

A new specimen of *Millerocaulis* (Osmundales: Osmundaceae) from the Cerro Negro Formation (Lower Cretaceous), Antarctica

Ezequiel Ignacio VERA

CONICET - División Paleobotánica, Museo Argentino de Ciencias Naturales «Bernardino Rivadavia»,
Av. Angel Gallardo 470, C1405DRJ, Buenos Aires, Argentina, evera@macn.gov.ar

Abstract: A new petrified stem of *Millerocaulis* Erasmus ex Tidwell *emend.* Vera, collected in the Aptian Cerro Negro Formation outcrops of Livingston Island (Antarctica), is described in detail. This specimen is probably conspecific with *Millerocaulis australis* (Vera), from the same unit, but it is smaller than the holotype and only known specimen of the latter species. Furthermore, differences between several characteristics of both specimens are observed. A discussion based on biological aspects of this group of plants is given, taking into account the ontogenetic variability. A conservative referral of the new specimen to *M. australis* is preferred over the proposal of a new morphotaxon for the inclusion of the new materials.

Key words: *Millerocaulis*, Osmundaceae, Cretaceous, Cerro Negro Formation, Antarctica.

Resumen: Un nuevo espécimen de *Millerocaulis* (Osmundales: Osmundaceae) de la Formación Cerro Negro (Cretácico Inferior), Antártida. Se describe en detalle un nuevo estípide petrificado de *Millerocaulis* Erasmus ex Tidwell *emend.* Vera, colectado en afloramientos de edad aptiana de la Formación Cerro Negro en Isla Livingston (Antártida). Este espécimen es probablemente coespecífico con *Millerocaulis australis* (Vera), procedente de la misma unidad, pero es mas pequeño que el holotipo (y único ejemplar conocido) de dicha especie. Además, existen diferencias entre ambos especímenes. Se brinda una discusión basada en aspectos biológicos de este grupo de plantas, teniendo en cuenta la variación ontogenética. Se opta por referir de manera conservativa el nuevo espécimen a *M. australis*, antes que proponer un nuevo morfotaxón para la inclusión de los nuevos materiales.

Palabras clave: *Millerocaulis*, Osmundaceae, Cretácico, Formación Cerro Negro, Antártida.

INTRODUCTION

The genus *Millerocaulis* Erasmus ex Tidwell *emend.* Vera includes ca. 40 morphospecies of osmundaceous affinities, spanning from the Triassic to the Late Cretaceous (Tidwell & Ash, 1994). Although a detailed review regarding the tempo-spatial distribution of the osmundaceous stems has been recently provided by Tian *et al.* (2008), it is important to note the high diversity of this morphogenus in the Mesozoic of Western Gondwana. Triassic rocks of Argentina and Antarctica have yielded many *Millerocaulis* species, including *M. beardmorensis* (Schopf) Tidwell, *M. woolfei* (Rothwell, Taylor & Taylor) Vera, *M. herbstii* (Archangelsky & de la Sota) Tidwell, *M. stipabonettii* Herbst and *M. lutzii* (Herbst) Herbst (Archangelsky & de la Sota, 1963; Schopf, 1978; Tidwell, 1986; Herbst, 1995, 2006; Rothwell *et al.*, 2002). In this region, Jurassic records of this genus are present exclusively in Patagonia, with the species *M. patagonica* (Archangelsky & de la Sota) Tidwell, *M. chubutensis* (Herbst) Herbst and *M. santaecrucis* (Herbst) Herbst (Archangelsky & de la Sota, 1962; Herbst, 1977, 1995; Tidwell, 1986).

On the other hand, Cretaceous species have been found only in Antarctica (*M. australis* (Vera) Vera and *M. livingstonensis* (Cantrill) Vera) (Cantrill, 1996; Vera, 2007, 2009).

In this work, a new osmundaceous stem from the Cerro Negro Formation outcrops at Byers Peninsula, Livingston Island (Antarctica) is described in detail and referred to the genus *Millerocaulis*.

