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FERTILE OSMUNDACEAE FROM THE EARLY JURASSIC OF PATAGONIA, ARGENTINA

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Two new compression-impression species of the Osmundaceae described from reproductive and vegetative remains are erected for the first time from the Early Jurassic of Argentina. *Todites cacereii* sp. nov. and *Osmundopsis rafaellii* sp. nov. demonstrate that two main osmundaceous reproductive morphologies; i.e., differentiated reduced or unreduced fertile laminae were already present and widespread in Gondwana by this time. On the basis of a discussion of relevant morphological characters, the phylogenetic meaning of the fossils *Todites* and *Osmundopsis* is explored. Likewise, the systematics and taxonomy of fossil taxa and their relationships with modern ones are discussed in light of current hypotheses. In this regard, because clear synapomorphies or apomorphies are not yet fully understood, it is suggested that fossil representatives are better placed in morphotaxa (*Todites*, *Osmundopsis*) than in any current genus. Nonetheless, the clear record of characters of the leptopteroid clade by the early Jurassic proves to be older than previously assumed, which also points to an earlier time of origination for the osmundaceous ferns.

Keywords: Jurassic, Patagonia, Osmundaceae, *Todites*, *Osmundopsis*.

Introduction

The Osmundaceae is a small family of leptosporangiate ferns that have been considered intermediate between leptosporangiate and eusporangiate ferns (see Taylor et al. 2009). This hypothesis, originally based on a mixture of characters present on the osmundaceous sporangia, has recently shown congruence from a number of molecular phylogenetic studies (Hasebe et al. 1995; Pryer et al. 2004; Smith et al. 2006). Pryer et al. (2004) estimated diverging times for the major groups of ferns by means of penalized likelihood (Sanderson 2002), using their Bayesian consensus tree and incorporating 21 fossil constraints. According to this study, the osmundaceous ferns originated in the Late Carboniferous (323 Ma).

Osmundaceae is characterized by unique and very distinctive rhizome anatomy (Hewitson 1962), sporangia without a definite soral-type organization, and sporangia with a rudimentary pathlike annulus, which is distinct from all other sporangial morphologies of leptosporangiate ferns (Gifford and Foster 1989). Within living representatives, three genera have been classically recognized: *Osmunda*, *Todea*, and *Leptopteris*; these genera are normally distinguished on the basis of the morphology of fertile pinnae (Hewitson 1962; Metzgar et al. 2008). *Todea* and *Leptopteris* share several morphological features, such as the presence of unreduced fertile pinnae and the absence of dimorphic leaves. Most phylogenetic analysis places these two genera as sister groups (Metzgar et al. 2008). *Osmunda*, on the other hand, is clearly distinguished by the presence of reduced fertile pinnae and is divided into three subgenera (Kramer 1990): *Osmunda*, *Ple-*

nasium, and *Osmundastrum*. However, a detailed study on fossil species of the subgenus *Osmundastrum* (Miller 1967, 1971) and recent molecular phylogenetic analyses (Yatabe et al. 1999, 2005; Metzgar et al. 2008) have questioned the monophyletic status of *Osmunda*. These studies have also suggested that *Osmunda cinnamomea* is not related to the other *Osmunda* species and occupies a basal position, sister to the rest of the family. A combined morphological and molecular analysis performed by Jud et al. (2008) also supports the basal position of *O. cinnamomea*, which now represents the only species of the genus *Osmundastrum*. Following this new approach, *Osmunda claytoniana* is now included in the monotypic subgenus *Claytosmunda*, which occupies a basal phylogenetic position within the genus *Osmunda* (Metzgar et al. 2008).

The Osmundaceae has a rich fossil record that can be traced back to the late Paleozoic. It is known mostly from permineralized stems (Gould 1970; Miller 1971), but there are also compression-impression fertile specimens (Naugolnykh 2002). Permineralized stems described as *Palaeosmunda* (Gould 1970), from the Upper Permian of Australia, possess a number of characters with osmundaceous affinity, suggesting that the family probably arose in the Southern Hemisphere and subsequently dispersed from there (Skog 2001). Despite these Permian records, it is during the Mesozoic that the family reached a more extensive distribution in both hemispheres and showed its major diversity in both compression and permineralized materials. For instance, fertile fronds indistinguishable from living species of *Osmunda* have been described from the late Triassic of Antarctica (Phipps et al. 1998), providing an example of evolutionary stasis. An additional example of taxa longevity within Osmundaceae is the occurrence of *O. cinnamomea* in the Upper Cretaceous of North America (Serbet and Rothwell 1999).

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Historically, two genera of fertile osmundaceous foliage have been described from the fossil record, *Todites* and *Osmundopsis*, which were originally erected to include materials that did not have sufficient characters to be included in modern taxa (in this case *Todea* and *Osmunda*). Additionally, sterile foliage of osmundaceous alliance was normally associated with the morphogenus *Cladophlebis*, which is characterized by bipinnate fronds, with alternate pinnae and lanceolate pinnules up to several millimeters long. The genus *Todites*, which appeared during the Late Triassic (Jung 1972; Kon'no 1972; Wang et al. 2005), has unreduced fertile pinnae related to the *Todea/Leptopteris* lineage. It is also characterized by bipinnate fronds, with pinnules having a midrib and diverging lateral veins. The large and almost sessile sporangia are disposed on the abaxial side of the pinnules along the veins. A triradiate scar characterizes the spores (Harris 1961). *Osmundopsis*, on the other hand, first occurs in the Early Jurassic (Harris 1961; van Konijnenburg-van Cittert 1996) and is principally characterized by the presence of sterile and fertile dimorphic fronds. The fertile pinnules have a strongly reduced or absent laminae. Based on these and other shared characters, such as the presence of sporangia arranged in clusters, *Osmundopsis* is related to living and fossil *Osmunda* and *Osmundastrum* species.

The Lower Jurassic ferns described here are assigned to the fossil genera *Todites* and *Osmundopsis*, both bearing the typical *Cladophlebis*-like foliage in clear association with reproductive fronds. Based on the preserved characters, the presence of the two main morphologies in osmundaceous fertile pinnae (i.e., reduced and unreduced) is confirmed, indicating their early co-occurrence in the Early Jurassic of Patagonia.

Material and Methods

A total of 100 well-preserved vegetative and reproductive specimens were collected at the Cerro Bayo locality, Chubut Province, Argentina (precise GPS location of this site is deposited at the Museo Paleontológico Egidio Feruglio and can be obtained from the authors on request), and described as *Osmundopsis rafaëlii* (36 specimens) and *Todites cacereii* (64 specimens). Plant horizons at this locality have been referred to unnamed silicoclastic deposits of fluvial origin. Fossil plant remains occur in silicified tuffaceous fine-grained sediments as part of a taphocenosis dominated by the cupressaceous conifer *Austrohamia minuta* (Escapa et al. 2008). The ferns are the second most common group and are represented by the osmundaceous ferns described here, along with dipteridaceous species of the genera *Dictiophyllum* and *Geoppertella*. Equisetaleans (*Equisetites*) and Caytoniales (*Sagenopteris*) complete the floral spectrum. In particular, the osmundaceous species were collected from the same single horizon. This association is considered to be early Jurassic in age based on similarities from nearby coeval floras (Escapa et al. 2008).

