Vera, 2008, has been recorded in both Northern and Southern hemispheres, in strata ranging from Triassic to Cretaceous age (Tian *et al*. 2008).

Several species of *Millerocaulis* have been described from Antarctica: the Triassic *M. beardmorensis* (Schopf) Tidwell, 1986 and *Millerocaulis woolfei* (Rothwell, Taylor & Taylor) Vera, 2008, both recovered from the Transantarctic Mountains; *Millerocaulis australis* (Vera) Vera, 2008 and *Millerocaulis* sp. cf. *M. australis* (Vera 2010), collected from Aptian deposits of the Cerro Negro Formation, Livingston Island; and the Late Cretaceous *Millerocaulis livingstonensis* (Cantrill) Vera, 2008, discovered at Williams Point (also on Livingston Island; Schopf 1978, Cantrill 1997, Rothwell *et al*. 2002, Vera 2007, 2008, 2010).

Here I describe a new species of *Millerocaulis* Tidwell *emend*. Vera, 2008 from the Cerro Negro Formation (Livingston Island, South Shetland Islands, Antarctica), with a heterogeneous ring in its petiole bases.

## Material and methods

Osmundaceous specimens were collected from exposures of the Aptian Cerro Negro Formation on Byers Peninsula, South Shetland Islands, Antarctica (Rotch Dome locality, Fig. 1), from strata composed of very rich and homogeneous pyroclastic material, probably corresponding to a lacustrine or low-energy fluvial environment. One specimen was found associated with a small thyrsopteridacean tree-fern stem. Several anatomical thin-sections were prepared and mounted in microscope slides. Photographs were taken with a Nikon Coolpix 995 adapted to an Olympus BX-51 or a Nikon SMZ-2t Microscope. The specimens are housed in the collection of the Museo

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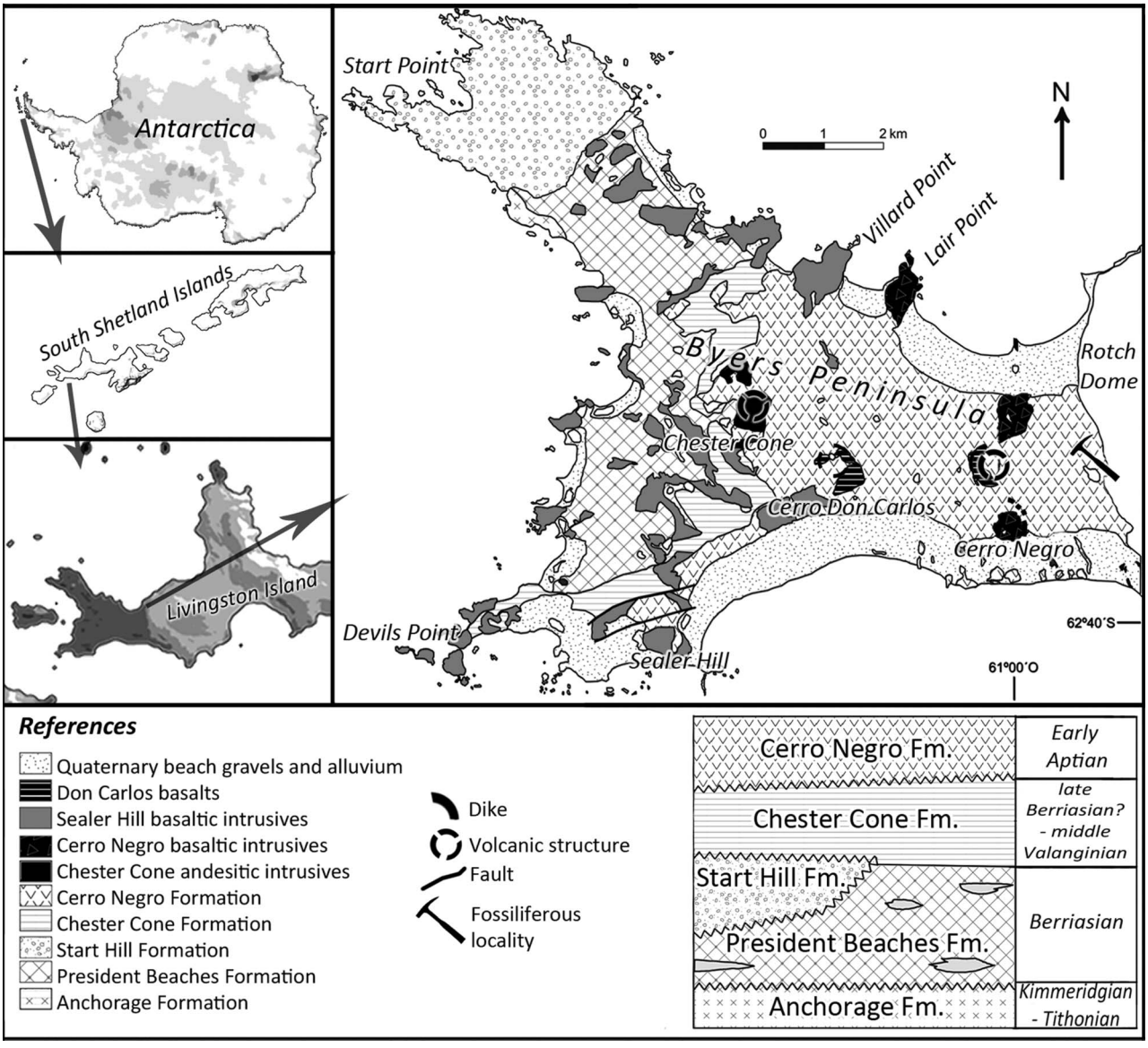


*Fig. 1.* Geologic map and stratigraphic scheme for Byers Peninsula. Modified from Hathway & Lomas 1998 (stratigraphic scheme) and Párica *et al.* 2007 (map).



