

New species of osmundaceous fertile leaves from the upper Triassic of Argentina

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ABSTRACT. A new species of *Osmundopsis* Harris is described based on several impression-compression fossils from the upper section of the Potrerillos Formation (Uspallata Group) at Cerro Cacheuta Hill, Mendoza Province, Argentina. *Osmundopsis zunigai* sp. nov. is characterized by having fertile pinnae with a slender striate rachis, bearing widely separate, opposite to subopposite short falcate pinnules with an entire margin, rounded apex, and a partially reduced lamina. The pinnules bear sporangia loosely disposed in clusters of four or five on the abaxial side. The sporangia are wedge- to heart-shaped, shortly stalked, with cells of the apical region thickened, and have a vertical dehiscence slit. The spores are trilete and laevigate. This is the first record of *Osmundopsis* in the Triassic of Argentina. The mutual occurrence or co-preservation of *Osmundopsis zunigai* sp. nov. with sterile fronds of *Cladophlebis kurtzi* suggests the possibility that these species formed part of a dimorphic bipinnate frond. The diversity and geographic extent of fertile leaves of the *Osmunda* lineage in the early Late Triassic, with records in South Africa and Antarctica and now with this new taxon, support the idea of a moist mesothermal climatic belt in southern Gondwana.

KEYWORDS: *Osmundopsis*, Osmundaceae, Carnian, Potrerillos Formation, Mendoza Province

INTRODUCTION

Osmundales is an order of leptosporangiate ferns which originated in the Late Carboniferous and diversified during the Triassic (Phipps et al. 1998, Pryer et al. 2004). They are characterized by distinctive rhizome anatomy, with an ectophloic siphonostele composed of a ring of discrete xylem strands, leaves dimorphic or with fertile portions dissimilar to sterile ones, sporangia without a definite soral-type organization, and sporangia with a lateral annulus, a character that differs from all other sporangial morphologies of leptosporangiate ferns (Gifford & Foster 1989, Smith et al. 2006).

The extant representatives comprise about 20 species currently classified across four genera: *Osmunda* L., *Osmundastrum* C.Presl, *Leptopteris* C.Presl and *Todea* Bernh. (Metzgar

et al. 2008, Christenhusz et al. 2011). As compared to its limited modern diversity, Osmundales has a rich and diverse fossil record, including more than 150 species and over 25 genera (Taylor & Taylor 1993). The fossil taxa consist of permineralized stems (Gould 1970, Miller 1971) and impression-compressions of sterile and fertile leaves (Taylor et al. 2009, Naugolnykh 2002). During the Mesozoic the family reached an extensive distribution in both hemispheres. For instance, the fossil record of fertile fronds begins in the Upper Permian with the occurrence of three species of *Todites* from Russia (Naugolnykh 2002).

In Argentina the Triassic record of Osmundales comprises several species of the sterile frond genus *Cladophlebis* Brogn. emend. Frenguelli, one species of the fertile frond genus *Todites* Seward, and three species of

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the permineralized stem genus *Millerocaulis* Erasmus *ex* Tidwell *emend.* Vera (Herbst 1994, 1995, 2006). Here we document fertile leaves from the Potrerillos Formation that constitute the first record of *Osmundopsis* Harris in the Triassic of Argentina.

GEOLOGICAL SETTING

The most stratigraphically complete Triassic basins of southwestern Gondwana are located near the Proto-Pacific margin of the South American Plate. They are narrow and elongate NW–SE depressions (Charrier 1979,

Spalletti et al. 2003) filled by continental strata in Argentina; in Chile they are filled by marine to deltaic, littoral and in some cases paralic transitioning to continental strata in Chile. The largest continental Triassic depocenter is the Cuyo Basin, floored on the Choiyoi Group, an intraplate Permian–Triassic plutonic–volcanic complex. It covers an area of 60 000 km² and includes several depocenters filled with siliciclastic continental deposits (Stipanovic 2001).

One of the thickest exposed sections of the Cuyo Basin situated in northern Mendoza Province crops out at Cacheuta Hill (Fig. 1). The Triassic units exposed on the southern