The Cerro Negro Formation is a sequence of volcanoclastic continental strata with an age estimated in 120.3 ± 2.2 My, 119.4 ± 0.6 My and 119.1 ± 0.8 My using the $^{40}\text{Ar}/^{39}\text{Ar}$ method (Hathway, 1997; Hathway *et al.*, 1999). Abundant plant specimens have been recovered from these sediments, including petrified stems assigned to the fern Family Osmundaceae and Order Cyatheaales (Césari *et al.*, 2001; Vera, 2007, 2009) and fern frond compressions with *in situ* spores (Césari, 2006).

MATERIAL AND METHODS

The specimen was collected in the Aptian Cerro Negro Formation outcrops at Rotch Dome

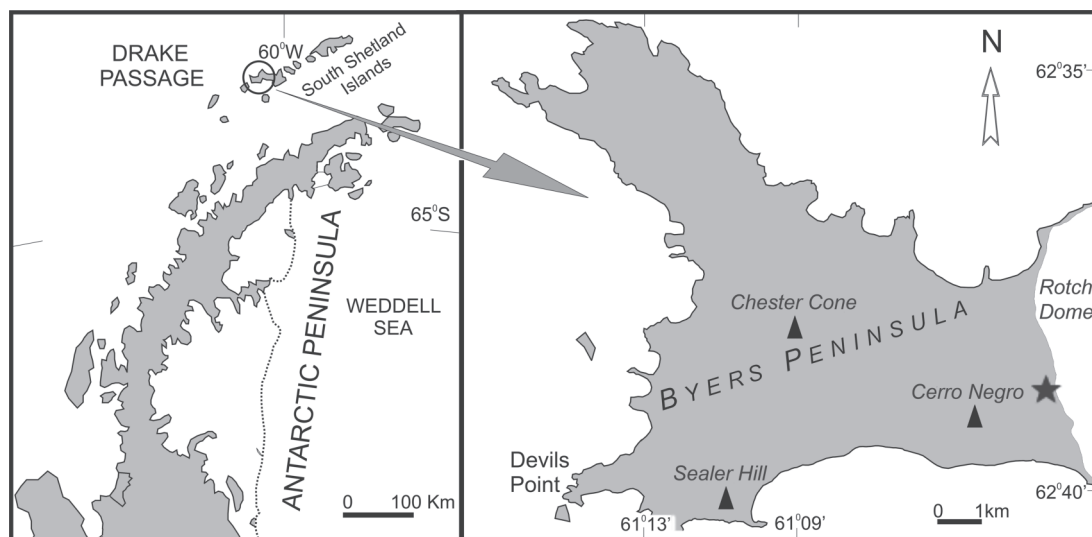


Fig. 1. Location map, showing fossiliferous locality (star). Modified from Césari *et al.* (1999) and Párica *et al.* (2007).

locality, Byers Peninsula, South Shetland Islands, Antarctica (Párica *et al.*, 2007, Fig. 1). 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. The specimens are housed in the collection of the Museo Argentino de Ciencias Naturales «Bernardino Rivadavia», División Paleobotánica, under BA Pb numbers.

Cortical Ratio (CR) was estimated using the following formula:

$$CR = OC/IC$$

Where OC is the outer cortex average width of the specimen, and IC is the inner cortex average width of the same specimen.

For comparative purposes, the holotype of *Millerocaulis australis* BA Pb 13510; BA Pb Pm 508, 509, 510, 511, 512, 513, 526, 527 was also examined.

SYSTEMATICS

Class Polypodiopsida (=Filicopsida)
Order Osmundales
Family Osmundaceae
Subfamily Osmundoidea Miller, 1971

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

Type species. *Osmundites dunlopia* (Kidston & Gwynne-Vaughan) Tidwell, 1986.

Millerocaulis sp. cf. *Millerocaulis australis* (Vera) Vera. (Figs. 2.A-H, 3B)

2001 *Ashicaulis* sp. Césari, Remesal & Párica, p. 45, figures. 1 A.