Argentino de Ciencias Naturales 'Bernardino R. Rivadavia', División Palebotánica, under BA Pb numbers. The Cortical Ratio (CR) was estimated using the following formula: CR = OC/IC, where OC is the average width of the outer cortex of the specimen, and IC is the average width of the inner cortex of the same specimen.

## Geological setting

The Byers Peninsula, covering 61 km$^2$, is located in the western part of Livingston Island (South Shetland Islands, Antarctica; Fig. 1). Most of this territory (*ca* 95%) is devoid of ice (Césari *et al.* 1999), exposing the Upper Jurassic–Lower Cretaceous sequences of the Byers Group, which represents the most complete record of the Pacific flank of the volcanic arc developed during the Mesozoic, resulting from the subduction of the palaeo-Pacific lithosphere along the continental margin of the Antarctic Peninsula (Hathway 1997). The Byers Group has recently been divided into five units: the marine Anchorage, President Beaches, Start Hill, Chester Cone and the non-marine Cerro Negro formations (Crame *et al.* 1993, Hathway & Lomas 1998; Fig. 1). Deposition of the Anchorage Formation took place during the Late Jurassic (Kimmeridgian–Tithonian), whereas the rest of the units are dated as Early Cretaceous (Hathway

& Lomas 1998). The base of the Cerro Negro Formation is marked by a low-angle unconformity, probably related to tectonic or volcano-tectonic uplift (Hathway 1997), whereas the top of the unit lies under the permanent ice of the Rotch Dome. The ages obtained using the $^{40}Ar/^{39}Ar$ method for the base ($120.3 \pm 2.2$ Ma, $119.4 \pm 0.6$ Ma or $119.1 \pm 0.8$) and the uppermost known sections of the unit ($119 \pm 3$ Ma) suggest that the Cerro Negro Formation was deposited rapidly (Hathway *et al.* 1999, Falcon-Lang & Cantrill 2002).

Hathway (1997) divided the Cerro Negro Formation into two units: a lower silicic unit and an upper basaltic unit. The lower unit is composed mainly of ignimbrites intercalated with reworked silicic pyroclastic and epiclastic strata, whereas the upper unit consists mainly of basaltic lapilli-tuffs and tuffaceous breccias, also including two welded silicic ignimbritic units, basaltic conglomerate lenses and intervals of basaltic sandstones and mudstones (Hathway 1997, Hathway & Lomas 1998). Syneruptive deposits of the Cerro Negro Formation are represented by pyroclastic strata, syneruption debris and flood-flow deposits (Hathway & Lomas 1998). On the other hand, intereruptive sedimentation took place in fluvial and lacustrine environments, recorded by conglomerates, sandstones and mudstones (Hathway & Lomas 1998).

Abundant plant specimens have been recovered from the Cerro Negro Formation strata, including permineralized stems assigned to the Osmundaceae and Cyatheales (Césari *et al.* 2001, Vera 2007, 2009, 2010) and fern frond compressions with *in situ* spores (Cantrill 1998, Césari 2006).

## Systematic palaeobotany

Order OSMUNDALES Link, 1833

Family OSMUNDACEAE *sensu* Tidwell & Parker, 1987

Subfamily OSMUNDOIDEA Miller *emend.* Tidwell & Parker, 1987

**Millerocaulis** Erasmus *ex* Tidwell, 1986 *non* 1994 *emend.* Vera, 2008

*Type species*. *Millerocaulis dunlopii* (Kidston & Gwynne-Vaughan) Tidwell, 1986.

**Millerocaulis tekelili** sp. nov. (Figs 2, 3, 4)

*Holotype*. BA Pb 14855 (BA Pb Pm 528, 529, 530, 531, 532, 533).

*Referred specimens*. BA Pb 14856 (BA Pb Pm 534-536), BA Pb 14857 (BA Pb Pm 537-538), BA Pb 15007 (BA Pb Pm 625-626), BA Pb 15008 (BA Pb Pm 627), BA Pb 15009 (BA Pb Pm 628-630).

*Type locality and stratigraphic horizon*. All the studied specimens, including the holotype, were collected at the Rotch Dome locality (*sensu* Párica *et al.* 2007), Byers Peninsula, Livingston Island. South Shetland Islands; Lower Cretaceous (Aptian) Cerro Negro Formation.

*Etymology*. The specific epithet derives from the word *Tekeli-li*, pronounced by fictional Antarctic inhabitants in the book 'The Narrative of Arthur Gordon Pym of Nantucket' by Edgar Alan Poe, and in the book 'At the mountains of madness' by Howard Phillip Lovecraft.