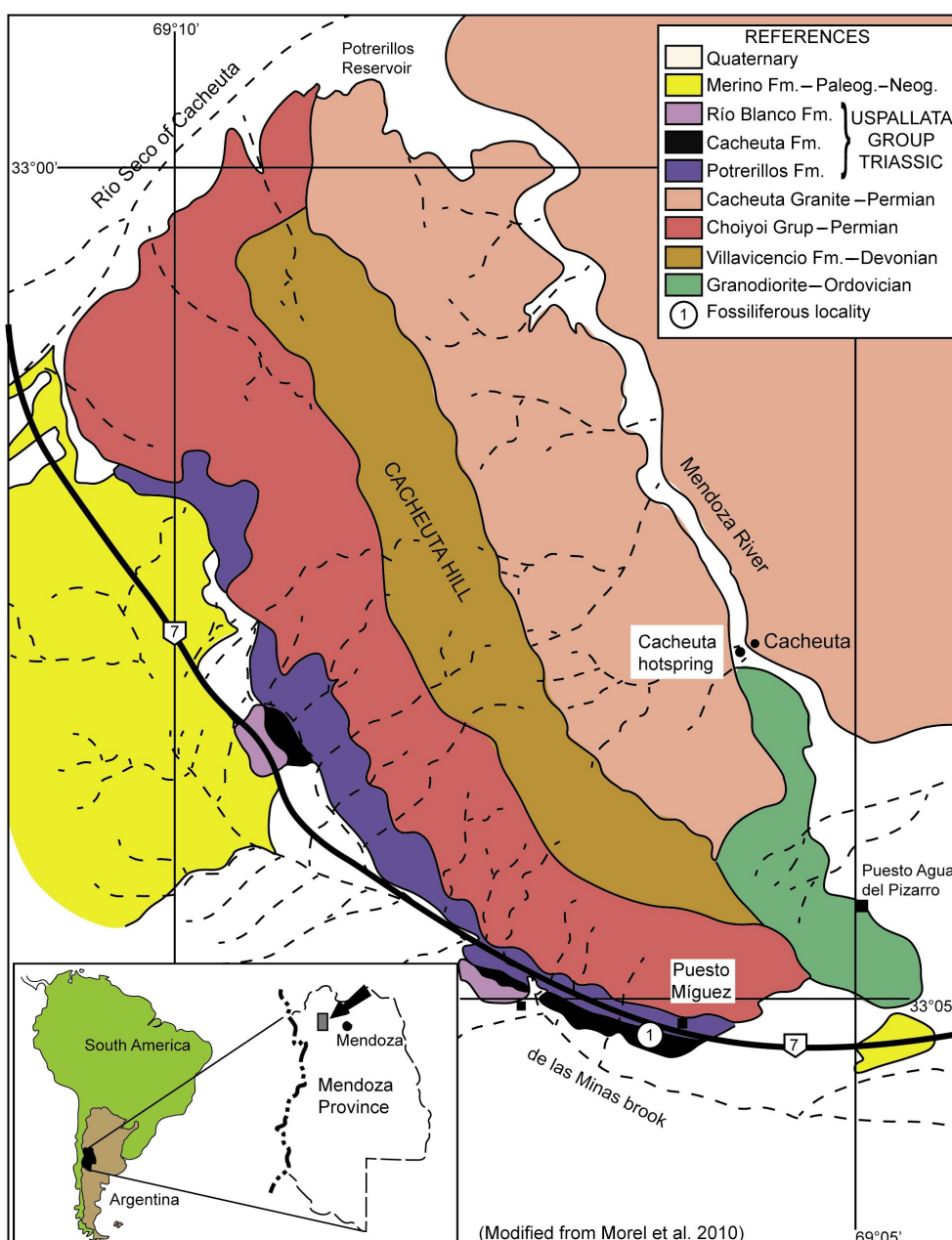


Fig. 1. Location and geology of study area in Mendoza Province, Argentina

flank of Cacheuta Hill form part of the upper section of the Uspallata Group (Groeber 1946), unconformably resting on the Choiyoi Group. The Triassic succession at Cacheuta Hills deformed into a homocline, with a dip direction towards the southwest (20–40°). In this area the Uspallata Group exposure comprises the Potrerillos Formation (upper section), and the Cacheuta and Río Blanco formations.

The exposed portion of the Potrerillos Formation at the Puesto Míguez locality reaches a thickness of 125 m. Its lithological characteristics and sedimentary facies were studied by Morel (1994) and Morel et al. (2010, 2011). It is characterized by net dominance of tabular and lenticular beds of yellowish, greenish grey and blackish, cross-stratified sandstones, subordinate laminated grey mudstones, and a minor proportion of conglomerates which are more abundant at the base of the unit. This succession was interpreted as facies generated in fluvial environments with distributary channels, wide interdistributary floodplains, and recurrent overflow channel episodes (Morel 1994).

PALAEONTOLOGICAL BACKGROUND

Cacheuta Hill is a well-known Triassic plant fossil site (Zuber 1889, Kurtz 1921, Frenguelli 1948, Jain & Delevoryas 1967); it was reviewed by Stipanovic (1983), Stipanovic et al. (1996), Kokogian et al. (2000), Artabe et al. (2001) and Stipanovic & Marsicano (2002).

Previous studies by the present authors (E.M., D.G.) included stratigraphic, sedimentological and palaeoenvironmental analyses (Morel 1994), as well as palaeobotanical and palaeoecological studies (Artabe et al. 2007, Morel et al. 2010, 2011) of the Potrerillos, Cacheuta and Río Blanco formations. Artabe et al. (2007) reported and reconstructed a petrified forest of corystosperms (*Elchaxylon*) with specimens in life position. Subsequently, Morel et al. (2010, 2011) made a systematic study of plant remains preserved as impression-compressions.

Three plant-bearing strata were recognized in the Potrerillos Formation at Cacheuta Hill, and labelled EP I, EP II and EP III. The palaeoflora recovered from these strata is diverse and is characterized by an abundance of ferns, corystosperms and ginkgoaleans, besides the

presence of conifers, peltasperms, sphenophytes and lycophytes (Morel et al. 2010, 2011). Although abundant, fern diversity is low, with representation limited to *Asterotheca* Presl. (Marattiales), *Coniopteris* Brongn. (Cyatheales) and *Cladophlebis* (Osmundales).

The plant assemblage has been referred to the early Late Triassic (=Carnian) BNP (*Yabeiella brackebuschiana*, *Scytophyllum neuburgianum*, *Rhexoxylon piatnitzkyi*) Biozone and the Cortaderitian Stage of the chronostratigraphical scheme of Argentina (Spalletti et al. 1999, Morel et al. 2003). Detailed palynological studies in the Puesto Míguez locality assigned the preserved microfloristic association to the Carnian and the Ipswich Subprovince (Rojo & Zavattieri 2005, Zavattieri & Rojo 2005).

With respect to the age of Potrerillos Formation, the lower section of this unit was dated at the Cerro Bayo and Cerro Cocodrilo localities, 10 km distant from the Puesto Míguez fossiliferous locality, resulting in a U-Pb SHRIMP age of 230±2.3 Ma (Spalletti et al. 2008). Thus, the upper section of Potrerillos Formation can be considered Late Triassic in age (Spalletti et al. 2008).

MATERIAL AND METHODS

The studied fossil plants are preserved as impression-compressions and come from the plant-bearing stratum EP II (“estrato plantífero II”) of the Potrerillos Formation at the locality named Puesto Míguez (69°06'34"W and 33°05'04"S) at Cacheuta Hill (Fig. 1). This site was previously known as “behind the former YPF administration building” (Frenguelli 1948). Fossils were collected by two authors of this paper (E.M., D.G.) in the 1980s. All the studied plant fossils are held in the Palaeobotanical Collection of the Museo de La Plata under the acronym LPPB.