Description. The specimen is 310 mm tall and its width ranges between 90 and 160 mm. It contains a small stem with an ectophloic-dictyoxyl siphonostele surrounded by a mantle of petiole bases and adventitious roots reaching 7 centimeters in thickness (Fig. 2A). The stem consist of a pith 1-3 mm in diameter with cells of unknown nature because of the poor preservation of this tissue. Surrounding the pith is located a ring of xylem (1 mm in radial diameter, up to 15 cells thick), interrupted by many definite leaf gaps. Up to 20 (12 using Hewitson's (1962) method of count) xylem strands can be observed in a transversal section of the stem (Fig. 2B, C). Metaxylem tracheids are 30-60 μ m in diameter. Protoxylem clusters were not observed in the material. The external tissues of the stele (phloem, pericycle and endodermis) are totally obliterated and this makes impossible a detailed study of the cellular characteristics.

Surrounding the stele are located the cortical tissues, differentiated in an internal parenchymatic inner cortex (0.45-0.75 mm thick) and an external cortex (1.2-3.7 mm thick), very poorly preserved, composed by sclerenchymatic cells (20-60 μ m thick) with cell walls 0.5-1.5 μ m thick. Cortical Ratio is approximately 4.2.

Scattered throughout the cortex are present about 17-20 leaf traces, approximately 5 of them in the inner cortex tissue and the rest in the outer cortex. Leaf traces originate from the central stele, and start as a small group of parenchyma in the middle of a xylem strand. This parenchymatic group of cells grows centripetally and, at the same time, the xylem bundle grows in the opposite direction (centrifugally). Finally, the xylem bundle is constricted and a reniform leaf trace with an endarch protoxylem cluster is released from the stele. The resulting leaf gap is immediate, being completely formed when the leaf trace is released (Fig. 2C).

When the trace is released from the central cylinder, the xylem bundle is surrounded by the phloem, pericycle and endodermis. During its development, the leaf traces are immersed in several tissues. First, the inner cortical fleshy parenchyma surrounds the structure. When it traverses through the external cortical tissue, it is covered by sclerenchymatic tissue, enclosing the trace and the inner cortex and resulting in a homogeneous petiole ring outside the stem. Inner cortical tissue of the petiole is not homogeneous, and when it is located outside the stem several small patches of sclerenchyma can be observed. During its traverse across the stem, the shape of the trace changes from reniform to C-shaped, and sclerenchyma associated with it start to develop in the concavity of the trace, first as a mass of tissue parallel and adaxial to the trace, but progressively developing in two sclerenchyma bundles located near the tip of the vascular strand after the fifth or sixth petiolar cycle (Fig. 2D, E; Fig. 3B). Since the preservation is not good, it is impossible to determine the place of the first protoxylem division.

Where they depart from the stem, the stipular wings of the petiole are up to 1 mm wide and 1.3 mm high, increasing its size to approximately 6 mm wide and 2.5 mm high in the most distal petioles of the specimen (6th cycle). Stipular wings contain mechanic groups of sclerenchymatic tissue. When the petiole departs from the stem, only one sclerenchymatic bundle is immersed in the stipular wings but, at more distal levels, several minor groups can be seen (between two to five), more or less aligned with the first one. The first group of sclerenchyma remains bigger than the others, having a size more or less twice the size of the smaller ones (Fig. 2E; 3B).

Root traces probably diverge from the leaf traces when they are released from the central cylinder. Apparently, two root traces are released at the same time, resulting in a characteristic arrangement of a central leaf trace and the two

root traces separated from it by the same distance (Fig. 2F). Almost all the root traces are cut transversally in the transverse sections of the stem.

Root traces are circular to oval in cross section (25-27.5 μ m in diameter), with a diarch configuration of the protoxylem. Metaxylem cells form a cluster of 12.5 μ m wide and 23 μ m high. As the leaf traces, when depart from the stem they are surrounded by an inner parenchymatic cortex and an outer sclerotic ring. Externally, they are covered by an indument of trichomes (Fig. 2G, H).

Studied specimen. BA Pb 14892; BA Pb Pm 521, 522, 523, 524, 525 (Museo Argentino de Ciencias Naturales «Bernardino Rivadavia». Colección Paleobotánica); Figures 2.A-H, 3.B.

Procedence. Byers Peninsula, Livingston Island. South Shetland Islands, Antarctica (S 62°38'12" - W 60°58'12").

Stratigraphic horizon. Cerro Negro Formation.

Age. Aptian.