Standard techniques for compression-impression fossils have been used in the study of these specimens, which are deposited at the Museo Paleontológico Egidio Feruglio Paleobotanical

Collection in Trelew, Argentina (hereafter MPEF-Pb). Fossils were analyzed using a Zeiss MC80DX stereoscope microscope with camera lucida attached. Photographs were obtained using a digital camera (Sony Alfa, DSLR-A100; 12 megapixels) under tungsten light. However, inner sporangia features of well-preserved, silicified *Todites* fertile fronds were observed under SEM (JEOL JSM-6460), without gold/palladium coat, at 15 kV, 28 Pa.

Systematics

Division—Pteridophyta

Order—Osmundales

Family—Osmundaceae Berchtold and Presl

Genus—*Todites* Seward emend. Harris, 1961

Type Species—*Todites williamsonii* (Brongniart)

Seward emend. Harris, 1961

Todites cacereii Escapa et Cúneo sp. nov. (Figs. 1–3)

Diagnosis. Fronds at least bipinnate with a robust rachis. Pinnae suboppositely inserted at open acute angles, with straight rachises. Pinnules oblong falcate, up to 0.5 cm long, with entire margins and obtuse apex, inserted at right angles by their entire bases, sometimes constricted. Venation pattern represented by a slightly straight to sinuous midvein extending up to two-thirds of the pinnule length. Secondary veins open dichotomous, arising in opposed or subopposed pairs. Fertile pinnules similar to sterile ones, except that dichotomies of secondary veins are more common. Densely covered by sporangia on their abaxial side. Sporangia ovoid or globose, 0.35 mm in diameter. Sporangia cells rectangular, with straight walls. Annulus located on the medial zone of the sporangia. Spores smooth, trilete, ovoid to globose.

Holotype. MPEF-Pb 1755.

Paratypes. MPEF-Pb 2869, MPEF-Pb 2697.

Locality. Cerro Bayo locality, NW Chubut Province, Argentina.

Age. Early Jurassic.

Etymology. The specific epithet *cacereii* refers to the last name of Don Julio Cáceres, the owner of the farm where the specimens were collected.

Specimens. Fertile fronds: MPEF-Pb 1495, 1725, 1755, 1788, 1858, 1862, 2697, 2702, 2704, 2729, 2809, 2810. Sterile fronds: MPEF-Pb 1732, 1735, 1759–1761, 1769–1770, 1775, 1779, 1782, 1785–1787, 1791–1793, 1850–1851, 1858, 1862, 2214, 2668, 2670, 2673, 2676, 2682, 2684–2685, 2689–2690, 2697, 2732, 2736, 2741, 2748, 2750, 2760, 2768–2769, 2773, 2783–2784, 2786, 2789, 2791, 2793, 2796, 2798, 2805–2806, 2808, 2812.

Description. Both fertile and sterile fronds are clearly bipinnate, at least 16 cm long and 15 cm wide. A strong, straight, or slightly sinuous frond rachis (0.8 cm in width) with longitudinal striations can be observed on sterile fronds. Pinnae are suboppositely arranged along the main rachis, with up to 0.4 cm separation between pinnae of the same pair and 0.7–1 cm of separation between consecutive pairs of pinnae (fig. 1A). Pinnae rachises (secondary rachises) are straight, up to 0.2 cm in width, and inserted on a primary

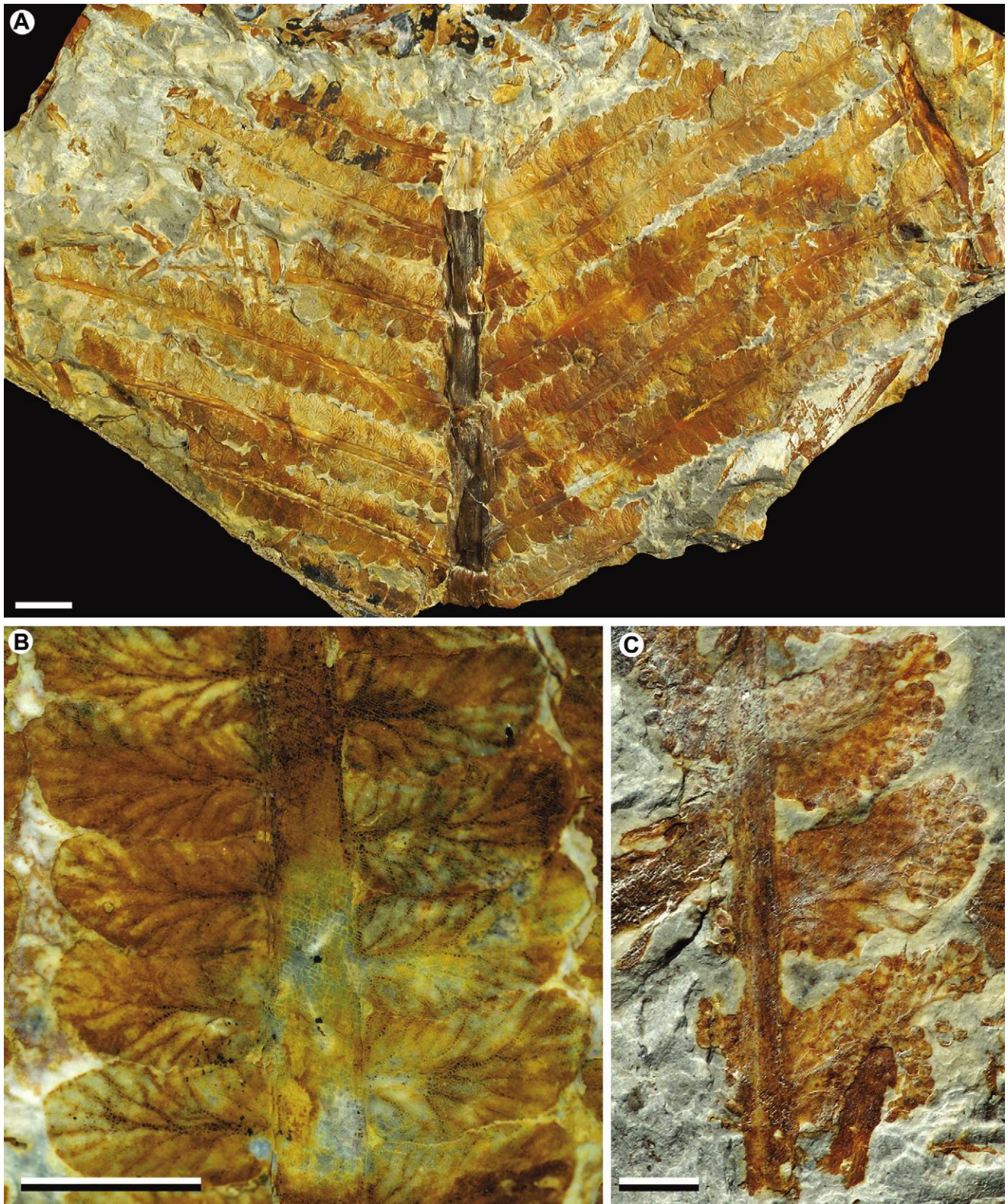


Fig. 1 *Todites cacerei* sp. nov. from Cerro Bayo, Chubut Province, Argentina. A, Sterile frond showing broad rachis and densely arranged pinnae. MPEF-PB 2869. Scale bar = 10 mm. B, Sterile pinnae showing venation and broad rachis. MPEF-PB 2869. Scale bar = 5 mm. C, Fragment of fertile pinnae. Note that the central pinnule is partially covered by sporangia but venation is observed. MPEF-Pb 2810. Scale bar = 2 mm.

frond rachis at acute angles (60°–70°). The longest pinnae can be up to 10 cm (incomplete); the width can be up to 1.1 cm and remains constant along the pinnae length. There is usually no overlapping between consecutive pinnae, although this is possible on apical zones.