*Diagnosis*. Stem erect, surrounded by stipulate petiole bases and adventitious roots. Protoxylem mesarch/sub-exarch; inner cortex parenchymatic; outer cortex sclerotic; outer cortex/inner cortex ratio approximately 4; leaf traces endarch, having one protoxylem cluster that first divides in the outer cortex; petiole bases with well-defined stipular wings at the sixth–seventh petiolar cycle, developing at this level a heterogeneous sclerotic ring, with a thick band composed of fibers that is narrow abaxially and enlarged laterally; no sclerenchyma associated with the vascular trace; sclerenchymatic strands present in the inner cortex of the petiole base; a large sclerotic bundle accompanied by several small strands in the petiole wings; when the outer cortex is approximately 2 mm thick, 25–33 leaf traces can be seen in cross-section, approximately 33% of them in the inner cortex and the rest in the outer.

*Description*. The following description is based on the holotype (BA Pb 14855), with additional comments relating to other specimens, where they provide important anatomical features.

The stele is an ectophloic–dictyoxylic siphonostele, included in a small stem (6–12 mm wide) surrounded by a mantle of stipulate petiole bases and adventitious roots (Fig. 2A–C). The pith is poorly preserved in BA Pb 14856 and shows two distinct zones (Fig. 2B), one central and the other in the periphery, distinguished essentially by differences in colour. Since the specimen's preservation is not ideal, it is difficult to determine whether this feature is an artefact of fossilization or represents genuine differentiation of tissues. Surrounding the pith is a vascular cylinder 1–1.2 mm in radial width (8–15 tracheids thick). Approximately 30 xylem strands are