DISCUSSION

Several studies have already shown the apparent evolutive stasis of the fern Family Osmundaceae, with the genus *Osmunda* represented in Triassic strata of Antarctica (Phipps *et al.*, 1998), the genus *Todea* in Cretaceous sediments of North America (Jud *et al.*, 2008), and the living species *Osmundastrum cinnamomeum* present in Upper Cretaceous rocks of USA (Serbet & Rothwell, 1999). These results suggest that living representatives of the group may be used as reference model for studying fossil osmundaceous specimens.

The specimen here studied may be considered a new species of *Millerocaulis*. However, a conservative view has been adopted, making a «biological» comparison (focusing in «structural characters» *sensu* Herbst (2003) and ontogenetic variability), taking into account the observations made on living representatives of the Osmundaceae.

Millerocaulis australis was defined as a fairly large osmundalean stem, containing *ca.* 60 leaf traces in the cortex (Vera, 2007), different from the number observed in the specimen BA Pb 14892, which possesses nearly 20. These differences may be related with the size of both specimens, since it is possible that in a small specimen the number of leaf traces may be lower than in a big one.

Another difference is the way in which the root traces are produced. In *Millerocaulis australis*, generally one root trace diverges dur-

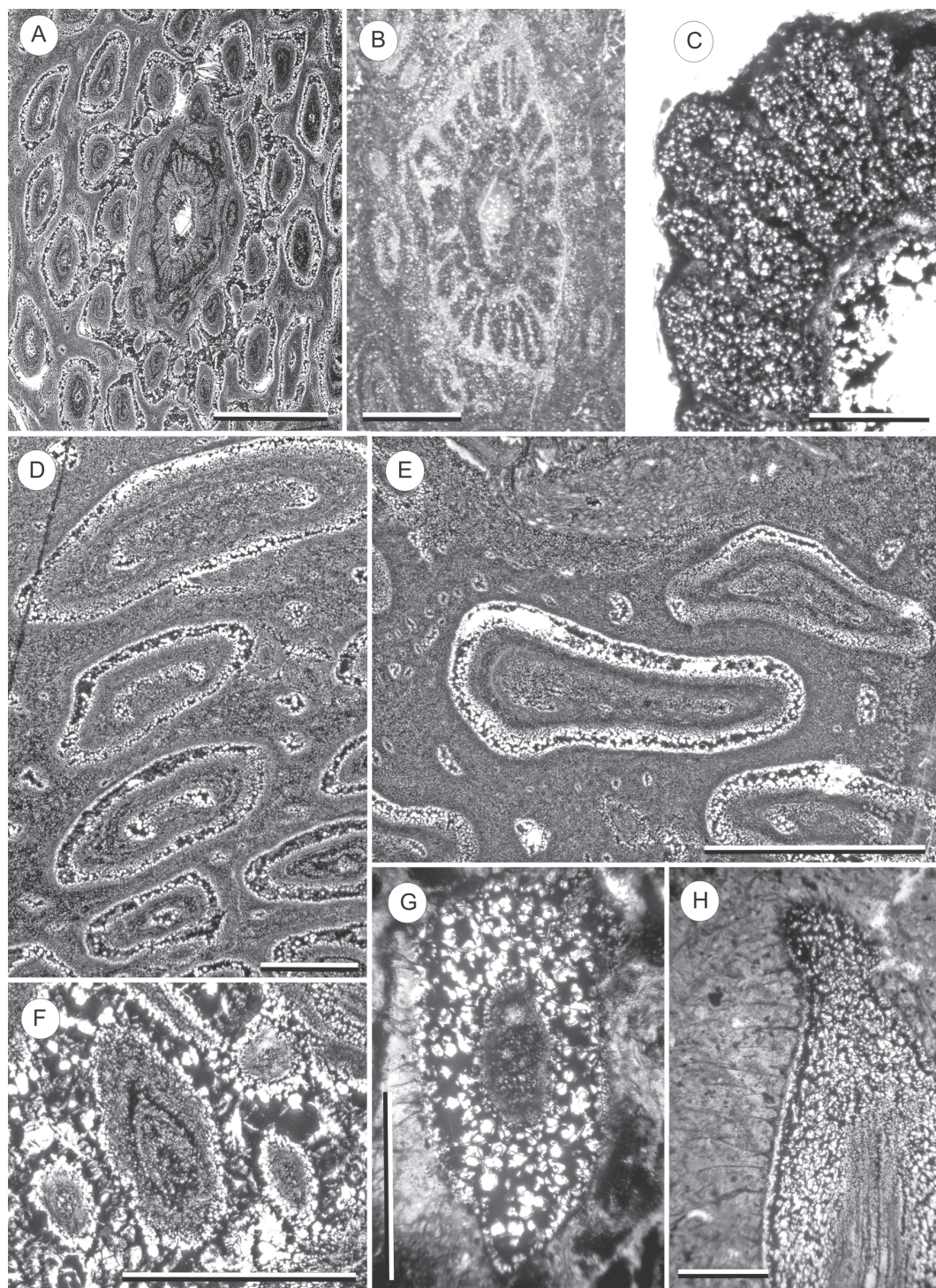


Fig. 2. A-F. *Millerocaulis* sp. cf. *M. australis*. BA Pb 14892. A, Stem surrounded by petiole bases and adventitious roots. B, detail of the stele. C, Detail of the xylem ring showing a departing leaf trace. D, Consecutive cycles of petiole bases, showing modifications in the arrangement of sclerenchyma in the concavity of the trace. E, Most external petiole bases, showing mechanic groups in the stipular wings and sclerenchymatic arrangement in the concavity of the trace. F, Detail of a leaf trace with associated root traces. G, Adventitious root, showing internal parenchymatic and outer sclerenchymatic cortex. H, Detail of an adventitious root, showing trichomes attached to the external surface. Scale bar: figures A and E = 5 mm; B, D and F = 2 mm; C, G and H = 500 μ m.