Pinnules are also suboppositely disposed, with the first basal pinnule basiscopically inserted on the pinna rachis (fig. 1B); all of the pinnules are basally inserted at right angles (85°–90°), sometimes slightly basally and acroscopically constricted, with margins partially superimposed. In general, pinnules are oblong, sometimes slightly falcate, with entire margins and an obtuse apex, up to 0.5 cm long and 3.5 cm wide (fig. 1B). The pinnule venation pattern shows a straight or slightly sinuous primary vein, up to 0.3 mm wide, gradually thinning toward the apex, disappearing at two-thirds of the pinnule length. Secondary veins originate from the primary vein in opposed or subopposed pairs, at angles varying from 45° in the proximal pinnule to more acute angles in the distal part (fig. 1B). In general, secondary veins have an open dichotomous pattern, dichotomizing once in the first 0.5 mm of their lengths, and then continue straight up to the pinnular margin. Occasionally, secondary veins may undergo a second dichotomy near the pinnule margin. The vein density is up to two veins per millimeter at the margins.

Fertile fronds are morphologically similar to sterile ones (fig. 1C). Fertile pinnae show nearly identical sizes and insertion angles (fig. 2A).

The fertile pinnules are up to 0.6–0.8 cm long and 0.35–0.45 cm wide (fig. 2B, 2C); in general they are morphologically similar to sterile pinnules, although they occasionally show a more falcate shape. Insertion and venation patterns are similar to those of sterile pinnules, although venation is not always visible, except for the midvein (fig. 2C); secondary veins are normally forked twice (fig. 1C). Sporangia are densely arranged on the abaxial side of the pinnules and come into contact with one another (figs. 2B–2D, 3A). Every fertile pinnule bears 140–180 ovoid or globose sporangia, measuring up to 0.35 mm in diameter (mean, 0.25–0.30 mm). Epithelial cells on the sporangia are rectangular, up to 50 μm long and 12–15 μm wide, with straight walls (fig. 3C). A dehiscence ring is laterally arranged on approximately the middle zone of the sporangia (fig. 3D). The ring is one cell thick and probably does not encircle the entire sporangia (fig. 3D). Ring cells are elongate, 50 μm long and 25 μm wide. Broken sporangia sometimes allow the spore contents to be visible, which are represented as endocasts of spores (fig. 3E, 3F) occurring in numbers of approximately 20; spores are ovoid or globose, up to 40 μm in diameter (fig. 3C–3F).

Spores occur preserved as molds (fig. 3); they are trilete, globose, approximately spherical in equatorial outline to ovoid (when compressed). In equatorial view they have a hemispherical distal side and a pyramidal proximal one. The spore surface wall is smooth and appears polished (fig. 3F), with a distinct to prominent trilete scar (laesurae), raised, extending across the whole proximal face, simple or frequently bordered by thickenings of the exine (margo). Contact facets either completely undelimited or suggested by low and ill-defined line in the spore wall continuing the tri-

date scar and then suggesting arcuate ridges. Mean spore diameter \sim 35–38 μm .

Genus—*Osmundopsis* Harris

Type Species—*Osmundopsis sturii* (Raciborsky) Harris
Osmundopsis rafaellii Escapa et Cúneo sp. nov. (Figs. 4, 5)

Diagnosis. Fertile and sterile pinnae dimorphic. Sterile fronds bipinnate, at least 25 cm long with a robust rachis. Pinnae up to 12 cm long, inserted at 45° angles in an alternate to subopposite form through secondary rachises up to 0.25 cm wide. Pinnules arranged opposite or alternate along pinnae; the largest measures up to 1.7 cm long and 0.8 cm wide; oblong to wedge shaped and falcate; apex obtuse and margins serrate. Venation pattern shows a strong midvein extending for \sim 90% of the pinnule length. Secondary veins arising in opposed or subopposed pairs, dichotomize once, reaching the margin at each tooth. Fertile pinnae up to 4.5 cm long, bearing reduced oblong to falcate pinnules, oppose to subopposedly inserted in a clearly separate way; oblong falcate in shape, up to 1 cm long and 0.35 cm wide, showing a strong midvein. Wedge-shaped, shortly stalked sporangia densely disposed in clusters of three or four on the abaxial side, all bearing a clear incision on the distal side corresponding to the dehiscence zone.

Holotype. MPEF-Pb 1793.

Paratypes. MPEF-PB 1769, 1862, 1757.

Locality. Cerro Bayo locality, NW Chubut Province, Argentina.

Age. Early Jurassic.

Etymology. The specific epithet *rafaellii* refers to the first name of Dr. Rafael Herbst, in honor of his numerous contributions to the understanding of the Jurassic floras of Argentina.

Studied materials. Fertile fronds: MPEF-Pb 1766, 1769, 1791, 1793, 1862, 2677, 2670, 2682, 2724, 2743, 2750, 2769, 2819; 1770, 1775, 1844, 2210, 2667, 2676, 2772. Sterile fronds: MPEF-Pb 1489, 1496, 1580, 1747, 1749, 1757, 1789, 1774, 1855, 2682, 2697, 2704, 2751, 2768, 2798–2799, 2809.

Description. The sterile fronds are bipinnate and at least 25 cm long and 24 cm wide. The frond rachis is straight and striated (fig. 4A), up to 0.8 cm wide at the base, gradually decreasing toward the apex. Pinnae originate from the frond rachis in an alternate or subopposite way, separated up to 4 cm on each frond half; they are up to 12 cm long and 3.2 cm wide, inserted at 45° angles or closer toward the apex (fig. 4A). Pinnae rachises are up to 0.25 cm wide and slightly curved. Pinnules are arranged in an opposite to alternate way along the pinna rachis and are inserted at open but acute angles (60°–70°). In general, pinnules are slightly overlapped, and the first one of each pinnae occurs on the basiscopic side. The largest pinnules occur on the medial sector of the pinnae, and they can be up to 1.7 cm long and 0.8 cm wide; they are oblong to wedge shaped in outline, falcate, and with an obtuse apex. Margins are serrate or dentate, with approximately two teeth every 1 mm (fig. 4B). The venation pattern shows a strong midvein evident for \sim 90% of the pinnule length. Secondary veins are born opposite to subopposite and can dichotomize once (very rarely twice), nearly to their ori-

