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Marattiaceae synangia from the Lower Cretaceous of Antarctica

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ABSTRACT

Marattiaceous ferns are conspicuous fossil element in upper Paleozoic and lower Mesozoic deposits, but become rarer to almost absent in Cretaceous to Holocene deposits. In this contribution, fragmentary synangia recovered from the Aptian Cerro Negro Formation (Livingston Island, Antarctica) are described. Synangia are bivalvate, containing at least four lachrymiform sporangia per valve. Valves are fused at the base, and connect to the leaf blade by a short peduncle. Sporangia contain more than 400 oval to reniform (probably monolete), smooth to microgranulate spores. The reproductive structures have morphological similarities with extant *Marattia* and *Ptisana*, and the apparent absence of labia suggests a closer relationship with the latter genus. The presence of Marattiaceae, along with previously described ferns (e.g. Cyatheales) supports warm climatic conditions during the Aptian in this region of Antarctica.

1. Introduction

Extant Marattiaceae is a small group of ferns restricted to wet tropical and subtropical regions, in primary and secondary forests, where the canopy is dense (Camus, 1990). Several classification schemes have been proposed for this group (see Murdock, 2008a, b, and cites therein, for a review). Despite the lack of consensus regarding the relationships among Marattiacean taxa, most authors agree in considering them as a single evolutionary unit of primitive eusporangiate ferns (Murdock, 2008a, b, and references therein).

Marattiaceae has one of the most extensive fossil records. Fossils referable to this group, preserved as impression/compression, petrification, charcoalification and isolated palynomorphs, can be found in strata ranging from the Carboniferous to the Holocene. However, as was highlighted by Hu et al. (2006), post Jurassic records of this family are very scarce. To date, Cretaceous specimens referred to the Marattiaceae include the charcoalified isolated synangia *Goolangia minnesotensis* Hu, Dilcher, Schneider et Jarzen and *Mesozoisynangia trilobus* Hu, Dilcher, Schneider et Jarzen, recovered from the Dakota Formation (Hu et al., 2006). Fragmentary fertile remains of Marattiaceae were also recorded as impression/compressions by Césari et al. (2001) in the Aptian Cerro Negro Formation (Antarctica). Cenozoic records of the group are even less common (Millay, 1979; Hill and Camus, 1986; Collinson, 2001; Kvaček, 2014).

In this contribution, permineralized synangia recovered from the Early Cretaceous Cerro Negro Formation are described in detail, and referred to the fern family Marattiaceae. Comparisons with extant and extinct representatives of this group of ferns are made, and climatic conditions are suggested.

2. Materials and methods

Studied specimens comprise isolated synangia preserved as permineralizations within the rock matrix surrounding a permineralized cyathealean tree fern axis currently under study, collected from outcrops of the Cerro Negro Formation at Byers Peninsula, Livingston Island (South Shetland Islands, Antarctica), at the Rotch Dome locality, sensu Párica et al. (2007), at 62°38′41″S–60°58′12″W coordinates (see Vera, 2012, for a brief geological description of the area).

Thin sections of the cyathealean stem were made, and the preserved marattialean structures were studied under light microscopy using a Nikon SMZ-2t Microscope.

Systematic treatment follows Smith et al. (2006) and Murdock (2008a, b). Terminology used follows Millay (1997) and Murdock (2008a, b), and is schematized in Fig. 1.

3. Systematic palaeontology

Division: Pteridophyta
Class: Marattiopsida Doweld 2001
Order: Marattiales Link 1833
Family: Marattiaceae Kaulf 1824

Remarks. The familial name Marattiaceae Kaulf 1824 is currently regarded as a junior synonym, since Danaeaceae C. Agardh 1822 has chronological priority. However, a proposal for *nomina*

