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Original article

A revision of the fern family Osmundaceae in Brazil

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ABSTRACT

As part of floristic surveys in the Southern Cone of South America and the Flora do Brasil 2020 project, we present a revision of Osmundaceae in Brazil. Osmundaceae is represented by two genera (*Osmundastrum* and *Osmunda*) and three species. One of them, *Osmunda piresii*, is endemic to the savannas of Central Brazil, occurring in the states of Goiás, Minas Gerais, and Mato Grosso. *Osmunda gracilis* is synonymized under *Osmunda spectabilis*. We present a dichotomous key, descriptions, diagnostic illustrations, distributions, and notes on taxonomy and ecology.

Keywords: *Osmundastrum*, *Osmunda*, Osmundales, Neotropics, taxonomy

Introduction

The royal ferns (Osmundales) are the most ancient surviving lineage of leptosporangiate ferns (Bomfleur *et al*. 2017). The order comprises two families. One of them is the Guaireaceae, which became extinct during the Early Jurassic. The Guaireaceae has seven recognized species, and one of them, *Guairea carnierii*, has fossil records from the Rio Grande do Sul state in southern Brazil (Late Permian to Middle Triassic - Bomfleur *et al*. 2017). The other family is the Osmundaceae, with 18 extant species currently classified into six genera, as follows: *Claytosmunda*, *Leptopteris*, *Osmunda*, *Osmundastrum*, *Plenasium*, and *Todea* (PPG I 2016). This small group of ferns is remarkable in many respects. Its members represent the earliest lineage of all leptosporangiate ferns, with features that have been interpreted to be intermediate between eusporangiatae and leptosporangiatae (Bomfleur *et al*. 2015). The only extant family of this lineage, Osmundaceae, is characterized by unique and very distinctive rhizome anatomy (Hewitson 1962), with a two-layered cortex of stems and stipes, differentiated into inner, primarily parenchymatous cylinder, and outer sclerenchymatous cylinder. The stipes have a pair of stipular wings, and the tips of the stipe bundle are incurved, *i.e.*, they are more or less horseshoe-shaped. The peripheral xylem siphon is typically presented with leaf gaps (Bomfleur *et al*. 2017). The sporangia are arranged without a definite soral-type organization but with a rudimentary pathlike annulus, which is distinct from all other sporangia of leptosporangiate ferns (Gifford & Foster 1989). Phylogenetic studies have been carried out in the last 20 years and have supported the monophyly of the family and its current circumscription (Yatabe *et al*. 1999; Schuettpelz & Pryer, 2007; Metzgar *et al*. 2008).

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Osmundaceae has a rich fossil record that can be traced back to the late Paleozoic. Fossils belonging to this family largely consist of permineralized stems (Gould 1970; Miller 1971), but compression-impression of fertile leaves have also been found (Naugolnykh 2002). Permineralized stems described as *Palaeosmunda* (Gould 1970) from the Upper Permian of Australia possess several 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, during the Mesozoic, Osmundaceae reached a more extensive distribution in both hemispheres, with a greater diversity of compressed and permineralized materials in the fossil record (Escapa & Cúneo 2012).

In Brazil, and South America more generally, extant representatives of Osmundaceae have been treated in regional floras (*i.e.*, Capurro 1961, 1969; Sehnem 1967; Charpin & Novara 1995; Tryon & Stolze 1990; Prado 2004; Arana & Ponce 2015; Kessler & Smith 2017) and catalogues (Hassler 1928; Capurro 1938; de la Sota & Ponce 2008; Sylvestre 2010). A list of lycophytes and ferns from Brazil was presented in the *Catalog of Plants and Fungi of Brazil* (Prado & Sylvestre 2010), where the family is represented by two genera and two species, as it does in the synthesis published by Prado *et al.* (2015).

Studies of herbarium specimens and fieldwork have shown that the Brazilian "osmundaceous" fern flora is overlooked. It is therefore necessary to update the taxonomy, nomenclature, and distribution of the extant representatives of these ferns in Brazil. Thus, the goal of the present study is to present a taxonomic revision of Osmundaceae in this country including an identification key, morphological descriptions, diagnostic illustrations, and ecological remarks for all species.