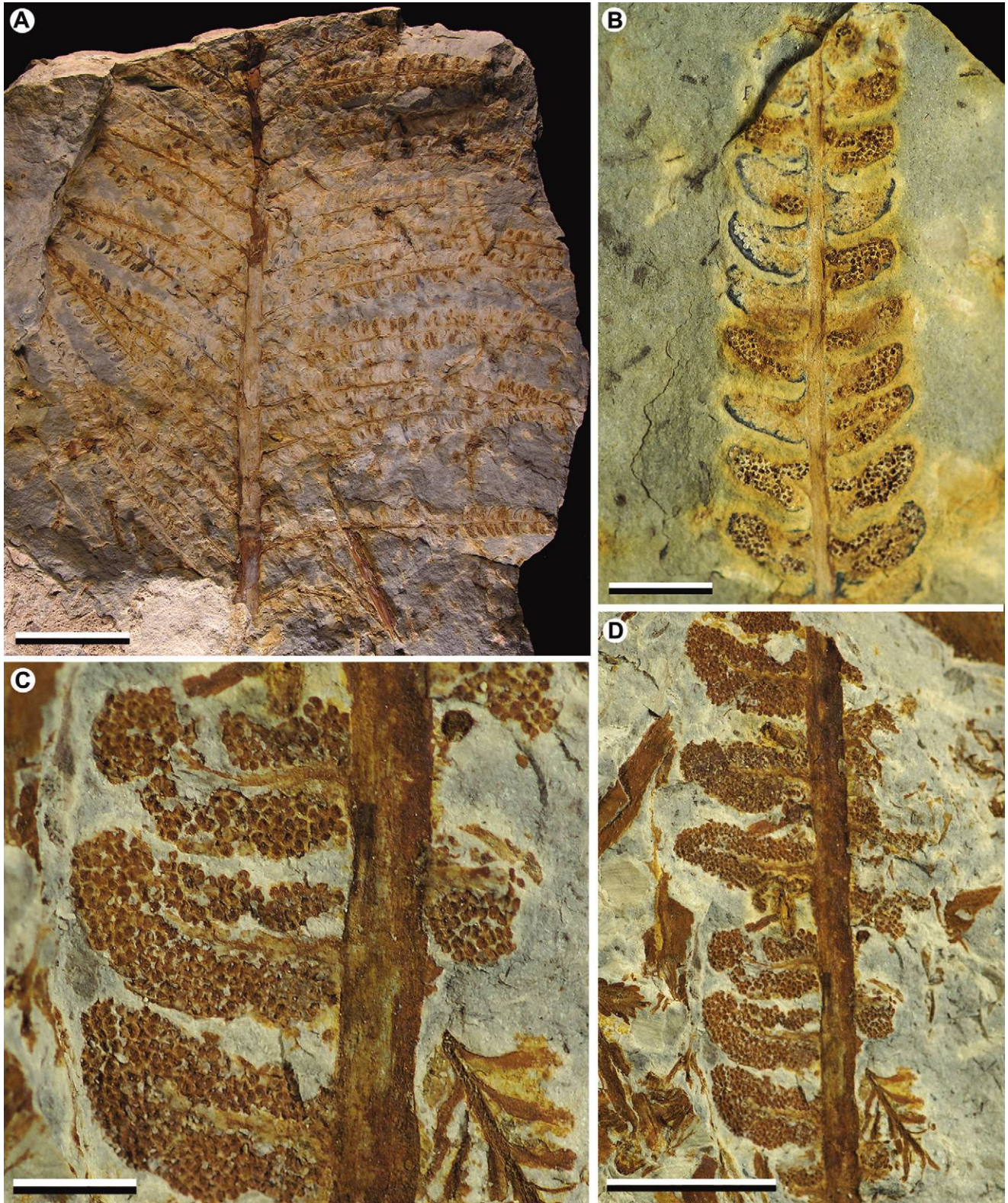


Fig. 2 *Todites cacerei* sp. nov. from Cerro Bayo, Chubut Province, Argentina. **A**, Bipinnate fertile frond showing lateral arrangement of pinnae and densely arranged fertile pinnules. MPEF-Pb 1755. Scale bar = 3 cm. **B**, Fragment of fertile pinnae showing abaxial side of pinnules covered with sporangia. MPEF-Pb 1755. Scale bar = 5 mm. **C**, Fragment of fertile pinnae showing fertile pinnules on abaxial side. MPEF-Pb 2697. Scale bar = 3 mm. **D**, Fragment of fertile pinnae showing broad rachis and laterally arranged fertile pinnules. MPEF-Pb 2697. Scale bar = 10 mm.

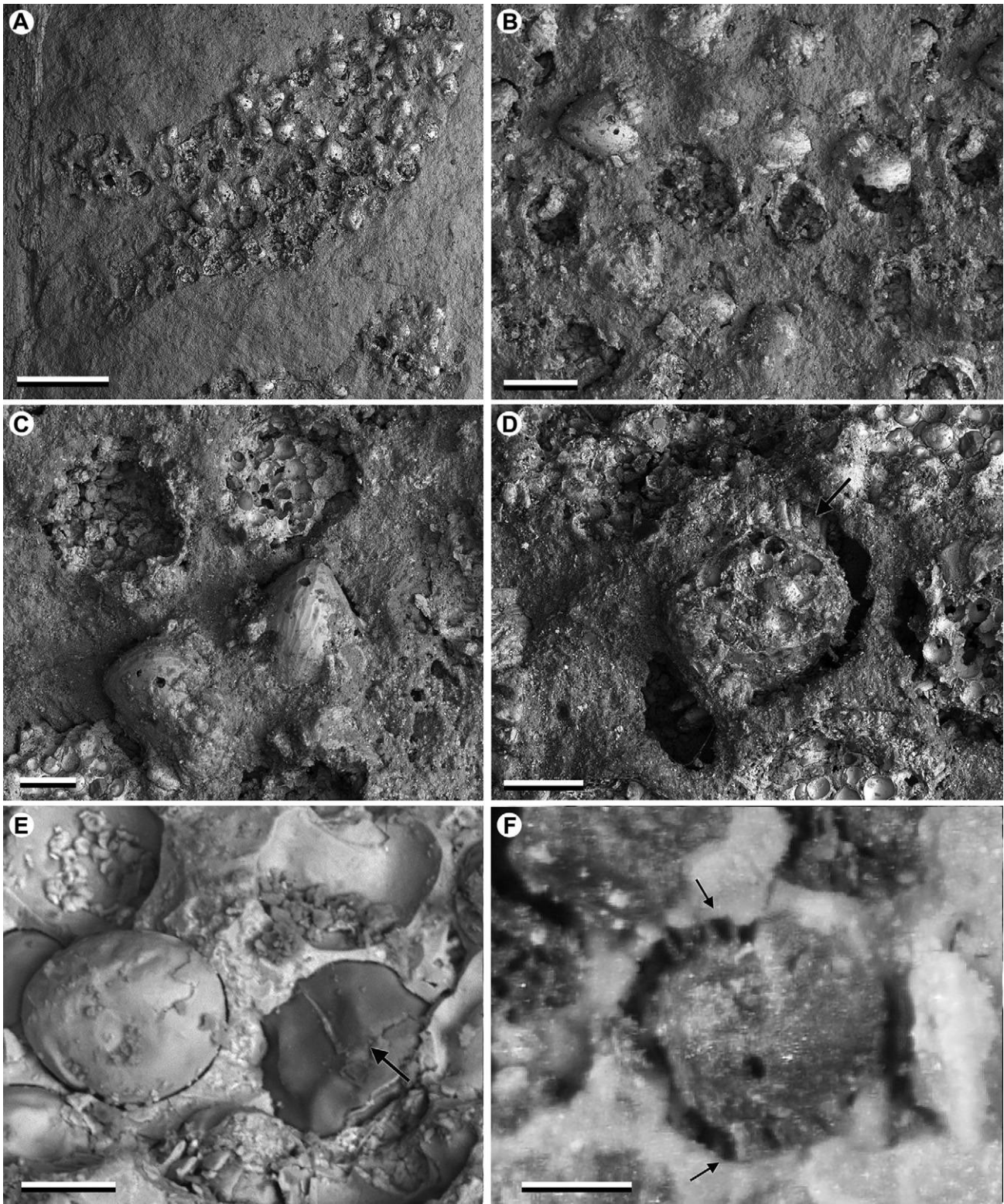


Fig. 3 *Todites cacereii* sp. nov. from Cerro Bayo, Chubut Province, Argentina. A–E, SEM images. MPEF-Pb 1755. A, Detail of fertile pinnule with sporangia covering its abaxial side. Scale bar = 1 mm. B, Detail of abaxial surface showing incomplete and complete sporangia. Scale bar = 200 μm . C, Detail of broken and entire sporangia. Note the molds of spores on the broken sporangia. Scale bar = 100 μm . D, Incomplete sporangia partially showing annulus cells (arrow). Scale bar = 100 μm . E, Detail of the sporangial contents. Note that some spores are preserved and in other cases they are represented by molds. Arrow indicates a spore in polar proximal view, in which contact areas (trilete scar) are visible. Scale bar = 20 μm . F, Sporangia showing equatorial annulus (arrows). Scale bar = 100 μm .