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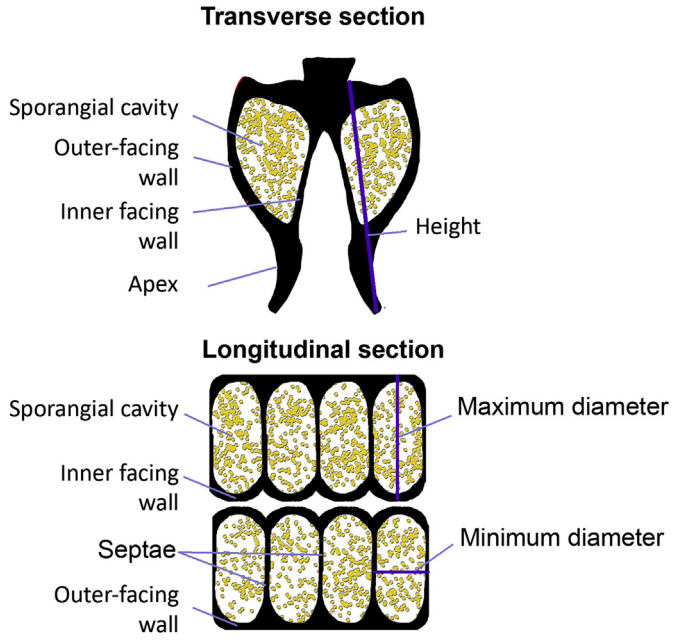

Fig. 1. Schematic representation of the Marattiace synangia studied in this work, showing terminology used in the text.

conservanda was recently submitted by Murdock et al. (2006), favoring the former name. For conservative purposes, the name Marattiaceae Kaulf is used here, since it has been widely employed for extant and extinct taxa.

Marattiaceae indet.

Studied Specimens: BA Pb 14,985 (Microscope slides BA Pb Pm 610, 625–628).

Repository: Paleobotanical Collection. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; Buenos Aires, Argentina.

Locality: Studied materials were collected at the Rotch Dome lotality (sensu Párica et al. 2007; see map in Vera, 2012) at Byers Peninsula, Livingston Island. (South Shetland Islands, Antarctica).

Stratigraphic unit: Cerro Negro Formation; Byers Group.

Age: Early Cretaceous (Aptian)

Description: This taxon is represented by abundant fragmentary pinnules and synangia containing spores. Synangia are connected to pinnules by short peduncles (Plate I, 1, 2, 4)

Synangia are linear, and bilaterally symmetrical, being approximately 450 μm wide, 600 μm in high, and at least 900 μm long (Plate I, 1, 2, 3, 4). Synangia are composed of at least eight sporangia, arranged in two opposed valves, being totally fused in each valve (Plate I 1, 2, 3, 4). Valves are connected by a small parenchymatous base, which extends for a short distance from the receptacle (Plate I, 1, 2, 4).

In transverse section, sporangia are lachrymiform in shape, with a height of 510–590 μm. Distal from the sporangial cavity, the apex of the sporangium extends for 150–230 μm (Plates 1, 2, 4). In longitudinal section, sporangia are rectangular to oval, with a maximum diameter of 180–215 μm, and a minimum diameter of 90–130 μm (Plate I, 3). Inner-facing walls (apertural walls) are one cell thick (approximately 10 μm) and, in some specimens, appear broken, probably owing to their delicate nature and sporangial dehiscence. Lateral (septae), and outer-facing walls are also narrow, probably 1–2 cells thick, but preservational quality precludes precise determination. Sporangia lack labia (Plate I, 2, 3, 4).

Each sporangium contains more than 400 spores (Plate I, 3, 4). Spores are small (ca. 20 μm in diameter), oval to reniform, suggesting a monolete character. The exine is laevigate to microganulate (Plate I, 5, 6).

4. Discussion

4.1. Affinities

Traditionally, eusporangiate ferns are included in the fern orders Marattiales and Ophioglossales. Both are characterized by sporangia lacking an annulus (Smith et al., 2006), as is the case with the studied specimens. However, fused sporangia forming synangia can be found only in Marattiales (Smith et al., 2006). Since the Antarctic remains are isolated synangia, they can be classified as a marattioid fern with a great degree of confidence.