Materials and methods

This study was based on a critical review of relevant literature, morphological data gathered from living specimens during fieldwork, and an examination of collections housed at BHCB, HB, MBM, MBML, R, RB, RBR, RFA, SI, SF, and UFMT herbaria. We also analyzed specimens received on loan and/or electronic images from the following herbaria: ALCB, B, BR, CEPEC, CESJ, FR, FUEL, HUEG, HUFSJ, HURB, K, LE, LINN-HL, NY, P, PACA, S, SJRP, SP, SPF, UB, UCS, UEC, UPCB, and US (acronyms according to Thiers 2020, continuously updated). The complete list of examined exsiccates is provided List S1 in the supplementary material. We studied the original description and type specimens of all names cited for Brazil, and the relevant information referred to the distribution and habitat features. All taxa were arranged alphabetically, and author names were abbreviated according to the International Plant Names Index (IPNI).

Results and discussion

Osmundaceae is represented in Brazil by two genera, *Osmunda* and *Osmundastrum,* and three species, *Osmunda piresii*, *O. spectabilis*, and *Osmundastrum cinnamomeum*. The richest genus is *Osmunda*, with two species, one of them, *Osmunda piresii*, endemic to Brazil.

Osmundaceae occurs in all states of the country's Central West, Southeast, and South regions, as well as the state of Bahia in the Northeast. Although this is a family with a nearly cosmopolitan distribution and wide occurrence in the Neotropical region, it is practically absent in Brazil's North and Northeast regions (Fig. 1A). There are scattered records, which could not be checked due to the absence of images in virtual herbariums: one collected in Serra dos Carajás, Pará state (*Dayle & Callejas 1803*, IAN), identified only as *Osmunda*, and another one collected in the region of Matriz do Camaragibe, Alagoas state (*Lyra 7894*, TEPB), with no genus assigned. The species are found in the Atlantic Forest, Cerrado, Pampa, and Pantanal biomes. Remarkably, the family is absent in the Amazon and Caatinga biomes.

Taxonomic treatment

Osmundaceae Martinov, Tekhno-Bot. Slovar. 445. 3-Ago-1820. Type: *Osmunda* L.

=*Osmundaceae* Bercht. & J.S. Presl, Prir, Rostlin 1: 272. 1-Nov-1820. Type: *Osmunda* L.

Terrestrial plants, with mostly unbranched, erect, or shortly creeping, ascending, sometimes treelike trunk, clothed in roots and persistent petioles, hairy at the apex. Rhizome anatomy distinctive, an ectophloic siphonostele (with a pith of parenchyma in center and phloem outside of vascular cylinder only), with a ring of discrete xylem strands, conduplicate or twice conduplicate in cross-section. Fronds 1- or 2-pinnate, bearing uniseriate hairs, these deciduous or persistent at axes, dimorphic or hemidimorphic; petiole caespitose, helicoidally arranged, with laterally winged stipules at bases, bearing mucilaginous hairs when young, with a single U-shaped vascular bundle; sclerenchyma strongly developed; base of lateral pinnae almost distinctly articulate or not; pinnule base auriculate or not; veins free, subpinnately furcate. Sporangia following veins or entirely covering strongly contracted fertile segments, not assembled in sori, sporangia with 128–512 spores, opening in an apical slit, annulus lateral; spores green, subglobose, trilete; gametophytes green, cordate, superficial. n = 22.

Six genera and about 18 species in temperate and tropical regions worldwide (PPG I 2016). Two genera and three species (one endemic) in Brazil.