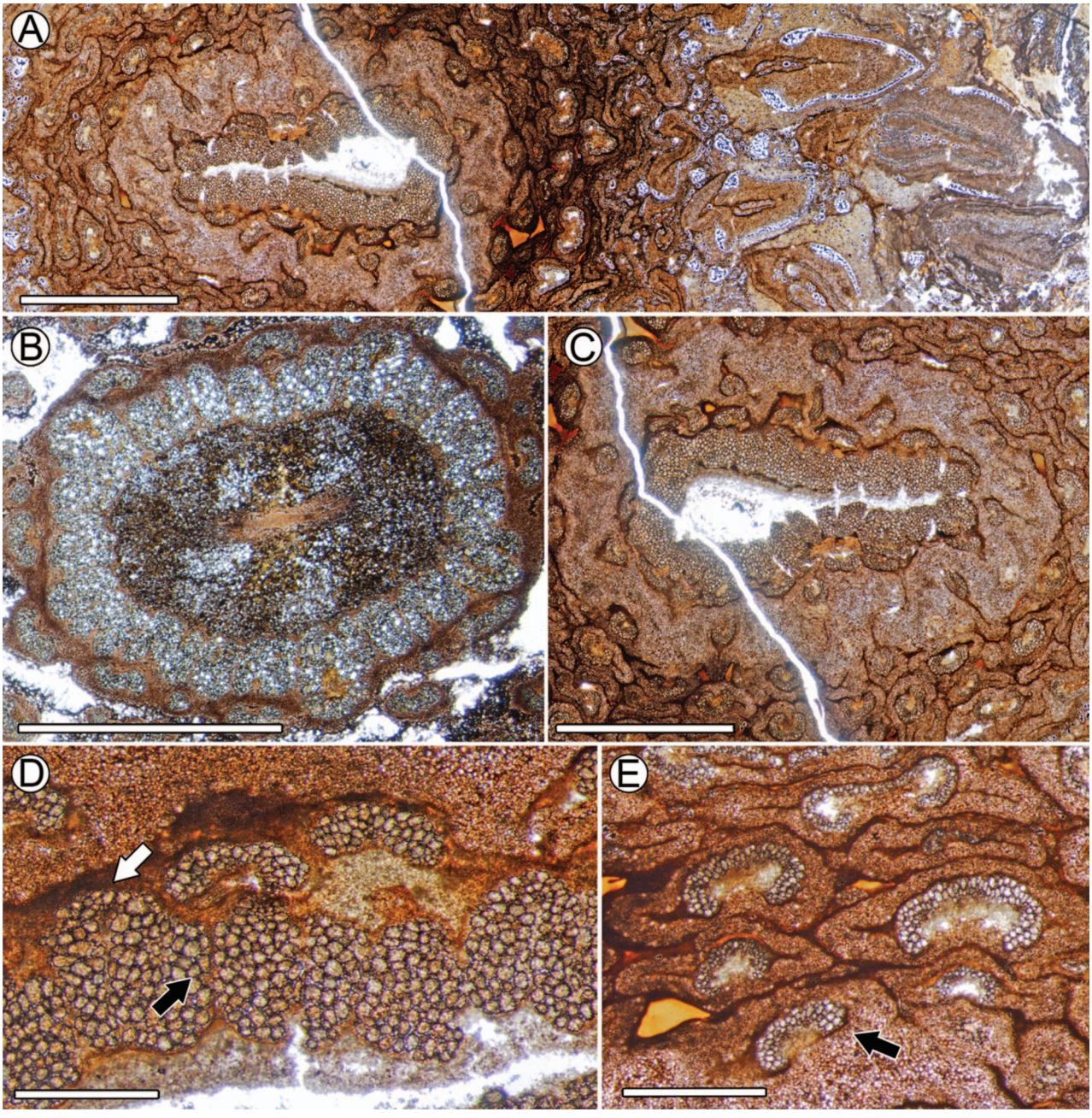


*Fig. 2.* Anatomy of *Millerocaulis tekelili* sp. nov. **A**, General view of the holotype (BA Pb 14855); **B**, Stele of the specimen BA Pb 14856; **C**, Detail of A, showing the central stem; **D**, Development of leaf traces, showing departing leaf trace (white arrow) and narrow leaf gap (black arrow), BA Pb 14855; **E**, Leaf trace in outer cortex (arrow) and internal petiole bases. Note the presence of two protoxylem clusters in the leaf trace (BA Pb 14855). Scale bar = 5 mm in A, B and C; and 1 mm in D and E.

present (Fig. 2B–C), and these are generally separated by very narrow (40 $\mu$m wide) leaf gaps, resulting from the departure of the leaf traces (Fig. 2C, D). Metaxylem tracheids are 60–140 $\mu$m in diameter, with cell walls 15–20 $\mu$m thick (Fig. 2D). Protoxylem clusters are mesarch/sub-exarch, located almost in the external region of the xylem strands. The external tissues of the stele (pericycle, endodermis and phloem) are not preserved in any of the specimens.

Surrounding the stele is a poorly defined inner cortex *ca* 0.5 mm wide (Fig. 2C–E) and, due to its homogeneous appearance, it was probably parenchymatic, like the cortical tissue present in the petiole bases. Surrounding this is the sclerotic outer cortex (1.8–2.2 mm wide; Fig. 2A, C). The quality of cortex preservation is poor in all specimens, and no cellular detail is evident. The cortical ratio is difficult to calculate, since the inner cortex is not well defined

(Fig. 2C–E) but it seems to be constant in the species, with a value near 4.

Scattered throughout the cortical tissues are 25–33 leaf traces, approximately 33% of them in the inner cortex and the rest in the outer. Leaf traces originate from the stele. First, a parenchyma cluster initiates adaxial to a protoxylem cluster. Where the xylem strand enlarges centrifugally, the parenchyma ray develops in the opposite direction, until it reaches the pith. The xylem strand continues its enlargement until a leaf trace with one endarch protoxylem cluster is released, leaving a narrow leaf gap in the xylem cylinder (Fig. 2D). The protoxylem cluster first divides in the outer cortex, and then more divisions occur in the petiole bases (Fig. 2E). Leaf traces are oblong or reniform (450 $\mu$m high and 900 $\mu$m wide) in the inner cortex, but as they pass through the outer cortex and petiole bases, their morphology becomes more C-shaped (Fig. 2C–E). Phloem, pericycle and endodermis are not preserved in the leaf traces.

Root traces are diarch, with a protoxylem cluster located in the poles of the trace, laterally surrounded by phloem (scarcely preserved in the studied material). Each root trace is approximately 250 $\mu$m in diameter and, when it is outside the stem, a sclerenchymatic ring (remnant of its development across the outer cortex) surrounds the structure forming an adventitious root (Fig. 3E). Apparently, only one root trace diverges from the stele when a leaf trace separates from the central cylinder. Almost all the root traces are seen in transverse section, indicating their orientation parallel to the stem (Fig. 3E).

Petiole bases are clearly delimited outside the stem, where sclerotic rings surround the trace (Fig. 3A). The inner cortex of the petiole is composed of parenchymatic cells 25–30 $\mu$m in diameter. The phloem, pericycle and endodermis can not be identified. Internal petiole bases have a xylem trace 170 $\mu$m (4–6 scalariform tracheids) thick (Figs 2F, G, 3B, C), which becomes progressively narrower [130 $\mu$m (2–3 tracheids) thick], until it reaches the most external cycles, where it is 1–2 tracheids thick (Fig. 3B, C). Internal petiole bases have a homogeneous sclerotic ring 250 $\mu$m wide, composed of the same tissue present in the outer cortex (Fig. 2E). Owing to poor preservation, it is difficult to discriminate between the sclerotic ring and the inner cortex of the petiole in some parts of the fossil.

Intermediate petiole bases (4–5 mm high and 7–9 mm wide) are stipulate and have a disctintive sclerenchymatic pattern in the stipular wings, inner cortex and outer cortex. Petioles have no sclerenchyma adaxial to the trace, but several sclerenchymatic strands are present in the inner cortex (Figs 3A, C, 4), composed of cells 50 $\mu$m wide, with walls 8 $\mu$m thick. Surrounding the vascular trace is a heterogeneous sclerotic ring, which has a slightly different arrangement of thick- and thin-walled fibers depending on the distance between the analyzed petiole section to the point of departure from the stem (Fig. 4). The final configuration of the heterogeneous ring (represented by the uppermost petiole sketch in Fig. 4), totally developed in the sixth to seventh petiolar cycle, reveals a narrow thick-walled fiber band (50 $\mu$m wide) abaxial to the trace, becoming enlarged laterally (700 $\times$ 325 $\mu$m; Fig. 3A–C).