Recently, Murdock (2008a) obtained a phylogenetic hypothesis for Marattiaceae, resulting in a taxonomic revision of the group (Murdock, 2008b), and providing detailed information about the extant representatives of the family. Among the results of the phylogenetic analysis, Murdock (2008a) found that *Danaea* was sister to the rest of Marattiaceae. This author included a key to the genera of Marattiaceae (Murdock, 2008b). In an attempt to understand the significance of the fossils studied here, Murdock's key (2008b) was followed. Although the key is broadly based on sporangial features, it also includes characters of the fronds and the rhizomes. The Antarctic remains possess raised synangia, as observed in most extant Marattiaceae except *Danaea* (Murdock, 2008b). *Christensenia* possesses radially symmetrical synangia (Murdock, 2008b), whereas the studied specimens have bilaterally symmetrical synangia. Species included in *Eupodium* possess prominently stalked synangia (Murdock, 2008b), a feature not present in Marattiaceae indet., where synangia are slightly raised. *Angiopteris* is characterized by the presence of non-fused sporangia (or slightly fused), where the synangia do not open as a unit (Murdock, 2008b). Marattiaceae indet. possesses sporangia fused into synangia, which open as a single unit. Murdock (2008b) proposed *Ptisana* for some species previously referred to *Marattia*. Although this separation was originally based on molecular phylogenies (Murdock, 2008b), morphological differences are evident between these two genera. Sporangia of *Marattia* possess labiate apertures, whereas in *Ptisana* these structures are absent. Marattiaceae indet. has sporangia apparently lacking labiate apertures, and may be more closely related to *Ptisana*. However, since this study is based only on sporangial remains, we prefer to not refer the specimens to that genus, which is based on extant plants. In addition, labia in *Marattia* are sometimes difficult to observe in fossil (or even in extant) remains (Escapa et al., 2015), and as a result affinities with *Marattia* s.s. cannot be discarded (a problem also present in impression/compression taxa, as summarized by Escapa et al. (2015). Despite this, it is clear that the Antarctic remains are comparable with extant Marattiaceae, representing a taxon probably more derived than *Danaea*. In addition, spores of extant Marattiaceae tend to be monolete and reniform, *Angiopteris* being an exception, with globose and trilete spores. This may be interpreted as a reversal to the ancestral condition, but the polarity of this character change is difficult to interpret, since fossil marattioids have both monolete and trilete spores, and other groups of ferns share these morphologies (Murdock, 2008b). The studied specimens lack well-preserved laesurae, but the morphology of the spores is similar to typical monolete spores, thus different from *Angiopteris*.

4.2. Comparison with other fossil marattioid ferns

The fossil record of post-Jurassic ferns referred to the Marattiaceae is very scarce. *Goolangia minnesotensis* Hu, Dilcher, Schneider et Jarzen and *Mesozoisynangia trilobus* Hu, Dilcher, Schneider et Jarzen are two charcoalified fossils collected from the Late Cretaceous Dakota Formation. *Goolangia minnesotensis* is represented by a single elongate sporangium, and can be separated from Marattiaceae indet. by its highly elongate nature and greater size. Furthermore, the presence of an attachment scar led the authors to suggest that it was part of a radially symmetrical synangium (Hu et al., 2006). *Mesozoisynangia trilobus* is a