Key to the species of ***Osmundaceae*** *in Brazil*

1. Fronds bipinnate, hemidimorphic with apical pinnae fertile; sterile pinnae glabrous; margin of the segments dentate to serrulate ..... 1. ***Osmunda***
   2. Laminae with 2–4 pairs of pinnae, remote, not overlapping one another; last segments ovate to elliptic, rarely subauriculate; apical segment larger than lateral ones; sporangia with interrupted distribution in fertile axes ..... 1.a. ***O. piresii***
   2. Laminae with 7–12 pairs of pinnae, proximate to almost overlapping; last segments oblong to elliptic, usually auriculate; apical segment conform; sporangia continuously distributed in fertile axes ..... 1.b. ***O. spectabilis***
1. Fronds pinnate-pinnatifid, dimorphic; sterile pinnae with a tuft of hairs on the abaxial surface near the rachises; margin of the segments entire ..... 2. ***Osmundastrum cinnamomeum***

1. *Osmunda* L., Sp. Pl. 2: 1063. 1753. Type: — *Osmunda regalis* L. (lectotype designated by Léman, Dict. Sci. Nat. 37: 9. 1825).

=*Aphyllocalpa* Lag., D.García & Clemente, Anales Ci. Nat. 5(14): 164. 1802. Type: — *Aphyllocalpa regalis* (L.) Lag., D.García & Clemente (= *Osmunda regalis* L.).

=*Struthopteris* Bernh., J. Bot. (Schrader) 1800(2): 126. 1801, nom. illeg. hom., non Scop. 1754. Type: — *Osmunda regalis* L. (lectotype designated by Pfeiffer, Nomencl. Bot. [Pfeiff.] 2(2): 1307. 1874).

Terrestrial plants. Rhizome erect to shortly creeping, stout, woody, without scales. Fronds dimorphic or hemidimorphic with dimorphic pinnae; petioles arising as a crown at the apex of the rhizome, more or less hairy when young, base of petiole swollen and with lateral flaplike stipules; laminae 2-pinnate, fertile portions positioned apically, reduced to a midrib with almost no laminae present; pinnae not articulate to the rachis. Sporangia large, naked, with a small patch annulus.

Five species; distribution nearly worldwide across tropical and temperate regions, two species in East and Southeast Asia, one in Europe, and two species (and one hybrid) in the New World, both present (one endemic) in Brazil.