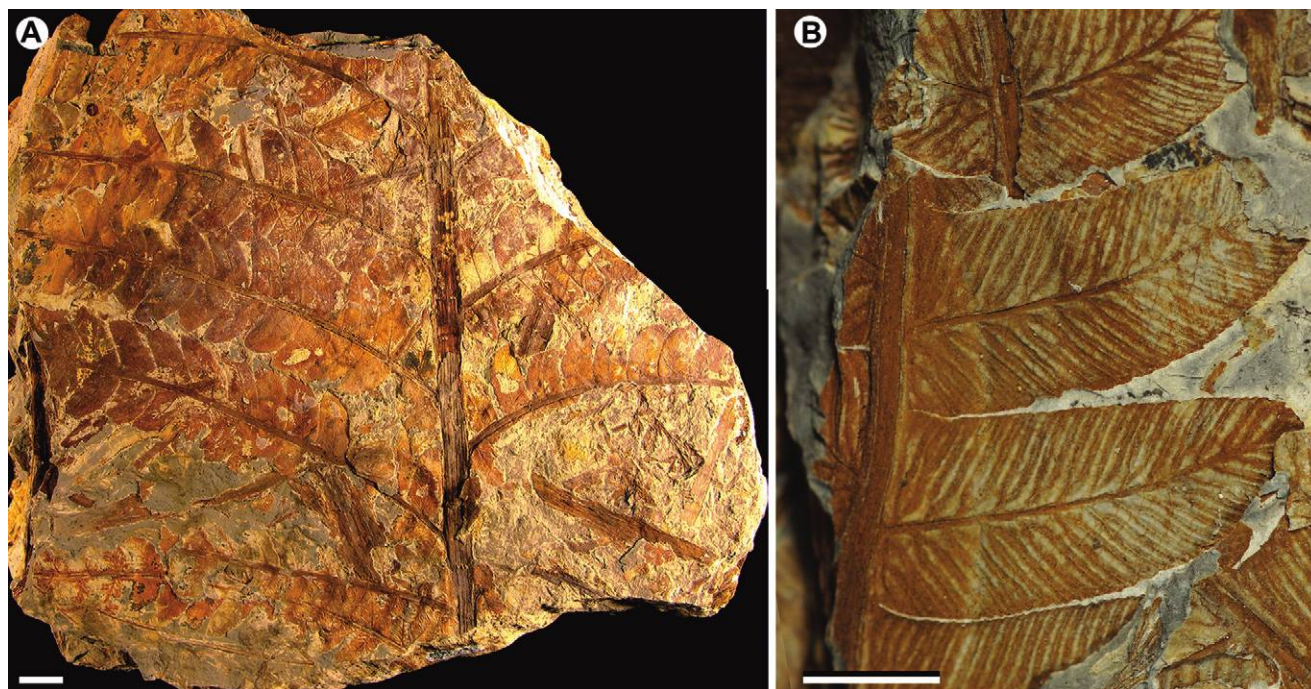


Fig. 4 *Osmundopsis rafaellii* sp. nov. from Cerro Bayo, Chubut Province, Argentina. A, Fragment of bipinnate frond showing alternate arrangement of pinnae. MPEF-Pb 1757. Scale bar = 1 cm. B, Detail of sterile pinnules showing open dichotomous venation and dentate margins. MPEF-Pb 2697. Scale bar = 5 mm.

gin in the midvein, reaching the margin coincident with one tooth (fig. 4B).

Almost complete fertile pinnae are 4.5 cm long and 1.5 cm wide (fig. 5A), with a winged, striated, and straight rachis up to 0.2 cm wide (fig. 5B). Pinnae are imparipinnate with a well-developed terminal pinnule 0.9 cm long and 0.2 cm wide. Along the rachis, fertile pinnules are oppositely to slightly suboppositely inserted at the pinna base, clearly subopposed at the middle sector, and definitely alternate at the distal pinna sector (fig. 5A–5C). There is a regular 0.4–0.5-cm separation in the insertion of pinnules on each side of the pinnae, which in turn are not overlapping. A slight decurrence is observed at the basiscopic and acroscopic sides of the pinnule base (fig. 5B). The fertile pinnules are reduced and oblong, up to 1 cm long and 0.15–0.35 cm wide. On their adaxial side, which lacks sporangia, a reduced lamina can be observed. When preserved, the venation pattern shows a prominent midvein (fig. 5A).

Sporangia are densely arranged in groups on the abaxial side of the pinnule (fig. 5D), which is not commonly seen. Because most of the fertile pinnules are compressed on their abaxial side, the sporangia look crushed and show up along the margin because of the reduced foliar pinnular lamina (fig. 5E). There they are grouped in 1-mm semicircles or tiny fans composed of three or four sporangia (fig. 5E). The sporangia are wedge shaped, 0.33 mm long and 0.5 mm wide, with a clear incision on their distal side that corresponds to the dehiscence zone (fig. 5F), and are probably attached on a short pedicel.

Discussion

The name *Todites* is commonly used for fossil osmundaceous ferns with unreduced fertile pinnules but without sufficient diagnostic characters to be included in the modern genera *Todea* or *Leptopteris* (Harris 1961). This separation is basically established using two criteria: (a) morphological differences in the sporangia, such as size, presence of thickened cells, and so on, and (b) preservational biases precluding the identification of the particular details that allow, in fossil cases, a safe assignment to *Todea* or *Leptopteris*. This ambiguity in the possible assignment of fossil specimens to either of these two modern genera is also apparently present in the proper distinction of both modern taxa. In this regard, most authors recognize *Todea* and *Leptopteris* as separate genera (Miller 1967; Metzgar et al. 2008), but others have suggested that a separation may not be possible and that every modern form should be included in the genus *Todea* (Hewitson 1962).

Todites has been used exclusively in fossil specimens that preserve their fertile pinnules and, in particular, the sporangia morphology (Halle 1913; Gee 1989; Naugolnykh 2002). When sterile fronds are found, they are usually assignable to the morphogenus *Cladophlebis*. Bodor and Barbacka (2008) developed a detailed morphometric study in order to distinguish *Cladophlebis* and *Todites* vegetative remains. Nonetheless, even when results with particular species can be obtained, the general morphology included in the form *Cladophlebis* has been related to different fern taxa and therefore represents a highly homoplastic kind of fern frond.