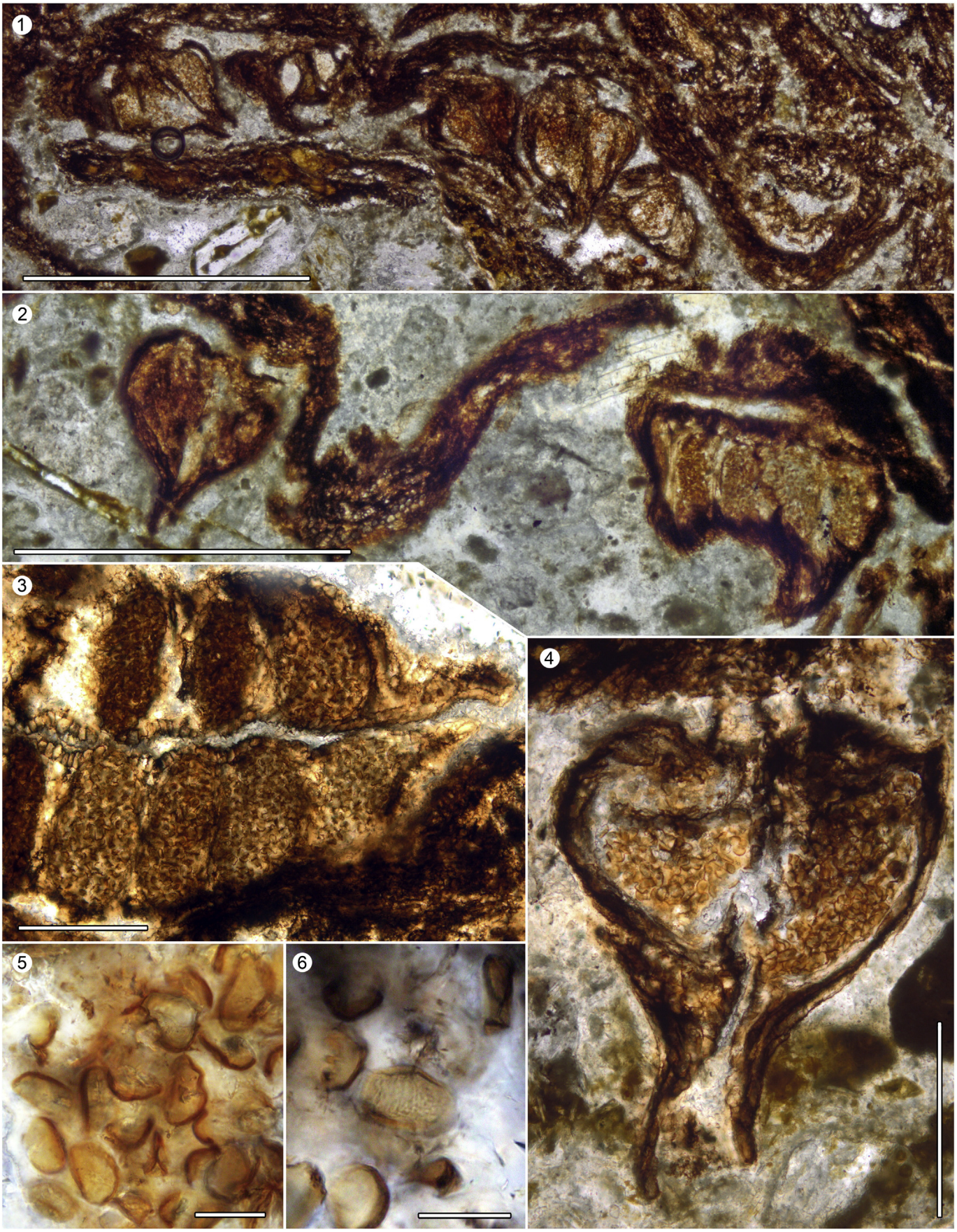

Plate I. Marattiaceae indet. BA Pb 14985. 1. General view of a leaf blade bearing at least four synangia. Scale bar: 1 mm. 2. Synangia in transverse (left) and lateral (right) section. Scale bar: 1 mm. 3. Synangia in longitudinal section. Scale bar: 200 μm. 4. Synangia in transverse section, showing spore content. Scale bar: 250 μm. 5. Detail of the content of a sporangial cavity, showing the morphology of the spores within. Scale bar: 20 μm. 6. Detail of spores contained in the sporangia, showing morphology and microgranulate exine. Scale bar: 20 μm.

taxon characterized by the presence of synangia formed by three sporangia (Hu et al., 2006), whereas the remains studied here possess synangia composed of more than eight sporangia, arranged in two valves.

Palaeozoic permineralized synangia of marattialean ferns are particularly abundant, and are generally referred to *Acaulangium* Millay 1977, *Araiangium* Millay 1982, *Acitheca* Schimper in Schimper and Schenk, 1879, *Eoangiopteris* Mamay 1950, *Grandeuryella* Weiss 1885, *Millaya* Mapes et Schabilion 1979, *Scolecopteris* Zenker 1837 and *Sturiella* Weiss 1885 (Millay, 1997; Liu et al., 2000). Species of *Scolecopteris* have been found in upper Palaeozoic strata of North America (Mamay, 1950; Millay, 1979; Lesnikowska and Millay, 1985), China (Hilton et al., 2004; He et al., 2006), Germany (Barthel et al., 1995; Weiss, 2002); and in Triassic strata of Antarctica (Delevoryas et al., 1992). This genus differs from Marattiaceae indet. by the presence of radially symmetrical synangia, whereas synangia of the studied specimens bilaterally symmetrical. Other genera, such as *Acitheca, Acaulangium* and *Araiangim*, also share radially symmetrical synangia (Millay, 1997; Liu et al., 2000). Few Palaeozoic taxa possess synangia similar to the Antarctic form. *Eoangiopteris*, containing the species *E. andrewsii* and *E. goodie* (Mamay, 1950; Millay, 1978) possesses sporangia arranged in bilateral synangia, similar to extant *Angiopteris*. As in the latter genus, it exhibits laterally free sporangia (Mamay 1950, Millay 1978), a condition different from Marattiaceae indet., where sporangia of each valve are totally fused. *Grandeuryella* also shares the presence of bilaterally symmetrical synangia with basally fused sporangia (Millay 1997). *Millaya* seems similar to extant *Danaea*, where synangia are completely embedded in the abaxial tissue of the pinnule (Millay, 1997), contrasting with the features observed in Marattiaceae indet. Finally, *Sturiella* is probably congeneric with *Acaulangium* (Millay, 1997), and thus different from the specimens studied here.