A Leica M50 stereoscopic microscope was used for study of the specimens. They were photographed with a Leica DC 150 system, Canon Powershot S40 and Canon T3i digital cameras. Drawings were made with a Wacom Intuos CTL-4100 graphical tablet. Leaf fragments (sporangia and spores) were also observed under SEM (JEOL JSM-6360 LV) at the microscopy facility of the Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Descriptions follow the terminology of Font Quer (1982) and Tryon (1960). Dimensions of morphological elements were averaged from 30 measurements in each case.

For the nomenclatural treatment, the International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code, Turland et al. 2018) was used. The suprageneric classification follows Smith et al. (2006).

SYSTEMATICS

Class POLYPODIOPSIDA

Order OSMUNDALES

Family OSMUNDACEAE

Genus: *Osmundopsis* Harris 1931 emend.
Harris 1961Type species. *Osmundopsis sturii*
(Raciborsky) Harris 1931*Osmundopsis zunigai* Coturel, Bodnar,
Morel, Ganuza, Sagasti and Beltrán **sp. nov.**

Plates 1, 2

Etymology. The specific name is dedicated to Lic. Adolfo Zuñiga, who was Curator of the Palaeobotanical Collection between 1988 and 2015.

Holotype. LPPB 11809, here designated, Pl. 1 figs 1, 4, 5; two fragments of fertile pinnae and a small fragment of a pinnae attached to the main rachis.

Paratype. LPPB 11812, Pl. 1 fig. 3, Pl. 2 figs 1–8.

Additional specimens. LPPB 11800, LPPB 11810.

Repository. Palaeobotany Division at La Plata Museum under the acronym LPPB.

Type locality. Puesto Míguez locality, Cacheuta Hill, Mendoza Province, Argentina.

Type horizon. EPII, Potrerillos Formation, Carnian.

Diagnosis. Fertile bipinnate leaf with striated main rachis. Pinnae with a slender, longitudinally striated secondary rachis, bearing widely separate, opposite to subopposite pinnules inserted at acute to right angles. Pinnules short, falcate, attached along the entire width of the base, with entire margins and rounded apex, and a reduced lamina showing a conspicuous midvein. Sporangia loosely disposed in clusters of four or five on the abaxial side. Sporangia wedge- to heart-shaped, shortly stalked, with cells of the apical region thickened, and a vertical dehiscence slit. Spores laevigate trilete.

Description. Fragment of the main rachis of a bipinnate frond, with the base of two secondary rachises and one pinnule (Pl. 1, fig. 1). Main rachis straight, up to 72 mm long and 4.7 mm wide. The distance between two pinna rachises from one side is 28 mm (LPPB 11809a). Five fragments of pinnae of bipinnate leaves up to 21 mm long and 8.5 mm wide (LPPB 11809b,c; LPPB 11800, 11810, 11812; Pl. 1, figs 2, 3, 4). Fertile pinnae have a striated and straight secondary rachis up to 1 mm wide, tapering towards the pinnae apices (Pl. 1, fig. 3, 4). Pinnae are imparipinnate with a very small terminal pinnule measuring 1 mm long and 1 mm wide, and at least eight pairs of pinnules (Pl. 1, fig. 4). Fertile pinnules are oppositely to suboppositely inserted on the secondary rachis at 90° in the proximal part and at 60–70° in the distal part of the pinnae (Pl. 1, fig. 4). Pinnules are short, falcate, attached along the entire width of the base, with entire margin and rounded apex, and a few have reduced laminae; up to 6 mm long in the proximal zone, shortening towards the apical zone. (Pl. 1, figs 3, 4, 5). There is a regular 2–3 mm separation at the insertion of the pinnules on each side of the pinnae, which do not overlap (Pl. 1, figs 4, 5). The basisopic side of the pinnules is slightly decurrent (Pl. 1, fig. 5; Pl. 2, figs 1, 3). When preserved, the venation consists of a thick midvein (Pl. 1, figs 4, 5; Pl. 2, fig. 1). The sporangia are arranged in clusters of four or five on the abaxial side of the pinnule sporangia in a peripheral position. The sporangia are wedge- or heart-shaped, short-stalked, and 0.3–0.4 mm in diameter (Pl. 1, figs 4, 5; Pl. 2, fig. 1). Most of the sporangia are closed. The cells of the apical region are thickened, and the sporangia have a vertical dehiscence slit (Pl. 1, figs 4, 5; Pl. 2, fig. 1). The spores are trilete, laevigate, and 15–20 µm in diameter (Pl. 2, fig. 8). The size and location (inside the sporangia) of the spores suggests that they are immature.

Sterile pinnae are unknown, but these fertile pinnae were found closely associated with sterile fronds of *Cladophlebis* in the same slabs (Pl. 3, figs 1, 2; see Discussion).

Generic assignment and comparisons. The remains studied here agree with the diagnosis of *Osmundopsis*, originally published by Harris (1931) and afterwards emended by the same author (Harris 1961). *Osmundopsis* includes: fossil dimorphic fern leaves with the sterile leaves bipinnate of *Cladophlebis*-type; fertile leaves bipinnate or