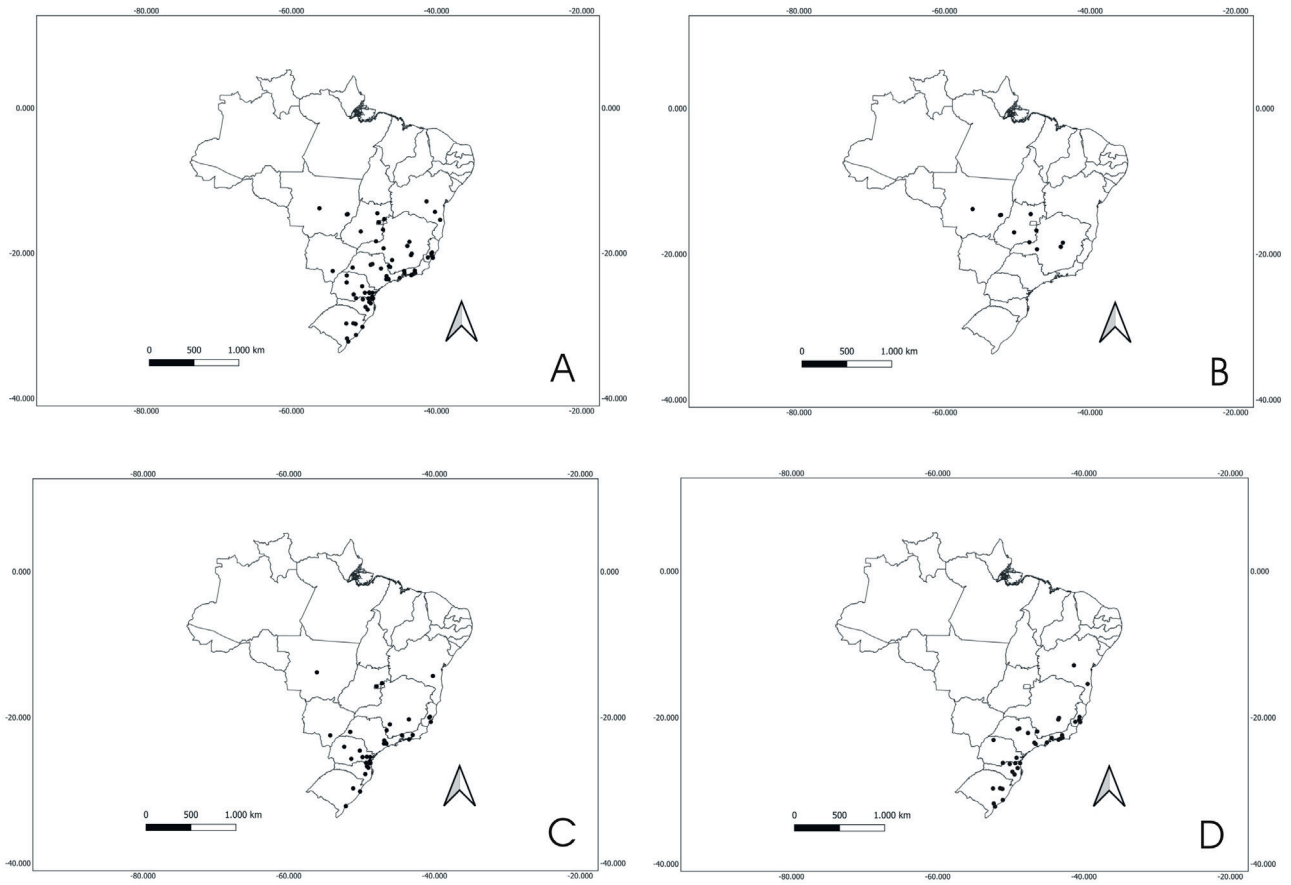

Figure 1. Distribution of species of the Osmundaceae in Brazil. **A**- General distribution of the family. **B**- *Osmunda piresii* Brade. **C**- *Osmunda spectabilis* Willd. **D**- *Osmundastrum cinnamomeum* (L.) C. Presl.

1a. *Osmunda piresii* Brade, Sellowia 17: 51. Fig. 1. 1965. Type: — "Brasilia, inter Brasilia et Niquelandia, margem do rio (barranco)", 10 May 1963, *J.M. Pires et al. 9674* (Holotype HB000027035!; Isotype UB0034479!).

Figs. 1B; 2A; 3A-B.

Rhizome short creeping; blackish, with persistent petiole bases, tips often erect, ascending, covered with reddish hairs. Fronds hemidimorphic, 2-pinnate; 15–20 x 10–15 cm; petioles 1/3–1/4 the length of the laminae, winged, glabrescent at maturity. Sterile part of the laminae broadly ovate; pinnae 2–4 pairs, remote, not overlapping each other, pinnules alternate or subalternate, subsessile or short-stalked (0.1cm), ovate to elliptic, rarely subauriculate, margins remotely dentate to serrulate, often with a single tooth near the base, apex rounded. Apical pinnae larger than the lateral ones. Fertile pinnae 2-4 pairs, positioned apically, rachis glabrous, with greatly reduced sporangia-bearing pinnae at the apex. Sporangia continuously distributed in fertile axes, greenish, turning rusty brown.

Selected material: **BRAZIL. Goiás:** Cristalina, *Filgueiras 1436* (UB); Paraúna: Ponte de Pedra, Parque Estadual de Paraúna, 16°5'16"' S 50°38'08" W, 1.VI.2013, *Faria, Moreira & Romão 3768* (RB, HUEG, UB); Rio Veríssimo, VII.1892, *E. Ule 240* (R). **Mato Grosso:** Nova Xavantina, 26.VIII.1967, *Richards & Argent 491* (NY, US); Rio Arinos, XI.1914, *Kuhlmann 58, 60* (R). **Minas Gerais:** Gouveia, 18°39'29.6" S 43°54'0.8" W, 900 m, 1.IX.2007, *Almeida 1260* (BHCB). Perdizes, 20.VII.1993, *Tameirão Neto 919* (BHCB, HB, RB); Santana de Garambeu, 18°37'51.9"S 43°56'47.1" W, 880 m, 6.VI.2007, *Almeida 1065* (BHCB); Santana de Pirapama, 21°35'23.4"S 44°08'33.8" W, 1100-1150 m, 7.VI.2001, *Salino 6958* (BHCB).