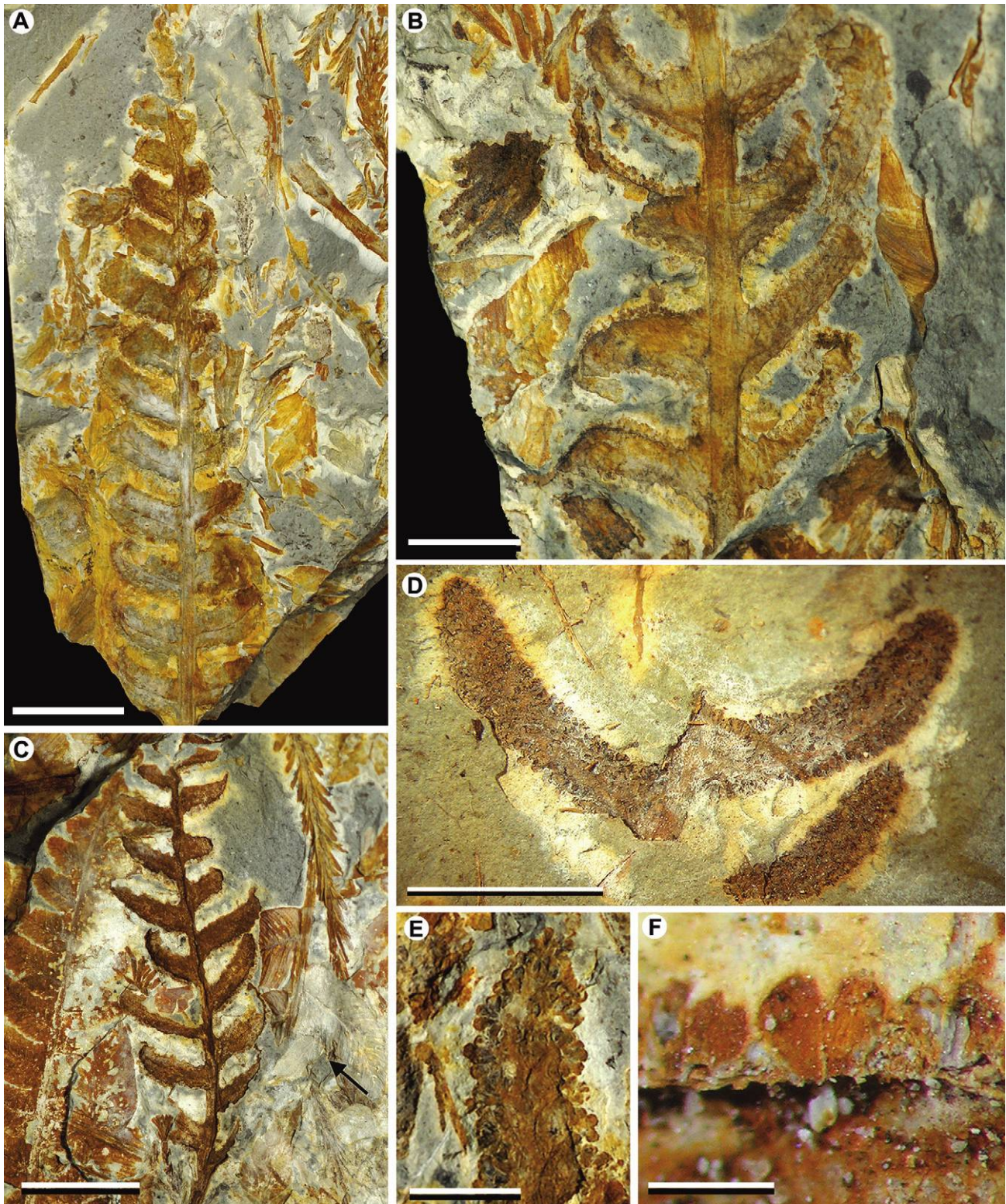


Fig. 5 *Osmundopsis rafaellii* sp. nov. from Cerro Bayo, Chubut Province, Argentina. **A**, Fertile pinnae in adaxial view showing the pinnae distal part. MPEF-Pb 1793. Scale bar = 10 mm. **B**, Fragment of fertile pinnae on adaxial side. Note the opposite arrangement of pinnules and the peripheral position of the sporangia. MPEF-Pb 1769. Scale bar = 10 mm. **C**, Fertile pinnae in adaxial view showing the alternate and subalternate arrangement of the reduced fertile pinnules. MPEF-Pb 1862b. Scale bar = 10 mm. **D**, Fragment of fertile pinnae on abaxial side. Note the sporangia covering the reduced pinnules. MPEF-Pb 1793. Scale bar = 10 mm. **E**, Detail of fertile pinnules in adaxial view. Note the arrangement of the sporangia in groups. MPEF-Pb 2819. Scale bar = 2 mm. **F**, Detail of sporangia showing the distal incision. MPEF-Pb 1776. Scale bar = 1 mm.

On the other hand, *Osmundopsis* was erected by Harris (1931) to include fertile fossil osmundaceous ferns with a differentially reduced foliar lamina and sporangia grouped in clusters, as seen in modern *Osmunda*. The genus is most commonly recorded from Jurassic localities in both hemispheres (see Tidwell and Ash 1994; Collinson 1996; van Konijnenburg-van Cittert 2002). The type species, in particular, is found in the Lias of Polonia and Iran and the middle Jurassic of England and China (van Konijnenburg-van Cittert 1996 and citations therein).

As a means to distinguish between the different fossil and modern *Osmunda* species, sporangia morphology becomes highly relevant (Phipps et al. 1998). However, according to Hewitson (1962), differences in sporangia do not appear as a definite character between the four modern genera of *Osmunda*, *Osmundastrum*, *Leptopteris*, and *Todea*. Nonetheless, there are some characters, such as the position of the dehiscence ring, that might become relevant. In *Leptopteris*, for instance, the ring occurs in a basal position near the sporangia pedicel; in *Osmunda* it occurs more medially, while in *Todea* it has a distal position. Phipps et al. (1998) emphasized that, in this apparent morphological continuum of the position of the ring, the fossil genus *Osmundopsis* clearly represents an extreme, with sporangia showing rings covering the entire apical sector (see also Harris 1961). This sector, interestingly, rather resembles those in *Todea*. In this way, *Osmundopsis* might represent a natural taxon combining the pinnular morphology of *Osmunda* (i.e., reduced laminae in fertile zones) with sporangial morphology closer to that of the genus *Todea*.

Criteria for Correlation of Vegetative and Reproductive Fronds of *Osmundopsis rafaellii*

In the absence of preserved sporangia, osmundaceous foliage is normally included in the form genus *Cladophlebis* (Brongniart 1849). However, *Cladophlebis* morphology is highly homoplastic and could represent the foliage of different fern families (e.g., Cyatheaceae, Schizaeaceae); thus, it should not be considered exclusive to any of these families after sporangia morphology and arrangement are known (Halle 1913). In this context, the record of unambiguous compressed Osmundaceae is drastically reduced when compared with the abundant record of vegetative foliage with possible osmundaceous affinities.

Because of the reduced laminae of fertile pinnules in *Osmundopsis rafaellii*, a clear venation pattern can be hard to distinguish. This makes it harder to correlate fertile fronds with sterile ones when they were not found organically attached. Nonetheless, in our locality, fertile fronds of *O. rafaellii* have always been found associated with sterile foliage of the *Cladophlebis* type.