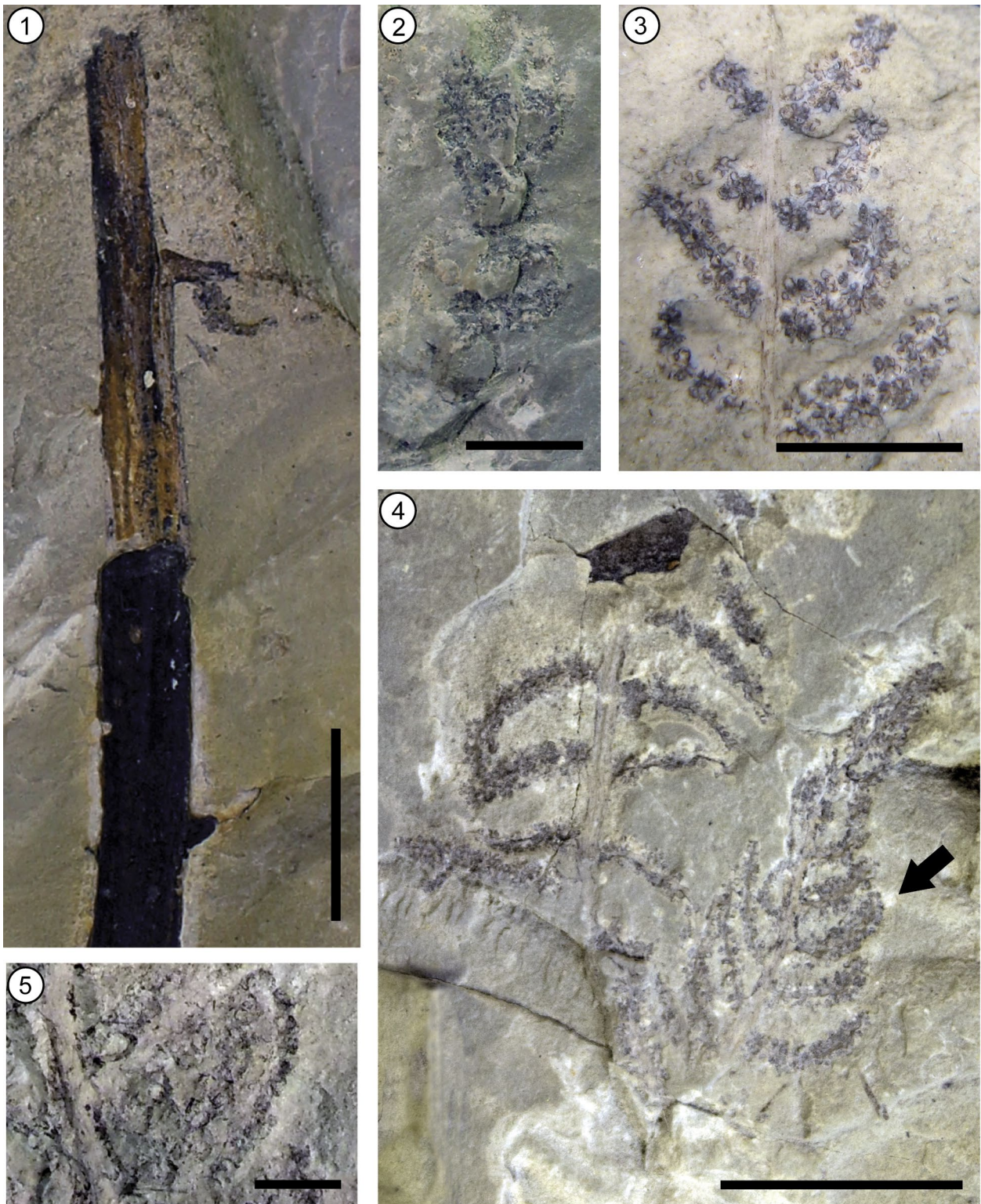


Plate 1. *Osmundopsis zunigai* sp. nov. 1. Main rachis with basal portion of the pinnae preserved, the upper with fertile pinnae, LPPB 11809a, scale bar – 10 mm; 2. Fragment of fertile pinnae, LPPB 11810, scale bar – 5 mm; 3. *O. zunigai*. Fragment of fertile pinnae, LPPB 11812, scale bar – 5 mm; 4. Two fragments of fertile pinnae with attached sporangia, arrow points to pinnule detailed in Figure 5, LPPB 11809b and c, scale bar – 10 mm; 5. Detail of figure 4, LPPB 11809c, scale bar – 1 mm

tripinnate, with their lamina strongly reduced (Escapa & Cúneo 2012) or absent with ultimate pinnulae filiform (Harris 1961); sporangia grouped, each sporangium pyriform, with the whole apical region of the wall thickened,

a dehiscence by the longitudinal stomium, and spores rounded and having triradiate scars.

Although more than 20 species of *Osmundopsis* have been described since the genus was established, several are based on fragmentary