Stipular wings (*ca* 3 mm wide in the sixth to seventh petiolar cycle) include a large sclerotic bundle (500 $\mu$m in diameter) near the sclerotic ring, accompanied by several smaller strands (100–120 $\mu$m in diameter) distributed along the petiole wings (Fig. 3A, D). Externally, petioles (5 $\times$ 9.5 mm in diameter) lack stipular wings, and the sclerotic ring seems to be homogeneous, lacking fibers and being of the same composition as the outer cortical tissues (Fig. 3F).

## Discussion

### *Affinities of* Millerocaulis tekelili

The subfamily Osmundoidea contains the four extant genera *Osmunda* (which includes the subgenera *Osmunda*, *Plenasium* and *Claytosmunda*), *Todea*, *Leptopteris* and *Osmundastrum* (Yatabe *et al*. 2005, Metzgar *et al*. 2008) and four genera recorded exclusively by fossil taxa (*Millerocaulis* Tidwell *emend*. Vera, 2008, *Osmundacaulis* Miller *emend*. Tidwell, 1986, *Palaeosmunda* Gould *emend*. Li, 1983 and *Aurealcaulis* Tidwell & Parker *emend*. Tidwell & Skog, 2002; Tian *et al*. 2008). *Osmundacaulis* is represented by species ranging from the Jurassic to the Cretaceous that are typically arborescent forms, with wide (more than 25 tracheids thick) dictyostelic vascular cylinders (Tidwell 1986), differing from *M. tekelili*. The leaf traces of *Aurealcaulis* bear exarch protoxylem and are formed by fusion of two vascular bundles after the divergence from the stele (Tidwell & Skog 2002), contrasting with the Antarctic species. The Permian genus *Palaeosmunda* is similar to extant Osmundaceae, but has rhombic petiole rings, that differ from the new taxon (Gould 1970, Tian *et al*. 2008). Among the extant genera, *Todea*, *Leptopteris* and *Osmunda* subgenus *Plenasium* have a sclerotic ring composed by thin-walled fibers, surrounded by a narrow ring of thick-walled fibers (Miller 1971, Cheng *et al*. 2007). *Osmundastrum*, including *Osmundastrum cinnamomeum* (L.) C. Presl (and most