Among the specimens studied from the Cerro Bayo locality, two types of *Cladophlebis* fronds have been identified: one of them is organically attached to fertile pinnules assigned to *Todites cacereii*. The second one, undistinguishable from *Cladophlebis denticulata*, occurs repeatedly associated with the fertile pinnules of *O. rafaellii*. The same *Cladophlebis/Osmundopsis* association has also been discovered in the Middle Jurassic of England, where the same

morphospecies *C. denticulata* was related to *Osmundopsis sturii* (van Konijnenburg-van Cittert 1996). Together, all of this evidence supports the hypothesis that the fertile pinnae of *O. rafaellii* possess sterile pinnae of the *C. denticulata* type.

Comparisons and Basis for the New Species

Todites nanjingensis from the early Jurassic of China has a venation pattern and sporangia distribution similar to those of *T. cacereii*. However, its fronds are considerably smaller, and the finer details of sporangia and spores are not preserved (Wang et al. 2005). Another comparable species from this group is *Todites denticulatus*, which is known from several Jurassic localities in the Northern Hemisphere (Harris 1961; Wang et al. 2005); however, it differs in the presence of clearly toothed pinnular margins that are never seen in *T. cacereii* nov. sp. The same can also be said for *Todites scoresbyensis*, a form quite similar to *T. denticulatus* (Harris 1931; Wang et al. 2005). *Todites recurvatus*, from the Triassic and Jurassic of Greenland (Harris 1931), has pinnules four times bigger than those of *T. cacereii*, while *Todites thomassii* from the Jurassic of Yorkshire (Harris 1961) differs in its bigger size and toothed pinnule margins.

Todites williamsoni (= *Todites grahamii*; Gee 1989), from the Jurassic of Hope Bay in Antarctica (Halle 1913; Rees and Cleal 2004), shares some vegetative and reproductive characters (e.g., sporangia densely covering the abaxial pinnule side, morphologically similar sterile and fertile pinnules, smooth spores) with *T. cacereii* nov. sp. However, the Antarctic species has much bigger pinnules and sporangia composed only of thickened cells without a clear ring of cells. This species has also been found in other Jurassic and early Cretaceous localities in Argentina (Baldoni 1979, 1980) but has been described only from poorly preserved specimens. The spores recovered from the sporangia of *T. cacereii* have main traits similar to smooth trilete spores previously found in situ on sporangia of the genus *Todites* (Harris 1931; van Konijnenburg-van Cittert 1978, 1996; Litwin 1985), although smooth trilete spores may result from preservational effects.

Osmundopsis rafaellii, on the other hand, is assigned to this morphogenus on the basis of fertile pinnules with a partially reduced lamina, sporangia organized in clusters, and a dehiscence ring distally located on the sporangia. Even though this genus has been characterized as having a drastic reduction in or even the absence of a foliar blade in fertile pinnules (Harris 1961; van Konijnenburg-van Cittert 1996), it is clear that this character could actually represent more than one state, resembling, to some extent, what is observed in some species of *Osmunda*. For example, *Osmunda regalis* shows, in the same individual, different degrees of foliar reduction on fertile pinnules.

Based only on morphological characters, it is not possible to determine well-established differences that separate *Osmundopsis* (including *O. rafaellii*) from the osmundaceous living genera with dimorphic fronds (i.e., *Osmunda* and *Osmundastrum*). However, most of the fossil species cannot be certainly included in any of these genera because morphological differences between them are principally restricted to anatomical characters such as the presence of a secondary endodermis in the stele and the presence of three clusters of

thick-walled cells in the sclerenchyma ring in the vascular strand of the petiole bases (see Hewitson 1962; Miller 1967, 1971). This point has become particularly relevant since the living genera with reduced fertile pinnae do not constitute a monophyletic group. In this context, in the absence of anatomical features, fossil species showing this morphology cannot be assigned to a particular clade within Osmundaceae with any certainty. *Osmundopsis rafaëlii* can then be included as a separate species based on the degree of reduction in fertile pinnule laminae, which differentiates it from any other known, designated species for the genus (see table 1).

Phylogenetic Meaning of Osmundopsis and Todites

As mentioned above, the family Osmundaceae has a well-defined phylogenetic status within the fern lineage as the sister group of the remaining leptosporangiate ferns; this hypothesis is supported by both molecular data and morphological data (Pryer et al. 2004; Smith et al. 2006). The paleobotanical evidence also suggests that the osmundaceous ferns are among the oldest representatives of the leptosporangiate ferns (see Taylor et al. 2009). Within the family, the latest phylogenetic results or phylogeny (fig. 6) places *Osmundastrum* as sister group to a clade formed by the remaining three living osmundaceous genera, which in turn is divided into two main clades. The genera *Todea* and *Leptopteris* constitute one of these main lineages (i.e., the leptopteroid clade) and are sister to *Osmunda* (Jud et al. 2008; Metzgar et al. 2008).

On the basis of the preserved characters, the species described here cannot be unambiguously placed within a particular extant genus. *Todites cacereii* has reproductive organs composed of nonmodified fronds, with their abaxial faces completely covered by sporangia, and vegetative leaves of the *Cladophlebis* type. This combination of characters is also observed in *Todea* and *Leptopteris* (leptopteroid clade; fig. 6), suggesting a close relationship of these genera with the Jurassic species described here.

The position of the sporangial annulus is frequently cited as the main feature used to separate *Todea* from *Leptopteris* (Hewitson 1962). In *Todea* the annulus is next to the top of the sporangium, while in *Leptopteris* the annulus is close to the stalk (see Hewitson 1962). On the other hand, Harris (1961)

defined *Osmundopsis* and emended *Todites*, including in both diagnoses the presence of an apical region with thickened cells. Phipps et al. (1998) considered that this condition was distinct enough to separate these forms into different genera. However, after the recognition of *Osmundastrum*, which basically had the same sporangial organization and annulus position of *Osmunda*, it is clear that the position of the annulus in the Osmundaceae constitutes a homoplastic feature that should not be used alone to define taxonomic issues. In this context, we refer to *Todites* as an artificial genus of fossil forms that may be referred to the leptopteroid clade (fig. 6) but cannot be unambiguously assigned to *Todea* or *Leptopteris*.

On the other hand, *Osmundopsis* has vegetative pinnules of *Cladophlebis* type and fertile pinnae with reduced laminae, as in the extant *Osmunda* and *Osmundastrum* (fig. 6). The last genera are morphologically distinguished by characters in the rhizomes and petiole bases (Miller 1967) but are highly similar in external morphology. In this sense, most of the nonanatomically preserved *Osmunda*-like fossils cannot be related to any of these extant genera, and therefore it would be correct and strongly suggested to include them in *Osmundopsis*. This is the case, for instance, for *Osmunda claytoniites* from the Triassic of Antarctica (Phipps et al. 1998), which has been frequently assumed as the oldest record of *Osmunda*. Following this, the name *Osmundopsis* is here restricted to nonleptopteroid Osmundaceae and cannot be unambiguously related to any monophyletic group. The position of the annulus and the degree of fertile pinnule reduction have been considered features that separate fossil *Osmunda* species from the genus *Osmundopsis* (Phipps et al. 1998). However, even when the emended diagnosis for *Osmundopsis* includes the presence of sporangia with a distal annulus, we think that a less restricted definition of the genus should include *Osmunda*-like species that cannot be assigned to *Osmunda* or *Osmundastrum*.