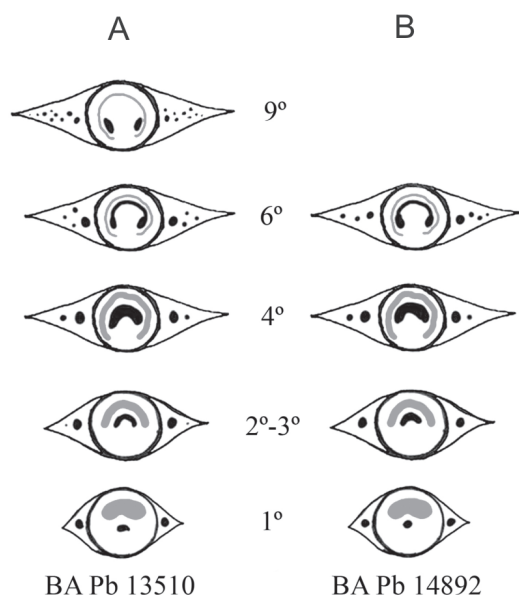


Fig. 3. Comparison between petiolar cycles of: A, the holotype of *Millerocaulis australis* (BA Pb 13510) and B, *Millerocaulis* sp. cf. *M. australis* (BA Pb 14892), showing the changing pattern of the sclerenchyma in the stipular wings and the concavity of the trace. In each case, the most external sketch corresponds to the preserved petiole with the greater expression of the sclerenchymatic tissues. Not at the same scale. From bottom to top: first cycle, second-third cycle, fourth cycle, sixth cycle, ninth cycle (only in the holotype). Black, sclerenchyma; grey, trace.

ing the development of a leaf trace (Vera, 2007). On the other hand, in BA Pb 14892 two root traces are typically observed in association with the production of a leaf trace. When compared with the living species *Leptopteris wilkesiana* (Brack.) H. Christ, a similar situation is observed. In basal (smaller) sections of the plant, the production of root traces is higher than in upper (bigger) sections of the plant (Miller, 1971), being this related with the mantle of adventitious roots that is more developed near the base of the stem and brings support to the plant.

Both specimens also differ in the type of leaf gap (immediate or delayed). In the type specimen of *Millerocaulis australis*, the leaf gap is delayed (Vera, 2007), but in BA Pb 14892 is immediate. Although in this particular case a conclusive justification for the observed differences can not be given, it is possible to suggest an explanation. If both plants belong to the same biological species, they should have a different degree of ontogenetic development. When the leaf trace separates from the cauline stele, the paren-

chymatic ray that interrupts the xylem cylinder possesses a similar degree of development. In the holotype of *M. australis*, since the siphonostele is wider, the interruption is not complete (producing a delayed leaf gap). On the other hand, in BA Pb 14892, the interruption of the stele is complete, and an immediate leaf gap is produced.