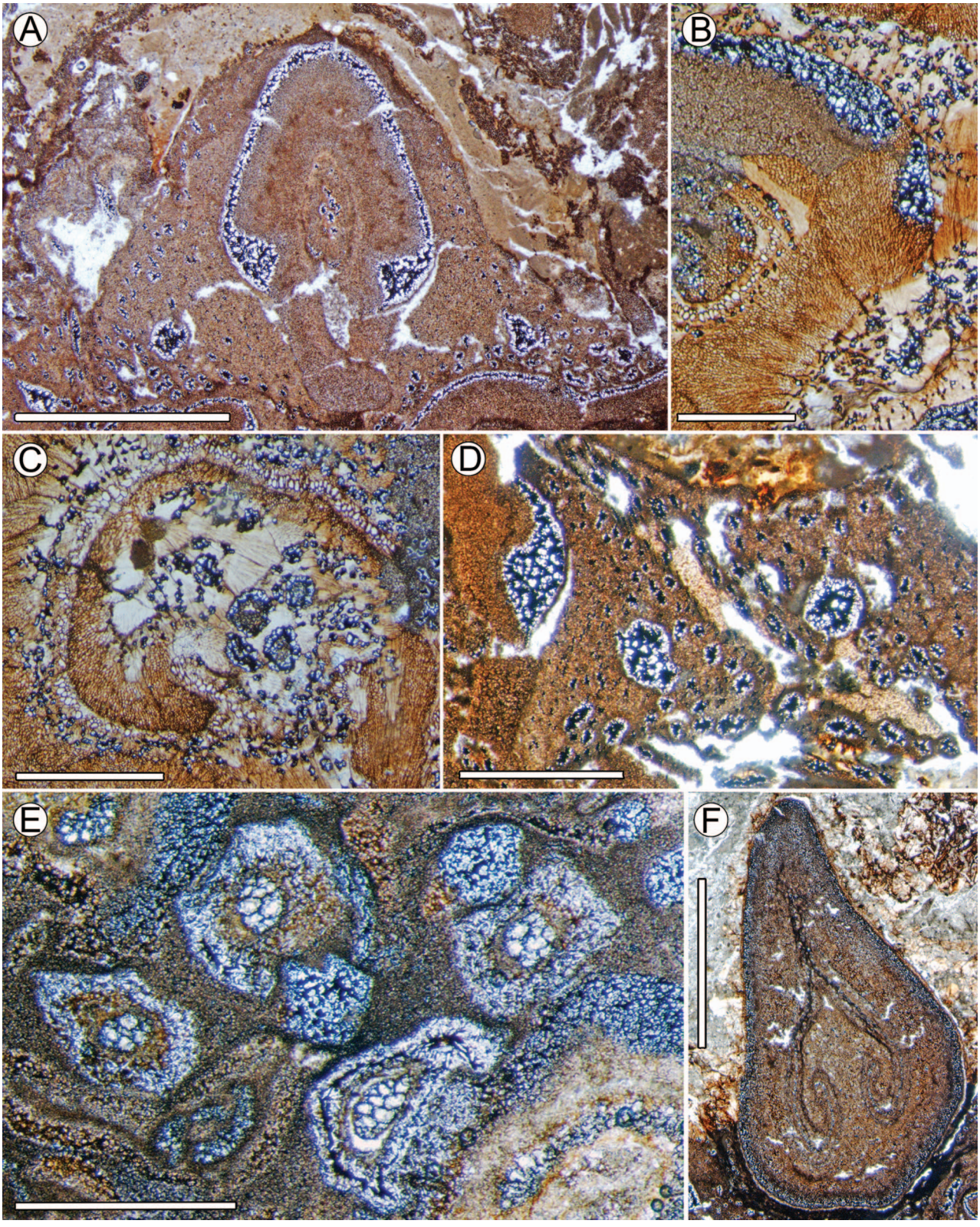


*Fig. 3*. Anatomy of *Millerocaulis tekelili* sp. nov. (BA Pb 14855). **A**, Petiolar base, showing heterogeneous ring and stipular wings; **B**, Detail of a petiolar base, showing the morphology of the ring; **C**, Detail of a petiolar base, showing the distribution of sclerenchyma strands in the inner cortex; **D**, Detail of a petiolar base, showing sclerenchymatic groups in the stipular wings; **E**, Adventitious roots; **F**, Most external petiole base, lacking stipular wings. Scale bar = 4 mm in A; 2 mm in B, C, D and F; and 1 mm in E.

certainly *Osmunda precinnamomea* Miller, 1967) is characterized by three masses of thick-walled fibres; differing from the specimens described here. Species of *Osmunda* subgenus *Osmunda* (e.g. *Osmunda regalis* L., *Osmunda lancea* Thunberg and *Osmunda japonica* Thunberg) share the presence of a characteristic adaxial band of thick-walled fibers (Miller 1971, Cheng *et al*. 2007) that are absent in *M. tekelili*. Among the extant taxa, *Osmunda* subgenus *Claytosmunda* is most similar to the new species, since it shares, at some point of development, the presence of a sclerotic ring with an abaxial arc of thick-walled fibers, with their ends greatly enlarged (see fig. 4A and B in Miller 1971). However, these features may also be present in *Millerocaulis*, a genus erected to encompass fossil (Mesozoic) osmundalean species similar to extant Osmundaceae that are impossible to refer to any of the extant taxa owing to the absence of key characters, or due to poor preservation (Miller 1971, Vera 2008). Since not all the features present in the *M. tekelili* were possible to determine (e.g. the nature of the pith), and taking into account that the overlap between subgenus *Claytosmunda* and *M. tekelili* is not absolute (e.g. there are differences in the distribution of sclerenchyma associated with the vascular trace and in the inner cortex of the petiole bases) and that the morphology of fertile and sterile fronds is unknown for the latter species, it is preferred to refer the described materials to *Millerocaulis*.

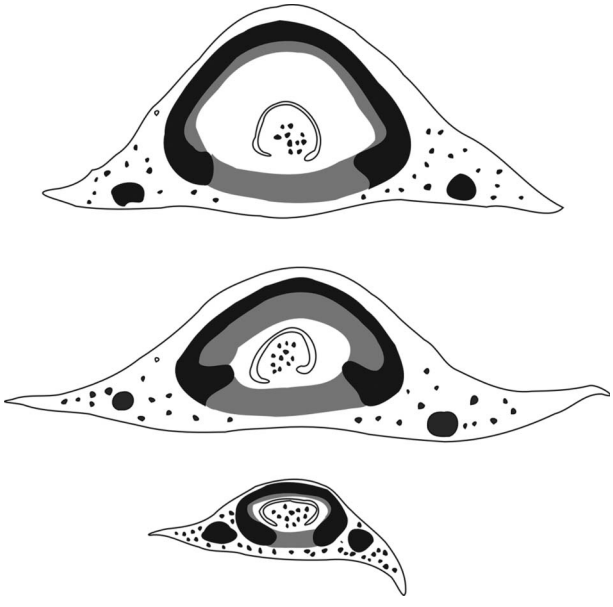

*Fig. 4*. Schematic transverse sections of the petiole bases of *Millerocaulis tekelili* sp. nov., showing changes in the arrangement of thick-walled (black) and thin-walled (grey) fibers (shown from inner to outer petioles upwards). Only stages with heterogeneous sclerotic ring are shown.

However, a brief discussion regarding a probable evolutionary significance of *M. tekelili* is given below.