Osmunda piresii differs from *O. spectabilis* in the number of pair of pinnae (2–4 pairs x 7-12 pairs), form of the segments (ovate to elliptic x oblong to elliptic), and sporangia distribution (interrupted x continuously distributed in fertile axes – Fig. 3B). *Osmunda piressi* has terminal pinnulae proportionally larger than the lateral ones (Fig. 3A).

This species is endemic in the central part of Brazil, and it has been recorded in the states of Goiás, Mato Grosso, and Minas Gerais. It grows in wet fields, banks of streams

Figure 2. A- *Osmunda piresii* Brade. – Isotype (UB0034479) - Digital specimen image at the INCT Virtual Herbarium of Flora and Fungi (http://inct.florabrasil.net/). **B-** *Osmunda gracilis* Link – Holotype – Digital specimen images at the Herbarium Berolinense. Version: 09 Aug 2017. Data Publisher: Botanic Garden and Botanical Museum Berlin. http://herbarium.bgbm.org/object/B200077286.

and rivers, and exposed and wet hillsides, especially in quartzite cracks. It occurs only in the *Cerrado* (Central Brazilian Savanna) biogeographic province, between 500–1,150 m in elevation.

1b. *Osmunda spectabilis* Willd., Sp. Pl. (ed. 4) 5: 98. 1810. *Osmunda regalis* var. *spectabilis* (Willd.) A.Gray, Manual (ed. 2): 600. 1856. *Osmunda regalis* subsp. *spectabilis* (Willd.) Á.Löve & D.Löve, Taxon 26(2/3): 324. 1977. Type: — United States. Pennsylvania. "Habitat in Canada, Pennsylvania, Virginia", 1805, *G. H. E. Muhlenberg s.n.* (lectotype B- W 19504-01 0!, designated by Tryon & Stolze, Fieldiana, Bot. 20: 23. 1989; isolectotype S-P-7269!).

Figs. 1C; 4A-B.

=*Osmunda spectabilis* var. *brasiliensis* Hook. & Grev., Bot. Misc. 3: 230. 1833. *Osmunda regalis* var. *brasiliensis* (Hook. & Grev.) Kunze, Linnaea 18: 308. 1844[1845]. Type: — Brazil. Rio de Janeiro, Serra dos Órgãos, *W. Swainson s.n.* (lectotype K000589312! Designated by Arana & Ponce, Darwiniana 3(1): 30.2015).

=*Osmunda palustris* Schrad., Gött. Gel. Anz.: 866. 1824. *Osmunda spectabilis* subsp. *palustris* (Schrad.) Á.Löve & D.Löve, Taxon 26(2/3): 324. 1977. Type : — Brazil, V-1816, *M. von Wied-Neuwied [36]*, (lectotype BR 0000005849567!; isolectotype BR0000005838035!, designated by Arana & Ponce, Darwiniana 3(1): 30. 2015).

=***Osmunda gracilis*** Link, Hort. Berol. 2: 145. 1833. Type: — "America meridionali", sine data, sine col. (holotype B 20 0077286!,). **Syn. Nov**. (Fig. 2B)

Terrestrial plants. Rhizome massive, creeping; apex often somewhat erect, covered with reddish hairs. Fronds hemidimorphic, 2-pinnate; 30–140 x 20–30 cm; petioles 1/3 length of the laminae, winged, with light brown hairs when young, glabrate at maturity. Sterile part of the laminae broadly ovate; pinnae 7–12 pairs, lanceolate, proximate to almost overlapping; pinnules alternate or subalternate, short-stalked (0.1cm), oblong to elliptic, usually auriculate, base oblique to somewhat truncate, margins dentate to serrulate, apex acute to rounded. Fertile pinnae 4–8 pairs, positioned apically, rachis glabrous, with greatly reduced sporangia-bearing pinnae at apex. Sporangia with dense distribution in fertile axes, greenish, turning red, then rusty brown.