4.3. Fossil ferns from the Cerro Negro Formation

Several studies outline the abundance and diversity of ferns in the Cerro Negro Formation. Leptosporangiate ferns are among the most abundant components of this palaeoflora, with representatives of Osmundaceae, Cyatheaceae, Dicksoniaceae, and Cyathealeans with unknown familial placement, among others (Askin, 1983; Césari et al., 1999, 2001; Cantrill, 2000; Césari, 2006; Torres et al., 1997; Vera, 2007, 2009, 2010, 2012, 2013, 2015). On the other hand, eusporangiate forms are almost absent from the unit. Césari et al. (2001) illustrated a fragment of a fertile frond with synangia, which they referred to Marattiaceae. Notably, these specimens are similar in size to Marattiaceae indet., and may have belonged to the same biological entity. However, the fragmentary nature of the specimen illustrated by Césari et al. (2001, Fig. 2A) and the specimens studied here, along with the few overlapping features between these fossils, precludes a more complete comparison.

4.4. Climatic inferences

Climatic inferences have been made previously, based on the pteridological content of the Cerro Negro Formation. The presence of abundant fern remains, including representatives of cyathealean tree ferns (Cantrill, 1998; Césari et al., 2001, Vera, 2009, 2013, 2015), suggests frost-free climatic conditions (Césari et al., 2001). The presence of *Lophosoria cupulata* Cantrill 1998, and the use of extant *Lophosoria quadripinnata* (J.F.Gmel.) C.Chr. 1920 as a modern analog, was used to estimate minimum annual temperatures of at least 8 °C (Cantrill, 1998). Recently, Bystriakova et al. (2011) estimated the ancestral climate of the core tree ferns clade (a Cyatheales clade containing Cyatheaceae, Dicksoniaceae, Metaxyaceae and Cibotiaceae) as characterized by relatively high annual rainfall (in excess of 1100 mm), and warm climate, with minimum temperatures not lower than 7.7 °C (thus, frost free), and maximum temperatures not lower than 23.3 °C. Given the presence of several core tree ferns clade representatives in the Cerro Negro Formation, similar climatic conditions were proposed (Vera, 2015). The presence of representatives of the Marattiaceae is another clue pointing to a warm climate regime during the Aptian of Antarctica.

Extant species of the Marattiaceae are essentially restricted to wet tropical or subtropical regions of the world (Camus, 1990), with representatives in the Neotropics (e.g. *Marattia*, *Danaea*, *Eupodium*), the Paleotropics (e.g. *Christensenia*, *Ptisana*), or with a pantropical distribution, such as *Angiopteris* (this taxon was originally paleotropical, but was later introduced and naturalized in the Neotropics) (Murdock, 2008b). Using the extant representatives of the family as modern analogs for Marattiaceae indet., it is suggested that during the deposition of the Cerro Negro Formation, the climatic conditions were similar to those ones of modern tropical/subtropical regions. On the other hand, the Antarctic taxon may represent a divergent lineage of Marattiaceae, more primitive than the extant recognized genera, which may have been able to inhabit non-tropical environments. However, the characteristics of the fossil studied here suggest that it is part of the Marattiales crown group, and probably closely related to *Ptisana* or *Marattia*. Consequently, the climatic requirements of the Antarctic taxon probably were similar to the requirements of extant representatives of the group. Fossil Marattiales comparable with *Marattia* and *Ptisana* also seem to show similar climatic distributions (Escapa et al., 2015), adding support to this proposal.