*Comparisons with other taxa*

*Millerocaulis tekelili* sp. nov. can be separated from all previously described Antarctic members of the genus (*Millerocaulis beardmorensis* (Schopf) Tidwell, 1986, *Millerocaulis woolfei* (Rothwell, Taylor & Taylor) Vera, 2008, *Millerocaulis livingstonensis* (Cantrill) Vera, 2008 and *Millerocaulis australis* (Vera) Vera, 2008) by the presence of a heterogeneous sclerotic ring in the petiolar bases of the former. Only a few other species of *Millerocaulis* have been recorded as having a heterogeneous sclerotic ring: *M. liaoningensis* Zhang & Zheng, 1991, *M. kidstoni* (Stopes, 1921) Tidwell, 1986, *M. johnstonii* Tidwell, Munzing & Banks, 1991, *M. embreei* Stockey & Smith, 2000, *M. juandahensis* Tidwell & Clifford, 1995, *M. indentata* (Hill, Forsyth & Green, 1989) Tidwell, 1986, *M. sinica* Cheng & Li, 2007, *M. preosmunda* Cheng, Wang & Li, 2007. *Ashicaulis claytoniites* Cheng, 2011, which under Vera's (2008) proposal would be included in *Millerocaulis*, also bears this type of petiole ring. All these species possess sclerenchyma in the concavity of the trace, a feature absent in *M. tekelili* (see Table 1 and Fig. 4 for this and all other observations in this paragraph). The Antarctic species shares with *M. embreei* the presence of sclerenchyma in the inner cortex of the petioles, whereas the rest of the compared species lack such tissue. Stipular wings of the Osmundaceae generally contain sclerenchyma strands. Stipes of *M. tekelili* have a single large mass of sclerenchyma, accompanied by several small strands of the same tissue, differing from the single mass present in *M. johnstoni*, *M. juandahensis* and *M. liaoningensis*. The place of first division of the protoxylem cluster of the leaf traces varies between osmundacean species. In some taxa, this division occurs in the petiole bases (e.g. *M. preosmunda*, *M. sinica, A. claytoniites*), whereas in others it takes place in the inner cortex (e.g. *Osmunda pluma*) or, in the outer cortex, as in *M. tekelili* and other species (e.g. *M. indentata*, *M. liaoningensis*). Heterogeneous petiolar rings generally have a different arrangement of thick and thin-walled fibers, depending on the species. In some taxa (e.g. *M. kidstonii*, *M. embreei*), thick-walled fibers form an abaxial arch, which in some species develops into two lateral bundles (e.g. *M. preosmunda*) or separates into an elongate abaxial strand and two lateral bundles (e.g. *M. indentata*), whereas in *M. tekelili*, the abaxial strand never divides and has enlarged ends.

| Species | Age | Source | Sclerenchyma in the trace concavity | Sclerenchyma in the inner cortex | Sclerenchyma ring | Sclerenchyma in stipular wings | First division of protoxylem |
|---|---|---|---|---|---|---|---|
| *Millerocaulis tekelili* sp. nov. | Early Cretaceous | Antarctica | None | Scattered | Abaxial arch, expanded at tips | 1 + numerous scattered | Outer cortex |
| *Millerocaulis johnstonii* | Late Triassic? | Australia | **Lining** | **None** | **Abaxial arch** | **1** | **Petiole bases** |
| *Millerocaulis kidstonii* | Jurassic–Cretaceous | Australia | **Two near trace** | **None** | **Abaxial arch** | 1 + 6 small | Unknown |
| *Millerocaulis indentata* | Triassic | Australia | **Two near trace** | **None** | Two lateral strands and one abaxial, the latter expanded | 1 + numerous scattered | Outer cortex |
| *Millerocaulis embreei* | Cretaceous | USA | **Lining** | Scattered | **Abaxial arch** | 1 + numerous scattered | **Petiole bases** |
| *Millerocaulis liaoningensis* | Middle Jurassic | China | **Lining** | **None** | **Abaxial arch** | **1** | Outer cortex |
| *Millerocaulis juandahensis* | Jurassic | Australia | **Two distant from trace** | **None** | **Two massess of thin-walled fibres inside ring** | **1** | Outer cortex |
| *Millerocaulis preosmunda* | Jurassic | China | **One mass** | **None** | Abaxial arch, upward forming two lateral bundles | 1 + numerous scattered | **Petiole bases** |
| *Millerocaulis sinica* | Jurassic | China | **One mass (crescent)** | **None** | **Abaxial arch** | 1 + numerous alligned | **Petiole bases** |
| *Ashicaulis claytoniites* | Jurassic | China | **One mass** | **None** | **Abaxial arch** | **1 (heterogeneous)** | **Petiole bases** |
| *Osmunda claytoniana* | Extant | Global | **Lining** | Scattered | Abaxial arch, upward forming two lateral bundles | **Elongate strip** | **Petiole bases** |
| *Osmunda pluma* | Paleocene | USA | **Lining** | Scattered | Abaxial arch, upward forming two lateral bundles | **Elongate strip + numerous scattered** | **Inner cortex** |
| *Osmunda oregonensis* | Eocene | USA | **Lining** | Scattered | Abaxial arch, upward forming two lateral bundles | **Elongate strip + numerous scattered** | **Inner cortex** |

*Table 1*. Comparison between Osmundaceae species with a heterogeneous sclerenchymatic ring. Key text in bold denotes differences between each taxon and *Millerocaulis tekelili* sp. nov. Data taken from Hewitson (1962), Miller (1967, 1971), Cheng *et al*. (2007), Cheng & Li (2007) and Vera (2007).

Some species included in *Osmunda* (*O. claytoniana* L., *O. pluma* Miller, 1967 and *O. oregonensis* (Arnold) Miller, 1967) have a petiole ring composed of an abaxial arch of thick-walled fibers, which in more distal regions has notably enlarged ends, until finally only these ends remain as two large masses (Miller 1967, 1971). Although none of the studied specimens of *M. tekelili* shows a petiolar ring with two masses of thick-walled fibers (these two masses always being connected by an abaxial band of the same composition), the arrangement of thick-walled fibers on the Antarctic species is strongly similar to the intermediate developmental stages of these *Osmunda* species. However, these *Osmunda* species differ from *M. tekelili* by having elongate strips of sclerenchyma in the stipular wings, and by the presence of sclerenchyma in the concavity of the trace (Table 1; Miller 1967, 1971). Since the studied specimens can not be referred to any previously known osmundalean species, the new taxon *M. tekelili* is proposed for including them.