Selected Material: **BRAZIL. Bahia:** Parque Nacional da Boa Nova, 6.I.2013, *Aona et. al 1915* (HURB, RB). **Distrito Federal:** Parque do Guará, s.d. *Heringer 13270* (R). **Espírito Santo:** Santa Maria do Jetibá, 19.XII.2007, *Kollmann 10221* (MBML). **Goiás:** s.d., *Ule 799* (R). **Mato Grosso:** Rio Arinos, XI.1914, *Kuhlmann 58* (R). **Mato Grosso do Sul:** Jataí, 9.XI.2004, *Lenhard 46* – UPCB. **Minas Gerais:** Serra do Picu, 9.IV.1879, *Netto et al. s.n.* (R 454); Poços de Caldas, 20.XI.1988, *Motta 1483* (MBM). **Paraná:** Morretes, 8.VIII.1968, *Hatschbach 19566* (MBM, RFA). **Rio de Janeiro:** Rezende, 10.V.1972, *Occhionni 4871* (RFA). **Rio Grande do Sul:** Cidreira, 12.I.2012, *Gonzatti 378* (FURB, RB, UCS). **Santa Catarina:** Bom Retiro, 25.XI.1985, *Smith*

Figure 3. *Osmunda piresii* Brade. **A-** Habit, showing the apical segment larger than the lateral ones (arrow); **B-** detail of the fertile pinna, showing sporangia with interrupted distribution in fertile axes (arrow). Images: *Faria et al. 3768* (RB01001189), Reflora – Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/).

Figure 4. *Osmunda spectabilis* Willd. **A-** General aspect of the fertile frond; **B-** Detail of fertile pinna, with sporangia completely covering the surface. Images: P. Labiak.

et al. 7946 (R). **São Paulo:** Ipiranga, VII.1941, *Lutz 1895* (R), Cotia, 25.XI.2011, *Lozano & Petean 792* (MBM).

This species has been classically treated as a synonym, variety, or subspecies of *Osmunda regalis* (Löve & Löve 1977; Smith 1981; Mickel & Beitel 1988; Tryon & Stolze 1989 (1990); Palacios-Ríos 1990, 1995; Kessler & Smith 2017), a European species that does not occur in America (Arana & Ponce 2015; 2016).

The species occurs throughout the New World, from Canada to Argentina and Uruguay. In Brazil, it occurs in Bahia, Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo. It can be found in the Cerrado and Atlantic Rainforest biomes, in ombrophilous or semideciduous seasonal forests, sandy coastal plains (*restinga*), and riverine forests. It grows in wet or marshy fields, streams, exposed hillsides, grasslands, and floodplains, in sunny or shaded places, from sea level to 1,700 m in elevation.

In the protologue of *Osmunda gracilis*, Link (1833) characterized the species mainly on the basis of the last segments ("pinnulae basis subauriculatae") and the overall reduced size of the specimen. After a morphological study of the holotype (Fig. 2B), we conclude that *Osmunda gracilis* was described using a specimen (collected in America meridionali?) under the morphological variation of *Osmunda spectabilis* and hence we propose synonymizing *Osmunda gracilis* under *Osmunda spectabilis*.

2. *Osmundastrum* C.Presl, Gefässbündel Farrn, 18. 1847. Type:—*Osmundastrum cinnamomeum* (L.) C.Presl (= *Osmunda cinnamomea* L.)

Terrestrial plants, moderate-sized to large. Rhizome erect, stout, woody, without scales. Fronds dimorphic; petioles arising as a crown at apex of rhizome, ± hairy when young, base of petiole swollen and with lateral flaplike stipules; laminae pinnate-pinnatisect, fertile portions reduced to a midrib with almost no laminar tissue present; pinnae articulate to rachis. Sporangia large, naked, with a small patch annulus.

One species; nearly worldwide in tropical and temperate regions in Asia and the Americas.

2. *Osmundastrum cinnamomeum* (L.) C.Presl, Gefässbündel Farrn: 18. 1847. *Osmunda cinnamomea* L., Sp. Pl. 2: 1066. 1753. *Struthiopteris cinnamomea* (L.) Bernh., J. Bot. (Schrader) 1801: 126. 1801. Type:— United States, Maryland ("Marilandia"), *P. Kalm s.n.* (lectotype LINN-HL-1244-12!, designated by Duek, Feddes Repert. 87: 329. 1976).