Nine cycles of petiole bases are preserved in the holotype of *Millerocaulis australis*. In the most external bases, 6-9 small sclerenchyma strands are present, accompanying a bigger one. In BA Pb 14892, the preserved mantle of petiole bases includes up to the sixth cycle, the arrangement of mechanical groups being different from the one observed in the most external petioles of *M. australis*. However, when petiolar bases of both holotype and BA Pb 14892 are compared at different petiolar cycles (Fig. 3), the sclerenchyma in the stipular wings, in the concavity of the trace, and in the petiolar ring (and also the sclerenchyma in the inner cortex of the petiole, not illustrated in the Fig. 3) was fairly comparable. Since this character was considered by many authors (Hewitson 1962; Miller 1971) as one of the most important features to separate species included in the Osmundaceae, and taking into account that most of the differences observed between the holotype of *Millerocaulis australis* and the specimen BA Pb 14892 may be considered a result of ontogenetic changes in the plant (Herbst's (2003) «variable» characters), these two specimens are here considered conspecific. As both stems were found in the same locality and stratigraphic horizon, and have a similar Cortical Ratio, also brings support to consider them conspecific. However, a conservative view is taken. Since only one specimen is described, it is here classified as *Millerocaulis* sp. cf. *M. australis*, until new material is found to eventually emend the original diagnosis of the species.

CONCLUSIONS

A new specimen of *Millerocaulis*, collected from sediments of the Aptian Cerro Negro Formation, is described. The distribution of the mechanic groups present in the petiole bases of the new specimen is fairly comparable with the arrangement observed in *Millerocaulis australis* (Vera) Vera, a taxon recorded in the same stratigraphic unit. However, both specimens differ in some characters, including the size of the stem, the diameter of the pith and vascular cylinder, etc.. Since these differences may be the result of ontogenetic changes in the plant, the new specimen is conservatively referred to *Millerocaulis* sp. cf. *M. australis*. Future findings will provide

helpful information to clarify if the specimen BA Pb 14892 should be referred to *M. australis* or if it represents a different taxon.

ACKNOWLEDGMENTS

Thanks are due to Dr. Silvia N. Césari for reading the manuscript and providing useful comments. The reviewers Drs. Rafael Herbst and Elías de la Sota, as well as the editor Dr. Sergio Archangelsky provided helpful comments which improved the quality of the final version of the manuscript. This work was a contribution to the PICT 32320.