*Evolutionary significance*

The phylogeny of extant Osmundaceae has been recently evaluated using molecular data (Yatabe *et al.* 1999, Metzgar *et al.* 2008), resulting in a partial reclassification of the group, recognition of the subgenus *Claytosmunda* (Yatabe *et al.* 2005), and placement of *Osmundastrum cinnamomeum* as sister group of the clade containing *Osmunda*, *Todea* and *Leptopteris*. However, few works have incorporated fossil representatives in such phylogenetic analyses. Miller (1971) utilized the Ground Plan/Divergence method of Wagner (1969), including extant and fossil species known at that time, and obtained results that more or less agree with the accepted phylogeny of the Osmundaceae (see Miller 1971 and Jud *et al.* 2008 for a more comprehensive discussion regarding this topic). More recently, Jud *et al.* (2008) carried out the first cladistic analysis for the family including fossil taxa, using a morphological dataset, together with the molecular data of Yatabe *et al.* (1999). However, that work focused on addressing the systematic affinities of *Todea tidwelli* Jud, Rothwell & Stockey, 2008, thus it was the only fossil species included in the dataset (Jud *et al.* 2008). A more exhaustive analysis, including extant and extinct species (and also encompassing species of the Thamnopteroidea and Guaireaceae) is needed to establish the phylogenetic relationships between the major clades of the Osmundales. However, such an analysis exceeds the aim of this contribution; thus the discussion of the phylogenetic significance of *Millerocaulis tekelili* is based mainly on comparisons between the morphoanatomical characters of the most similar species.

As previously discussed, *Millerocaulis tekelili* shares more features with the extant *Osmunda claytoniana* L. than with the rest of the extant Osmundaceae. Interestingly, the anatomy of several fossil species suggests that they may represent transitional forms in the lineage leading from *Millerocaulis* to *Osmunda claytoniana*. This has been recently discussed by Cheng *et al.* (2007) and Cheng (2011), who proposed that *Millerocaulis preosmunda*, *Ashicaulis claytoniites* and *Osmunda pluma* Miller may be intermediate forms in the evolution from *Millerocaulis* to subgenus *Claytosmunda*. It is clear that the petiole bases of these *osmundalean* species (*M. preosmunda*, *A. claytoniites*, *O. pluma* and *O. claytoniana*) share not only the characteristics of the sclerenchymatic ring, but also the presence of a large sclerenchyma mass associated with the vascular trace, and the absence of sclerenchyma strands in the inner cortex of the petiole bases. The sclerenchyma pattern of the petiolar ring of *M. tekelili* is also similar to the one present in this lineage. However, the new species lacks sclerenchyma associated with the vascular trace, and has sclerenchyma strands in the inner cortex of the petiole suggesting that it may represent an earlier stage in the evolutionary lineage between *M. preosmunda*—*A. claytoniites* and *O. claytoniana*. Interestingly, there is strong evidence that subgenus *Claytosmunda* was established in Antarctica during the Triassic (Phipps *et al.* 1998), thus lending support to this hypothesis.

One conflict with the proposed phylogenetic hypothesis that *Millerocaulis tekelili* may represent a more primitive stage than *Millerocaulis preosmunda* and *Ashicaulis claytoniites* is that *M. tekelili* is Early Cretaceous in age, whereas *M. preosmunda* and *A. claytoniites* are from Middle Jurassic sediments (Cheng *et al.* 2007, Cheng 2011). However, this apparent inconsistency may be the result of probable exceptional longevity in *M. tekelili*, as evident in some other species of Osmundaceae (e.g. *Osmundastrum cinnamomeum*, Serbet & Rothwell 1999).

## Conclusions

A new species, *Millerocaulis tekelili*, is defined, based on several permineralized stems recovered from Aptian strata of the Cerro Negro Formation on Livingston Island, South Shetland Islands (Antarctica). This new species is characterized by the presence of an ectophloic–dictyoxylic siphonostele surrounding a probable heterogeneous pith, inner parenchymatic and outer sclerotic cortices (cortical

ratio approximately 4), heterogeneous sclerotic ring in the petiole bases, absence of sclerenchyma associated with the petiolar xylem trace, petiolar inner cortex with sclerenchyma strands and stipular wings having a large sclerenchyma bundle and several smaller ones. The presence of root traces equally distributed in all directions and the abundance of these structures cut in transverse section suggest an erect habit for this osmundalean plant.

Similarities between this new species and *Millerocaulis preosmunda*, *Ashicaulis claytoniites*, *Osmunda pluma* and *Osmunda claytoniana* suggest that they may represent evolutionary stages leading from *Millerocaulis* to *Osmunda* subgenus *Claytosmunda*. In addition, this new find increases the number of fossil plants recovered from the Cerro Negro Formation, allowing better characterization of the palaeoflora, and expanding the record of fossil Osmundales that inhabited Antarctica during the Mesozoic.

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