Figs. 1D; 5.

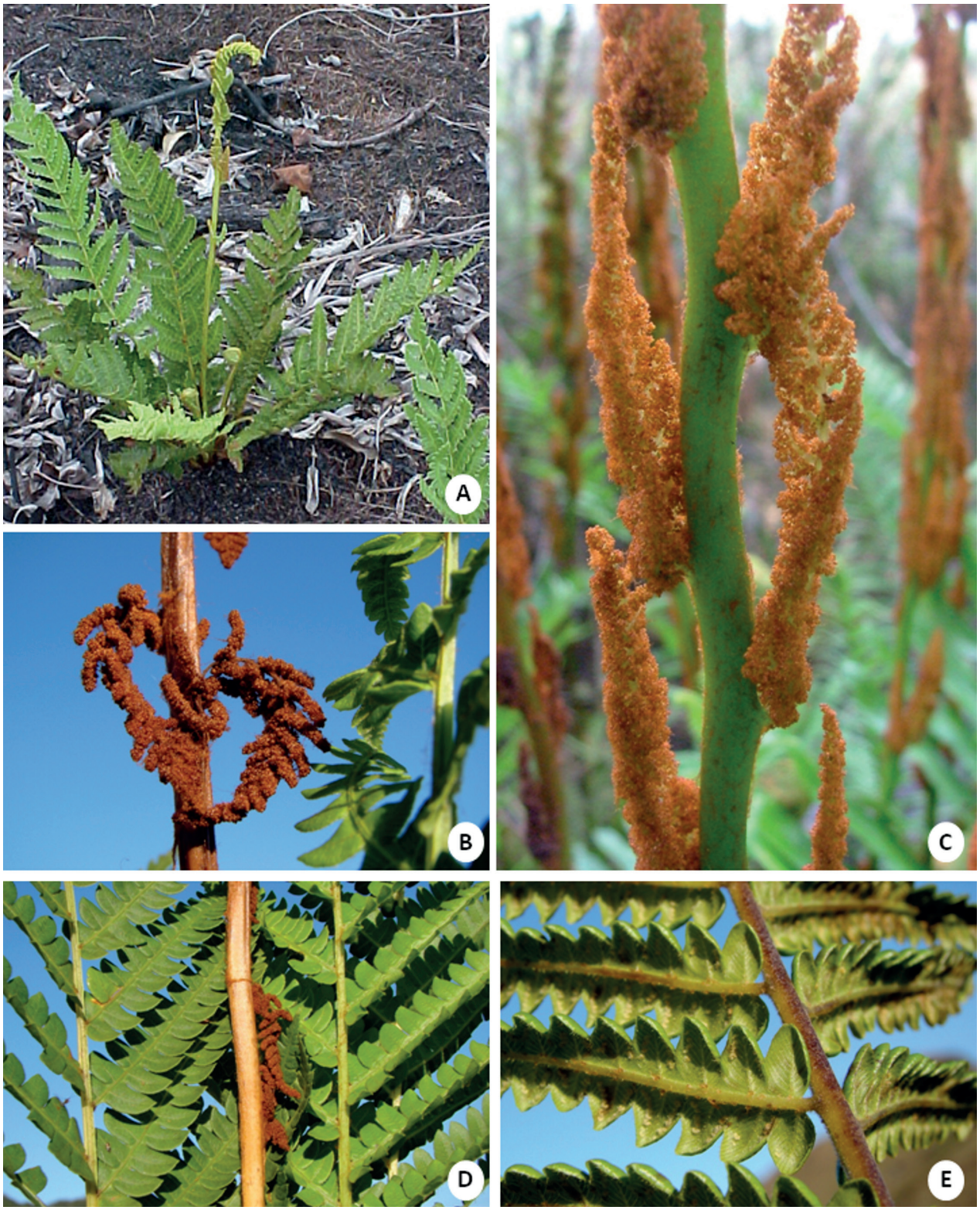

Figure 5. *Osmundastrum cinnamomeum* (L.) C. Presl. **A-** Habit; **B-** Fertile Pinnae; **C**- Fertile Pinnae in detail; **D-** Adaxial surface of a sterile pinna; **E-** Abaxial surface of a sterile pinna. Images: A: L. Sylvestre. B-E: P. Labiak.