BIBLIOGRAPHY

- Archangelsky, S. & E. de la Sota. 1962. Estudio anatómico de un estípite petrificado de «*Osmundites*», de edad jurásica, procedente del Gran Bajo de San Julián, Provincia de Santa Cruz. *Ameghiniana* 2: 153-164.
- 1963. *Osmundites herbstii*, nueva petrificación triásica de El Tranquilo, Provincia de Santa Cruz. *Ameghiniana* 3: 135-140.
- Cantrill, D.J. 1997. The pteridophyte *Ashicaulis livingstonensis* (Osmundaceae) from the Upper Cretaceous of Williams Point, Livingston Island, Antarctica. *N.Z. J. Geol. Geophys.* 40: 315-323.
- Césari, S.N., 2006. Aptian ferns with in situ spores from the South Shetland Islands, Antarctica. *Rev. Palaeobot. Palynol.* 138: 227-238.
- Césari, S.N., C. Párica, M. Remesal & F. Salani. 1999. Paleoflora del Cretácico Inferior de península Byers. *Ameghiniana* 36: 3-22.
- Césari, S.N., M. Remesal & C. Párica. 2001. Ferns: a palaeoclimatic significant component of the Cretaceous flora from Livingston Island, Antarctica. *Asociación Paleontológica Argentina. Publicación Especial* 7, pp 45-50.
- Hathway, B. 1997. Nonmarine sedimentation in an Early Cretaceous extensional continental-margin arc, Byers Peninsula, Livingston Island, South Shetland Islands. *J. Sedim. Res.* 67: 686-697.
- Hathway, B., A.M. Duane, D.J. Cantrill & S.P. Kelley. 1999. 40Ar/39Ar geochronology and palynology of the Cerro Negro Formation, South Shetland Islands, Antarctica: a new radiometric tie for Cretaceous terrestrial biostratigraphy in the Southern Hemisphere. *Aust. J. Earth Sci.* 46: 593-606.
- Herbst, R. 1977. Dos nuevas especies de *Osmundacaulis* (Osmundaceae, Filices) y otros restos de Osmundales de Argentina. *Facena* 1: 19-44.
- 1995. *Millerocaulis stipabonetti* nov. sp. (Osmundaceae, Filices) from the Late Triassic Cepeda Formation of San Juan Province, Argentina. *Med. Rijks Geol. Dienst* 53: 13-19.
 - 2003. *Osmundacaulis tehuelchense* nov. sp. (Osmundaceae, Filices) from the Middle Jurassic of Santa Cruz Province (Patagonia, Argentina). *Cour. Forsch.-Inst. Senckenberg* 241: 85-95.
 - 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* 8: 185-193.
- Hewitson, W.H. 1962. Comparative morphology of the Osmundaceae. *Ann. Missouri Bot. Garden* 49: 57-93.
- Jud, N.A., G.W. Rothwell & R.A. Stockey. 2008. *Todea* from the Lower Cretaceous of Western North America: implications for the phylogeny, systematics and evolution of modern Osmundaceae. *Am. J. Bot.* 95: 330-339.
- Miller, C.N. 1971. Evolution of the fern family Osmundaceae based on anatomical studies. *Contr. Mus. Paleont. Univ. Michigan* 23: 105-169.
- Párica, C.A., F.M. Salani, E. Vera, M. Remesal & S.N. Césari. 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: 553-567.
- Phipps, C.J., T.N. Taylor, E.L. Taylor, N.R. Cúneo, L.D. Boucher & X. Yao. 1998. *Osmunda* (Osmundaceae) from the Triassic of Antarctica: an example of evolutionary stasis. *Am. J. Bot.* 85: 888-895.
- Rothwell, G.W., E.L. Taylor & T.N. Taylor. 2002. *Ashicaulis woolfei* n. sp.: additional evidence for the antiquity of osmundaceous ferns from the Triassic of Antarctica. *Am. J. Bot.* 89: 352-361.
- Schopf, J.M. 1978. An unusual osmundaceous specimen from Antarctica. *Can. J. Bot.* 56: 3083-3095.
- Serbet, R. & G.W. Rothwell. 1999. *Osmunda cinnamomea* (Osmundaceae) in the Upper Cretaceous of Western North America: additional evidence for exceptional species longevity among filicalean ferns. *Int. J. Plant Sci.* 160: 425-433.
- Tian, N., Y.D. Wang & Z.K. Jiang. 2008. Permineralized rhizomes of the Osmundaceae (Filicales): diversity and tempo-spatial distribution pattern. *Paleoworld* 17:183-200.
- Tidwell, W.D. 1986. *Millerocaulis*, a new genus with species formerly in *Osmundacaulis* Miller (Fossils: Osmundaceae). *Sida* 11: 401-405.
- 1994. *Ashicaulis*, a new genus for some species of *Millerocaulis* (Osmundaceae). *Sida* 16: 253-261.
- Tidwell, W.D. & S.R. Ash. 1994. A review of selected Triassic to Early Cretaceous ferns. *J. Plant Res.* 107: 417-442.
- Vera, E.I. 2007. A new species of *Ashicaulis* Tidwell (Osmundaceae) from Aptian strata of Livingston Island, Antarctica. *Cret. Res.* 28: 500-508.
- 2008. Proposal to emend the genus *Millerocaulis* Erasmus ex Tidwell to recombine the genera *Ashicaulis* Tidwell 1994 and *Millerocaulis* Tidwell emend. Tidwell. *Ameghiniana* 45: 693-698.
 - 2009. *Alienopteris livingstonensis* gen. et sp. nov., enigmatic petrified tree fern stem (Cyatheales) from the Aptian Cerro Negro Formation, Antarctica. *Cret. Res.* 30: 401-410.