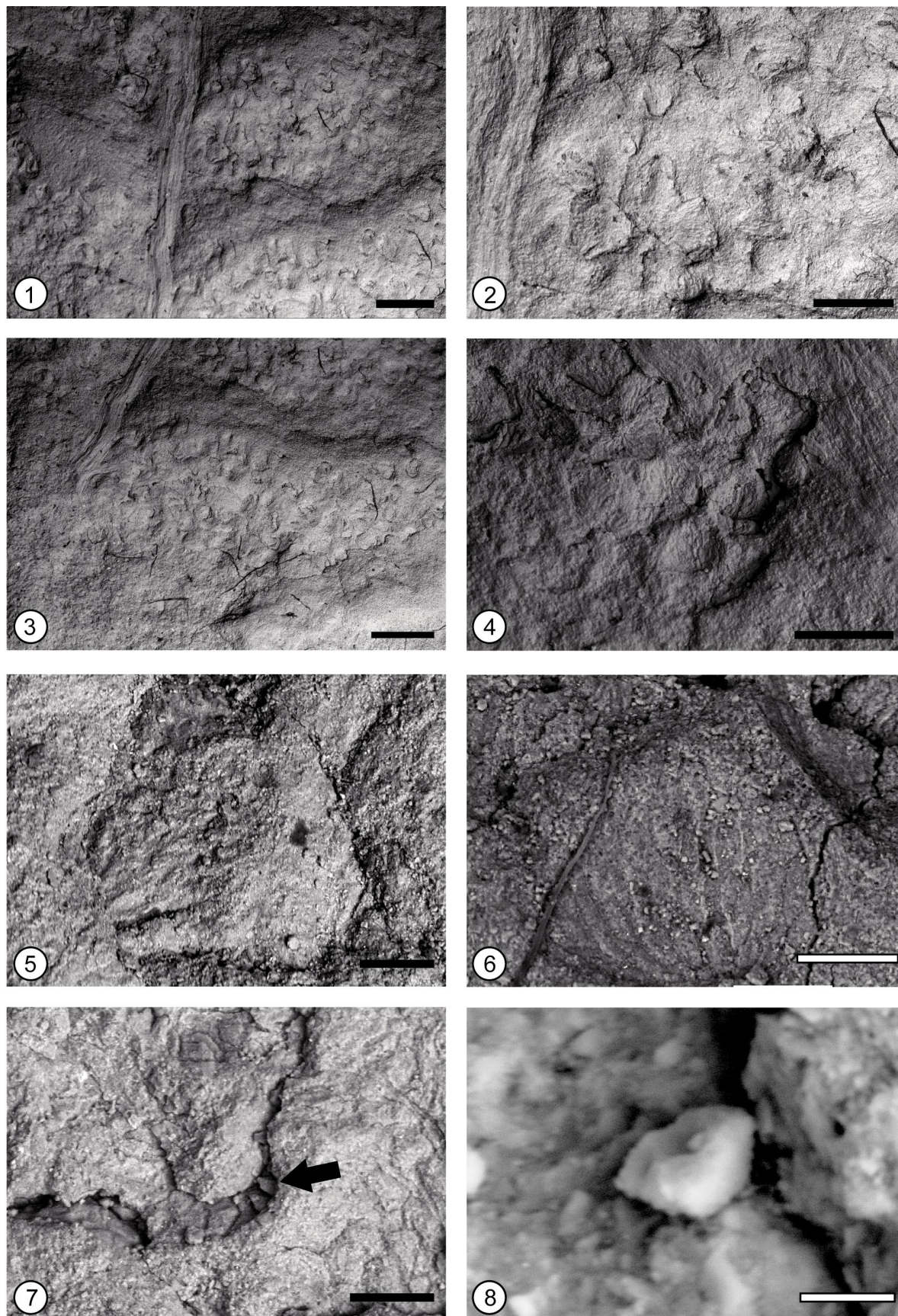


Plate 2. *Osmundopsis zunigai* sp. nov., LPPB 11812. **1, 3.** Pinnula showing arrangement of sporangia in clusters along reduced lamina, scale bar – 1 mm ss; **2, 4.** Clusters of sporangia, 2 is detail of 1, scale bar – 0.5 mm; **5.** Heart-shaped sporangium with distal thickened cells, scale bar – 100 μ m; **6.** External surface of sporangium wall with preserved detail of cells, scale bar – 100 μ m; **7.** Broken sporangium showing thickening of cells from dehiscence ring (arrow), scale bar – 100 μ m; **8.** Trilete spore, immature, scale bar – 10 μ m