5. Conclusions

Fertile remains of unambiguous Marattialean ferns are described from the Cerro Negro Formation. This record represents one of the few Cretaceous reports for Marattiaceae, an otherwise well-represented clade in Carboniferous–Jurassic strata (Hu et al., 2006). Comparisons with extant and extinct taxa suggest that the Antarctic fossil is closely related to the species included in the recently erected genus *Ptisana*, and to *Marattia* s.s. The climatic requirements of extant representatives of Marattiaceae suggest that the Livingston Island examples inhabited an area with a tropical/subtropical climate, supporting previous climatic inferences made for this Antarctic region during the Early Cretaceous.

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References

Askin, R.A., 1983. Tithonian (uppermost Jurassic)–Barremian (Lower Cretaceous) spores, pollen and microplankton from the South Shetland Islands, Antarctica. In: Oliver, R.L., James, P.R., Jago, J.B. (Eds.), Antarctic Earth Science: Fourth International Symposium (1982). Cambridge Univ. Press, New York, pp. 295–297.

Barthel, M., Reichel, W., Weiss, H.-J., 1995. "Madensteine" in Sachsen. Neue Funde von *Scolecopteris elegans* in der Typuslokalität. Abh. Staatl. Mus. Mineral. Geol. Dresden 41, 117–135.

Bystriakova, N., Schneider, H., Coomes, D., 2011. Evolution of the climatic niche in scaly tree ferns (Cyatheaceae, Polypodiopsida). Bot. J. Linn. Soc. 165, 1–19.

Camus, J.M., 1990. Marattiaceae. In: Kramer, K.U., Green, P.S. (Eds.), The Families and Genera of Vascular PlantsPteridophytes and Gymnosperms vol. 1. Springer-Verlag, Berlin, pp. 174–180.

Cantrill, D.J., 1998. Early Cretaceous fern foliage referable to Lophosoriaceae from President Head, Snow Island, Antarctica. Alcheringa 22, 241–258.

Cantrill, D.J., 2000. A Cretaceous (Aptian) flora from President Head, Snow Island, Antarctica. Palaeontogr. Abt. B 253, 153–191.

Césari, S.N., 2006. Aptian ferns with in situ spores from the South Shetland Islands, Antarctica. Rev. Palaeobot. Palynol. 138, 227–238.

Césari, S., Parica, C., Remesal, M., Salani, F., 1999. Paleoflora del Cretácico Inferior de península Byers, Islas Shetland del Sur, Antártida. Ameghiniana 36, 3–22.