=*Osmunda bipinnata* L., Sp. Pl. 2: 1065. 1753. *Anemia bipinnata* (L.) Sw., Syn. Fil.: 157. 1806. Type:—"Habitat in America meridionali". "*Osmunda latis crenis incisa*" in Plumier, Traité Foug. Amér.: t. 155. 1705! (lectotype designated by Proctor, Ferns Jamaica: 66. 1985).

=*Osmunda imbricata* Kunze, Farrnkräuter 2: 29, t. 112. 1849. *Osmunda cinnamomea* var. *imbricata* (Kunze) Milde, Monogr. Osmund.: 95. 1868. Type:—Venezuela. Mérida, 1846, *N. Funck & L. J. Schlim 1221* (lectotype LE 00000272! Designated by Arana & Ponce 2015; isolectotype, FR 0031898!).

Terrestrial plants. Rhizome creeping or ascending, short, bearing approximate fronds seemingly in a crown. Fronds dimorphic, young fronds densely covered with long, lax hairs, glabrescent and nearly naked when mature; petiole short, enlarged and winged at base; sterile fronds pale yellowish-green, pinnate-pinnatifid, ovate-lanceolate, 30–150 x 8–30 cm, chartaceous or papyraceous, gradually narrowed toward an acuminate apex; pinnae sessile, more than 20 pairs, 5–15 × 1.5–3 cm, incised ca. 2/3 toward costa, apex acuminate; lobe margins entire, margin with hairs, apex rounded; lateral veins forked; fertile fronds usually shorter and developing earlier than sterile, 2-pinnate; pinnae sessile, 2–4 × ca. 1.5 (2) cm, incised almost to costa; ultimate segments 0.2–0.4 cm wide, covered throughout with sporangia.

Selected material: **BRAZIL. Bahia:** Município de Água Quente. Arredores de Pico das Almas, 26.III.1980, *Mori & Benton s.n.* (RB 225411). **Espírito Santo:** Castelo. Parque Estadual do Forno Grande. Trilha do Rio Manso, 20.VII.2008, *Labiak et al. 4884* (RB, MBML, CEPEC, UPCB). **Minas Gerais:** Tacambira, Santa Cecília, Carandaí, I.1960, *Duarte 5075* (RB, SF). **Paraná:** São José dos Pinhais, Guaricana, 22.X.2008, *Cordeiro & Vaz 2998* (MBM). **Rio de Janeiro:** Marambaia, Restinga da Marambaia, 15.IV.2003, *Condack & Sylvestre 61* (RBR); Rio de Janeiro, Recreio dos Bandeirantes, Parque Zoobotânico do Marapendi, 9.IV.1992, *Sylvestre & de La Sota 784* (RB). **Rio Grande do Sul:** Pelotas, 19.X.1960, *Brauner & Sehnem 141* (HB). **Santa Catarina:** Atalanta, 08.XI.2014, *Bittencourt et al. 297* (FURB). **São Paulo:** Analândia, 10.V.2012, Lombardi & Souza 9313 (MBM); Serra da Bocaina, 12.V.1951, *Brade 20958* (RB).

In the New World, the species is represented by two varieties: *O. cinnamomeum* var. *cinnamomeum*, present in Brazil, and *O. cinnamomeum* var. *glandulosum*, endemic to the Atlantic coastal plains of the United States (McAvoy 2011).

Osmundastrum cinnamomeum occurs in Southeast Asia and the Americas, where it is found in Canada, the United States, Mexico, Guatemala, Honduras, Costa Rica, Colombia, Ecuador, Peru, Bolivia, Paraguay, Argentina, Uruguay, and Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo states). This species probably occurs in Mato Grosso do Sul, but we were unable to verify the single specimen collected there. It can be found in wet, marshy places and the banks of streams and watercourses. It grows in the Atlantic Rainforest, Cerrado, and Pampa biomes, in ombrophilous or semideciduous seasonal forests, sandy coastal plains (*restinga*), and riverine forests, from sea level to about 1,900 m.

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