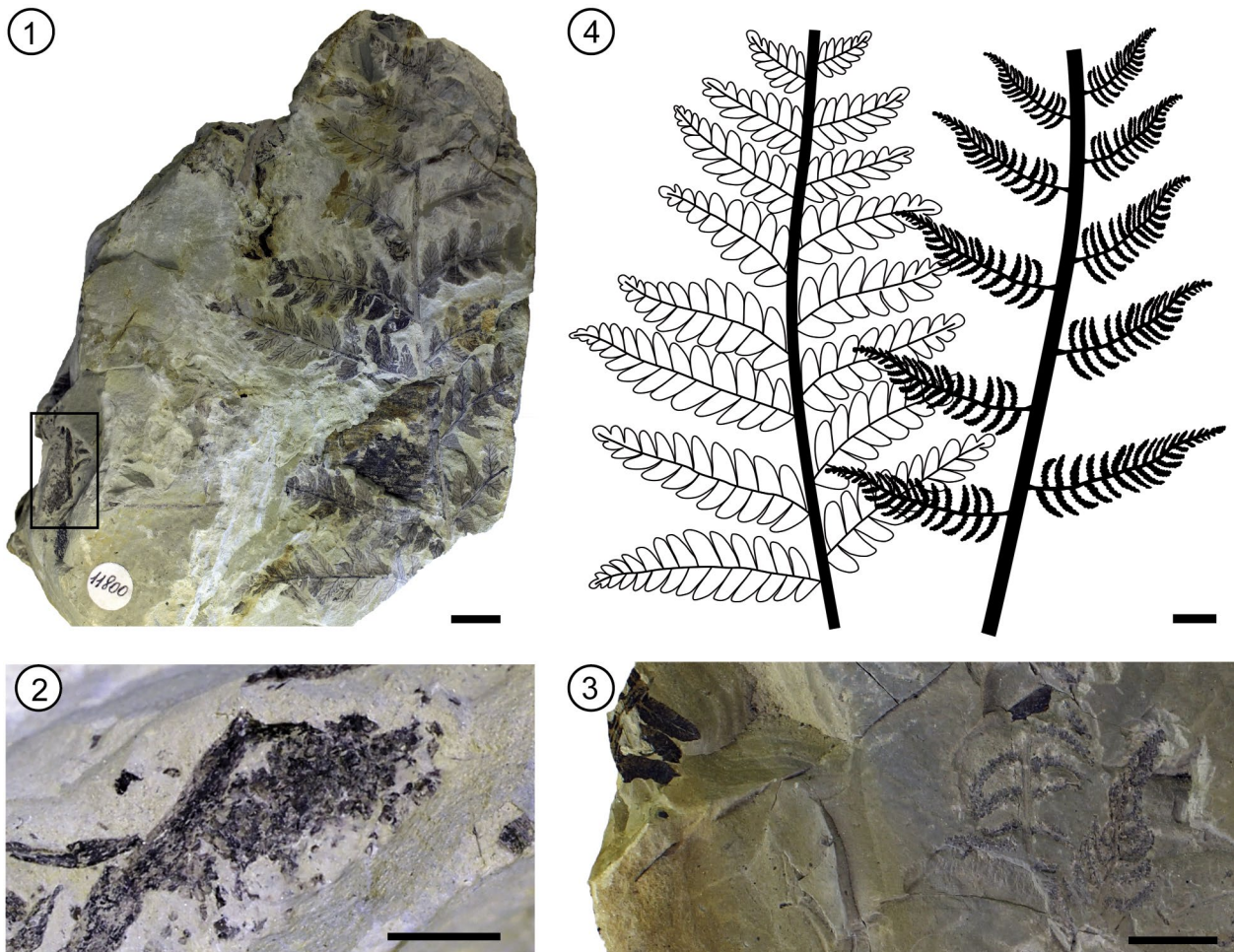


Plate 3. Reconstruction of *Osmundopsis zunigai* sp. nov. with *Cladophlebis kurtzii* sterile leaves. 1. Frond of *Cladophlebis kurtzii* in same slab of fragment of fertile pinnule, LPPB 11800, scale bar – 10 mm; 2. Detail of the fertile pinnule with sporangia in clusters, LPPB 11800, scale bar – 2.5 mm; 3. Associated pinnae of *O. zunigai* sp. nov. with pinnulae of *C. kurtzii*, LPPB 11809, scale bar – 10 mm; 4. Proposed reconstruction

material or uncertain characters, and others are used for dispersed spores (see supplementary material). For example, *Osmundopsis microcarpa* (Raciborski) Harris 1931 is represented by a fragment of a pinnule with unclear morphology (Miller 1971) and *O. prigorovskii* Kryštofovich et Prynada 1933 would correspond to *Todites* (Harris 1961). According to Van Konijnenburg-van Cittert (1996), these two species, together with *O. prynadae* Delle 1967, are very similar to *O. sturii* and probably are synonymous. On the other hand, *Osmundopsis petiolaris* Anderson et Anderson 2008 and *O. racemosus* Anderson et Anderson 2008 from the Triassic of South Africa are both regarded as putative species of the genus because the sporangia are probably arranged in synangia, but they are still included in our analysis because of their Gondwanan provenance. In this manner we recognise a total of eight species of leaves certainly belonging to *Osmundopsis*, and two with doubts (Tab. 1).

In a comparison with the better-known species of *Osmundopsis*, *O. zunigai* sp. nov. shows similarities with *O. scalaris* Holmes 2001 (Triassic, Australia), *O. sturii* (Raciborsky) Harris 1931 (Jurassic, Eurasia) and *O. rafaelii* Escapa et Cúneo 2012 (Jurassic, Argentina), due to the partial reduction of the pinnule lamina, the pinnule insertion, and its dimensions within the measurable ranges of pinnule and sporangia size (Tab. 1). However, *O. zunigai* sp. nov. differs from *O. scalaris* in the insertion angle of the pinnules, which is almost 90° and is uniform along the second-order rachis in the former, while in the latter it is variable (90° in the proximal part and at 60–70° in the distal part). *O. zunigai* sp. nov. differs from *Osmundopsis sturii* in the number of sporangia per cluster, being up to 20 in the Eurasian taxon and four to five in the new species. Moreover, *O. zunigai* sp. nov. differs from *O. scalaris* and *O. sturii* in having shorter pinnules, smaller sporangia and

Table 1. Comparison of *Osmundopsis* species

Species	Precedence	Distance between pinnules (mm)	Fertile pinnule				Sporangia		Mean spore diameter (µm)	Width of sterile pinnule laminae (mm)
			Insertion angle	Lamina	Shape	Length (mm)	Number per cluster	Size (µm)		
<i>Osmundopsis scalaris</i> Holmes 2001	Middle Triassic, Australia	1–3	80–90°	partially reduced	oblong	6–12	?	1000	3–4	
<i>Osmundopsis botryoides</i> Anderson et Anderson 2008	Late Triassic, South Africa	1.5–2	60–70°	completely reduced	?	1.2–2.5	?	500	?	
? <i>Osmundopsis petiolaris</i> Anderson et Anderson 2008	Late Triassic, South Africa	2.5–4	45–70°	partially reduced	petiolate, lanceolate	3–5	?	300–500	?	
? <i>Osmundopsis racemosus</i> Anderson et Anderson 2008	Late Triassic, South Africa	2–4	60–80°	partially reduced	sessile constricted at base, obovate	2.5–5	?	100–1000	?	
<i>Osmunda claytoniites</i> Phipps et al. 1998 ^b	Late Triassic, Antarctica	?	90°	completely reduced	?	10–13	?	300–375	Up to 5	
<i>Osmundopsis zuingai</i> sp. nov. Coturel et al.	Late Triassic, Argentina	2–3	90–60°	partially reduced (2–2.5 mm width)	attached along the entire width of the base, falcate	up to 6		400×300	3–7 ^c	
<i>Osmundopsis plectrophora</i> Harris 1931	Early Jurassic, Greenland	3	45°	completely reduced	filiform	>20		800×500	7–9	
<i>Osmundopsis rafaëlii</i> Escapa et Cúneo 2012	Early Jurassic, Argentina	4–5	60–70°	partially reduced (3.5 mm width)	falcate	up to 10	?	500×300	Up to 8	
<i>Osmundopsis nipponica</i> Kimura et Tsujii 1980	Early Jurassic, Japan	1.5	90°	completely reduced	filiform	7.5–8	?	400	?	
<i>Osmundopsis sturii</i> (Raciborski) Harris 1931 emend. Harris 1961	Early–Middle Jurassic, Eurasia	2–3	70–85°	partially to completely reduced	filiform to falcate	>10		600×400	5–7 ^d	
<i>Osmundopsis hillii</i> Van Konijnenburg-van Cittert 1996	Middle Jurassic, England	3–5	80–90°	completely reduced	filiform	up to 5		500×300	1–2 ^d	

^a *O. petiolaris* and *O. racemosus* probably have sporangia arranged in synangia, thus the assignment to *Osmundopsis* is equivocal.