Césari, S.N., Remesal, M., Parica, C., 2001. Ferns: a palaeoclimatic significant component of the Cretaceous flora from Livingston Island, Antarctica. Asociación Paleontológica Argentina. Publicación Especial 7 (7° International Symposium on Mesozoic Terrestrial Ecosystems. pp. 45–50.
Collinson, M., 2001. Cainozoic ferns and their distribution. Brittonia 53, 173–235.
Delevoryas, T., Taylor, T., Taylor, E., 1992. A marattialean fern from the Triassic of Antarctica. Rev. Palaeobot. Palynol. 74, 101–107.
Escapa, I.H., Bomfleur, B., Cúneo, N.R., Scasso, R., 2015. A new marattiaceous fern from the Lower Jurassic of Patagonia (Argentina): the renaissance of *Marattiopsis*. J. Syst. Palaeontol. 13 (8), 677–689.
He, X.Y., Wang, S.J., Hilton, J., Zhou, Y.L., 2006. A new species of the marattialean fern *Scolecopteris* (Zenker) Millay from the uppermost Permian of Guizhou Province, south-western China. Bot. J. Linn. Soc. 151 (2), 279–288.
Hill, C.R., Camus, J.M., 1986. Evolutionary cladistics of marattealean ferns. Bull. Br. Mus. Nat. Hist. (Bot.) 14 (4), 219–300.
Hilton, J., Wang, S.-J., Galtier, J., Glasspool, I.J., Stevens, L., 2004. A Late Permian permineralized plant assemblage in volcaniclastic tuffs from the Xuanwei Formation, Guizhou Province, China. Geol. Mag. 141, 661–674.
Hu, S., Dilcher, D., Schneider, H., Jarzeny, D.M., 2006. Eusporangiate ferns from the Dakota Formation, Minnesota, U.S.A. Int. J. Plant Sci. 167 (3), 579–589.
Kvaček, J., 2014. *Marattiopsis vodrazkae* sp. nov. (Marattiaceae) from the Campanian of the Hidden Lake Formation, James Ross Island, Antarctica. Acta Mus. Nat. Pragae Ser. B Hist. Nat. 70 (3–4), 211–218.
Lesnikowska, A.D., Millay, M.A., 1985. Studies of Paleozoic Marattialeans: new species of *Scolecopteris* (Marattiales) from the Pennsylvanian of North America. Am. J. Bot. 72, 649–685.
Liu, Z.H., Li, C.S., Hilton, J., 2000. *Zhutheca* Liu, Li et Hilton gen. nov., the fertile pinnules of *Fascipteris densata* Gu et Zhi and their significance in marattialean evolution. Rev. Palaeobot. Palynol. 109, 149–160.
Mamay, S.H., 1950. Some American Carboniferous fern fructifications. Ann. Mo. Bot. Gard. 37, 409–477.
Millay, M.A., 1978. Studies of Paleozoic marattialeans: the morphology and phylogenetic position of *Eoangiopteris goodii* sp. n. Am. J. Bot. 65, 577–583.
Millay, M.A., 1979. Studies of Paleozoic marattialeans: a monograph of the American species of *Scolecopteris*. Palaeontogr. Abt. B 169, 1–69.
Millay, M.A., 1982. Studies of Paleozoic marattialeans: an early Pennsylvanian species of the fertile fern *Scolecopteris*. Am. J. Bot. 69, 728–733.
Millay, M.A., 1997. A review of permineralized Euroamerican Carboniferous tree ferns. Rev. Palaeobot. Palynol. 95, 191–209.
Murdock, A.G., 2008a. Phylogeny of marattioid ferns (Marattiaceae): inferring a root in the absence of a closely related outgroup. Am. J. Bot. 95, 626–641.
Murdock, A.G., 2008b. A taxonomic revision of the eusporangiate fern family Marattiaceae, with description of a new genus *Ptisana*. Taxon 57, 737–755.
Murdock, A.G., Reveal, J.L., Doweld, A., 2006. Proposal to conserve Marattiaceae against Danaeaceae (Pteridophyta). Taxon 55, 1040–1042.
Párica, C.A., Salani, F.M., Vera, E.I., Remesal, M., Césari, S.N., 2007. Geología de la Formación Cerro Negro (Cretácico) en Isla Livingston: aportes a su geocronología y contenido paleontológico. Rev. Asoc. Geol. Argent. 62, 553–567.
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.
Torres, T., Barale, G., Thevernard, F., Philippe, M., Galleguillos, H., 1997. Morfología y sistemática de la flora del Cretácico Inferior de President Head, Isla Snow, archipiélago de las Shetland del Sur, Antártica. Inst. Antárt. Chil. Ser. Cient. 7, 59–86.
Vera, E.I., 2007. A new species of *Ashicaulis* Tidwell (Osmundaceae) from aptian strata of Livingston Island, Antarctica. Cretac. Res. 28, 500–508.
Vera, E.I., 2009. *Alienopteris livingstonensis* gen. et sp. nov., enigmatic petrified tree fern stem (Cyatheales) from the Aptian Cerro Negro Formation, Antarctica. Cretac. Res. 30, 401–410.
Vera, E.I., 2010. A new specimen of *Millerocaulis* (Osmundales: Osmundaceae) from the Cerro Negro Formation (Lower Cretaceous), Antarctica. Rev. Museo Argent. Cienc. Nat. "Bernardino Rivadavia" Nueva Ser. 12 (1), 41–46.
Vera, E.I., 2012. *Millerocaulis tekelili* sp. nov., new species of osmundalean fern from the Aptian Cerro Negro Formation (Antarctica). Alcheringa 36, 35–45.
Vera, E.I., 2013. New cyathealean tree fern, *Yavanna chimaerica* gen. et sp. nov., from the Early Cretaceous of Livingston Island, Antarctica. Cretac. Res. 44, 214–222.
Vera, E.I., 2015. Further evidence supporting high diversity of cyathealean tree ferns in the Early Cretaceous of Antarctica. Cretac. Res. 56, 141–154.
Weiss, H.J., 2002. Beobachtungen zur Variabilität der Synangien des "Madenfarns". Veröff. Mus. Naturkunde Chemnitz 25, 57–62.