Temporal and Biogeographic Implications

The occurrence of *T. cacereii* and *O. rafaëlii* in the early Jurassic of Argentina suggests that the two main morphologies of osmundaceous ferns were already present and diversified in the Southern Hemisphere. During the Early Jurassic, the family was well established in both hemispheres (Gould

Table 1

Comparison of Species of the Genus *Osmundopsis*

Species	Distance between pinnules (mm)	Length of pinnules (mm)	No. sporangia/cluster	Sporangia size (µm)	Mean spore diameter (µm)	Width of sterile pinnules laminae (mm)	Fertile pinnule laminae
<i>O. hillii</i>	3–5	Up to 5	Up to 8	500 × 300	42	1–2 ^a	Completely reduced
<i>O. sturii</i>	2–3	>10	Up to 20	600 × 400	48	5–7 ^b	Completely reduced
<i>O. plectrophora</i>	3	>20	Up to 12	800 × 500	50	7–9	Completely reduced
<i>O. rafaëlii</i>	4–5	Up to 10	?	500 × 300	?	Up to 8	Partially reduced (3.5-mm width)

Note. Modified from van Konijnenburg-van Cittert (1996).

^a Van Konijnenburg-van Cittert (1996) suggested *Cladophlebis harrissii* as the sterile foliage of *O. hillii*.

^b Van Konijnenburg-van Cittert (1996) suggested *Cladophlebis denticulata* as possible sterile foliage of *O. sturii*.

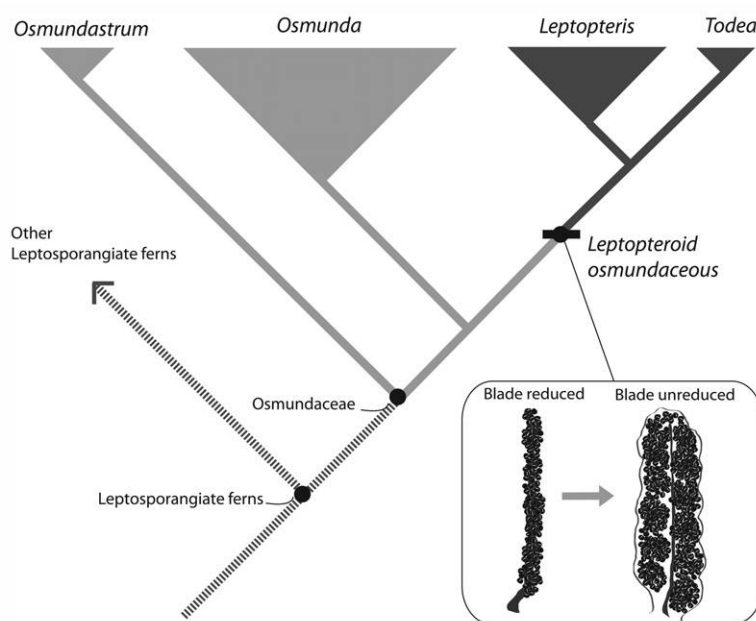


Fig. 6 Phylogenetic relationship of extant Osmundaceae (modified from Metzgar et al. 2008). Osmundaceae crown group is indicated by continuous line. Dark gray line is indicating the leptopteroid clade (*Todea* + *Leptopteris*). Light gray line indicates the *Osmunda*-like genera, which represent a paraphyletic group. The main morphological change in the fertile pinnules (blade reduced or unreduced) is indicated.

1975; Skog 2001). However, the highest diversity of the family is recorded during the Middle and Late Jurassic, when drier conditions probably competitively favored this family over other ferns with larger fronds (e.g., *Dipteridaceae*).

Until now, *O. claytoniites* from the Triassic of Antarctica (Phipps et al. 1998) has been considered the oldest record of the *Osmunda* crown group. Although this species can still be regarded as the first clear record of *Osmunda*-like ferns based on both vegetative organs and reproductive organs, it can no longer be considered the first record for the *Osmunda* crown group since its separation from *Osmundastrum* is not possible based on the preserved characters. In this sense, *O. claytoniites* possesses a phylogenetic meaning similar to that of *O. rafaëlii* and should probably be considered part of this fossil genus. Nonetheless, *O. claytoniites* constitutes the oldest unequivocal record for the crown group of the Osmundaceae (Vavrek et al. 2006), which is dated to the early Late Triassic (Escapa et al. 2010).

The minimum age for the crown group Osmundaceae has also been suggested to be Late Triassic (Norian, 206 Ma) based on a molecular estimation of phylogenetic divergence times (Pryer et al. 2004). A penalized likelihood approach was used for the estimation, and 21 fossil species were used as constraints. The same authors also estimated a minimum age of 98 million years (Cenomanian, Upper Cretaceous) for the leptopteroid clade. However, Jud et al. (2008) described a permineralized fossil rhizome from the Lower Cretaceous (Hauterivian-Valanginian) of Canada, which was included in the genus *Todea* on the basis of well-documented morphological synapomorphies. Consequently, a minimum age of 136 million years was suggested for the *Todea* clade (Jud et al. 2008), and an older age can be assumed for the leptopteroid

node. These results are highly congruent with the occurrence of *Todites cacerensis*, a taxon with unequivocal leptopteroid synapomorphies, in the Early Jurassic of Argentina.

The geographic origin for the osmundaceous ferns has been hypothesized to have been in the Southern Hemisphere (Tidwell and Ash 1994; Tian et al. 2008). However, it is clear that definitive osmundaceous synapomorphies (i.e., those present on the fertile fronds) have not yet been recorded from strata older than Triassic. Nonetheless, an indication, although weak, of their likely presence could be estimated from the record of *Cladophlebis* fronds in Permian strata from Australia, South Africa, and Argentina, along with other leptosporangiate ferns (McQueen 1954; Cúneo 1989; Césari et al. 1998). Besides, a relatively diverse record of rhizomes of osmundaceous alliance in Gondwana (Miller 1971; Tidwell and Ash 1994) would set the stage for the successful and diverse Mesozoic descendants. On the basis of the early Jurassic fossil materials described herein, the osmundaceous fern distribution was probably at its peak by this time, a fact most likely due to the wet and warm conditions that have been interpreted for SW Gondwana (Rees et al. 2000).

Concluding Remarks

Based on the preservation of definitive characters, in particular the fertile foliage, the studied materials from the early Jurassic represent the second-oldest record of truly osmundaceous plants from the Southern Hemisphere. As it has been historically recognized, the Osmundaceae represents an intermediate “experimental transition” between leptosporangiate and eusporangiate ferns. Likewise, from the character evidence

shown in the present contribution and others, it seems likely that a “transitional experiment” was somehow also occurring inside the group. In this regard, the nonmonophyletic status shown by the *Osmunda*-like genera with reduced fertile pinnales indicates a more complex scenario of character evolution than previously thought. The new species from Cerro Bayo show the coeval presence of the two main morphologies in the family as early as the basal Jurassic in Patagonia.

In light of current phylogenetic systematics knowledge, the inclusion of fossil remains in living taxa, when the preserved characters are not enough, can potentially lead to biases and misinterpretations in studies from other fields such as work with molecular clocks. This is the case for the osmundaceous remains analyzed here, which seem to be more plausibly included in morphotaxa other than extant ones. This represents a more conservative transitory solution because definitive synapomorphies (to include the fossils in a natural genus) or apomorphies (to create a new genus) are not yet recognized. Progressive reconstruction of whole plants, and its concomitant

increase in the number of characters, followed by their inclusion in integrative phylogenetic analyses, should lead to a better resolution in the taxonomy of both fossil and extant taxa.

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