^b Although *Osmunda claytoniites* was not included in *Osmundopsis*, the characteristics of the species agree with the generic diagnosis.

^c *Osmundopsis zuingai* sp. nov. is proposed here to be associated with *Cladophlebis hurtzi*.

^d Van Konijnenburg-van Cittert (1996) suggested that *Cladophlebis harrissii* was sterile foliage of *O. hillii*, and *C. denticulata* was possibly sterile foliage of *O. sturii*. References: Holmes (2001), Schweitzer et al. (1997)

less reduced pinnule lamina. Of the putative South African species, we found that *O. petiolaris* is the one more clearly assignable to the genus *Osmundopsis*, and *O. zunigai* sp. nov. lacks its distinctive petiole. Finally, *O. zunigai* most closely resembles *Osmundopsis rafaellii* Escapa et Cúneo 2012 from the Lower Jurassic of Chubut Province, Argentina (Tab. 1), but it differs from *O. rafaellii* based on the longer pinnulae and less reduced laminae in the latter. These differences are the basis for our decision to create the new species *Osmundopsis zunigai* sp. nov.

DISCUSSION

SYSTEMATIC AFFINITIES

Fertile fronds of Osmundaceae from the Mesozoic are generally assigned to *Todites* or *Osmundopsis*; these fossil genera were erected to include material that did not have enough characters to be included in extant taxa (e.g. *Todea* and *Osmunda*, Escapa & Cuneo 2012). Leaves of *Todites* have entire pinnulae with sporangia on both sides of the midvein and over the lateral veins; the sporangia are big and have a much reduced stalk. *Todites* appeared during the Late Triassic (Jung 1972, Kon'no 1972, Wang et al. 2005) and may be affiliated with the *Todea/Leptopteris* lineage (Escapa & Cuneo 2012). *Osmundopsis* fronds can be recognized as having pinnulae with a strongly reduced or absent lamina and small clustered sporangia. The sterile and fertile dimorphic or hemidimorphic fronds, the absence of a lamina or the presence of a strongly reduced one in the fertile pinnules, and sporangia arranged in clusters, have been interpreted to indicate affinities of *Osmundopsis* with living and fossil *Osmunda* and *Osmundastrum* species.

RECONSTRUCTION

Sterile osmundaceous leaves are normally included in the genus *Cladophlebis* Brongniart 1849. However, the morphology of *Cladophlebis* is highly homoplastic and has also been linked to other fern families such as Cyatheaceae and Schizaeaceae; thus it should not be considered exclusive to any of these families in the absence of information about reproductive morphology (Halle 1913). Despite this, close association of

Cladophlebis/Osmundopsis was found in the Early Jurassic of Argentina (Escapa & Cuneo 2012) and in the Middle Jurassic of England (Harris 1961, Van Konijnenburg-van Cittert 1996).

In fossiliferous stratum EPII of the Potrerillos Formation we have not found specimens of *Osmundopsis zunigai* sp. nov. in organic connection with sterile pinnae. Nevertheless, specimens LPPB 11800 and LPPB11809 are closely associated in the same slab with sterile fronds of genus *Cladophlebis kurtzi* Frenguelli 1947 (Pl. 3.1, 2), characterized by having bipinnate leaves with falcate pinnules and dichotomizing lateral veins (Herbst 1971). This species (Pl. 3.2) is similar to *Osmundopsis zunigai* sp. nov. due to the pinnule shape (falcate with entire margins) and size.

Although we have not discovered sterile pinnae of *C. kurtzi* attached to fertile pinna of *O. zunigai* sp. nov., we suggest a hypothetical reconstruction following the proposal of Anderson and Anderson (1985). These authors proposed the following criteria for linking two or more plant organs (from most reliable to least reliable): organic attachment, morphological similarity, kindred reinforcement, and mutual occurrence. In the case of *C. kurtzi* and *O. zunigai* sp. nov. the three last criteria are fulfilled, since they share the shape and size of the pinnules (“morphological similarity”), both genera were linked in other reconstructions (see Harris 1961, van Konijnenburg-van Cittert 1996, Escapa & Cuneo 2012) and were assigned to the same family (“kindred reinforcement”), and the two taxa were found in the same fossiliferous stratum (“mutual occurrence”) in the same rock a few centimetres apart. On the basis of general morphology we suggest that they constitute a dimorphic frond with fertile leaves of *Osmundopsis* and sterile leaves of *Cladophlebis* (Pl. 3.4).

PALAEOBIOGEOGRAPHY AND EVOLUTION

The osmundaceous ferns first appeared in the Permian, based on rhizomes and fertile fronds from Australia and Russia (Grimm et al. 2015, Naugolnykh 2002). During the end-Permian extinction event, the basal families became extinct but the core Osmundaceae survived (Collinson 2002, Van Konijnenburg-van Cittert 2002). *Osmundopsis* is known from the Middle Triassic of Australia (Holmes 2001)

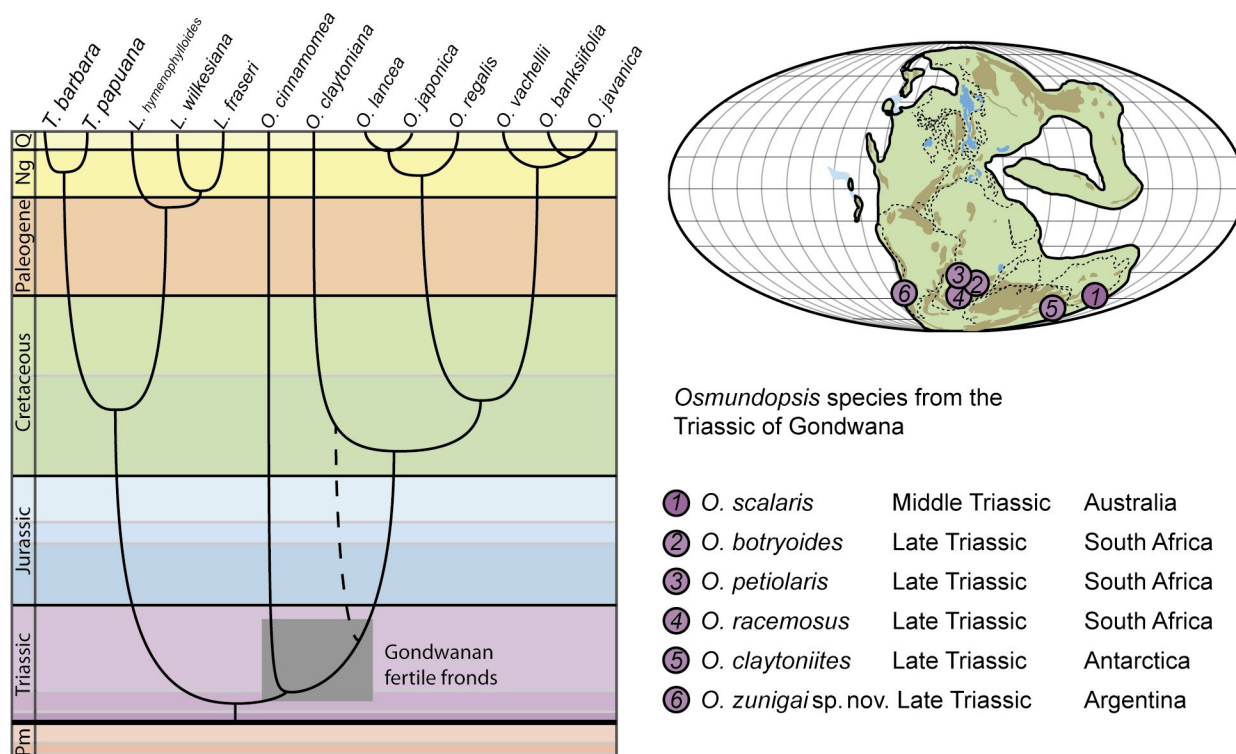


Fig. 2. *Osmunda* and *Osmundopsis*: proposed phylogeny of Grimm et al. (2015), and geographic and stratigraphic distribution in the Triassic

and became widespread by the early Late Triassic, with records from South Africa, Antarctica and Argentina, consistent with a moist temperate climatic belt in southern Gondwana (Fig. 2).

The phylogeny and evolution of the osmundaceous clade has been discussed recently. Grimm et al. (2015) used fossil fronds to calibrate their cladogram, adjusting the separation of the basal *Osmunda claytoniana* lineage in the Lower Cretaceous, but it is worth noting that *Osmunda claytoniites* from the Late Triassic of Antarctica was described as identical to *O. claytoniana*, so it should be reconsidered if the time of separation of *O. claytoniana* with the rest of the *Osmunda* species dates back at least to the Late Triassic (dashed line in Fig. 2). All the Triassic fossils come from Gondwana, the oldest – *O. scalaris* – being from the Middle Triassic of Australia, which leads us to posit a Late Triassic radiation of the *Osmunda* lineage.

Given that the strata in which *Osmundopsis zunigai* sp. nov. occurs are Carnian in age, and Osmundales is indicative of moist environments, this radiation could have been assisted by the extensive peat-forming environments recorded across temperate Gondwana (Retallack 1996), and could be evidence of the globally recognised Carnian Humid Episode

(Colombi & Parrish 2008, Ruffel et al. 2016) or Carnian Pluvial Event (Kustatscher et al. 2018) in South America.

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SUPPLEMENTARY MATERIAL

Table of *Osmundopsis* species based on isolated spores.

Species	Occurrence
<i>Osmundopsis acutispinosa</i> Kara-Murza 1954	Early Triassic to Middle Jurassic; Russia, Siberia, Kazakhstan
<i>Osmundopsis angrenica</i> Kuzichkina et al. 1959	Triassic to Middle Jurassic; Russia, Kazakhstan, Tajikistan, Uzbekistan
<i>Osmundopsis breviapiculatus</i> Kara-Murza 1954	Middle Jurassic; Russia
<i>Osmundopsis jurassica</i> Aliev et al. 1981	Jurassic; Kazakhstan
<i>Osmundopsis kugartensis</i> Kuzichkina 1962	Triassic to Jurassic; Russia, Kazakhstan, Siberia Uzbekistan
<i>Osmundopsis minuta</i> Kara-Murza 1954	Early Triassic to Middle Jurassic; Russia, Kazakhstan, Kyrgyzstan
<i>Osmundopsis plicatus</i> Kara-Murza 1960	Jurassic; Russia, Kazakhstan, Kyrgyzstan
<i>Osmundopsis pseudoregalis</i> Dubrovskaya 1967	Late Triassic to Early Jurassic; Kyrgyzstan
<i>Osmundopsis rostrata</i> Kara-Murza 1954	Early Triassic to Early Jurassic; Russia, Kazakhstan, Kyrgyzstan
<i>Osmundopsis rotunda</i> Klimko 1961	Middle Jurassic to Early Cretaceous; Russia
<i>Osmundopsis sparsaetuberculata</i> Dubrovskaya 1967	Late Triassic to Early Jurassic; Kyrgyzstan
<i>Osmundopsis spinosa</i> Kara-Murza 1954	Early Permian to Middle Jurassic; Russia, Siberia, Kyrgyzstan
<i>Osmundopsis spinosella</i> Kara-Murza 1954	Early to Middle Jurassic; Russia