CECÍLIA VIEIRA MIRANDA

ESTUDOS TAXONÔMICOS E FILOGENÉTICOS EM *Oleandra* CAV. (OLEANDRACEAE, POLYPODIOPSIDA) PARA A REGIÃO NEOTROPICAL

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientador: Pedro Bond Schwartsburd

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Assentimento:

Cecília Vieira Miranda

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Autora

Pedro Bond Schwartsburd
Orientador

Dedico este trabalho aos meus pais
Ronaldo e Celina

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BIOGRAFIA

Cecília Vieira Miranda, filha de Ronaldo Miranda e Celina de Cássia Baião Vieira Miranda, nasceu em Viçosa/MG em 27/01/1992.

Cursou parte do ensino fundamental na Escola Municipal Ministro Edmundo Lins, e o restante e o ensino médio no Colégio Equipe de Viçosa, ambos na cidade de Viçosa/MG.

Possui graduação em Ciências Biológicas pela Universidade Federal de Viçosa (2015). Tem experiência na área da Biologia Vegetal, atuando principalmente na Taxonomia e Sistemática de Samambaias. Foi estagiária durante 3 anos no Herbário VIC-UFV, onde realizou trabalhos usuais de herbário, trabalhos de informatização de herbário (BRAHMS), acompanhou trabalhos de Etnobotânica e iniciou sua Iniciação Científica na linha de pesquisa Taxonomia e Sistemática de Criptógamas. Também durante a graduação participou de projetos de extensão, na área de Educação Ambiental, principalmente fazendo parte do grupo Trilheiros do Sauá.

No Mestrado em Botânica, também concluído pela Universidade Federal de Viçosa (2017), Programa de Pós-Graduação em Botânica, realizou a revisão do gênero de samambaias aquáticas *Salvinia* Ség. (Salviniaceae) para as regiões sul e sudeste do Brasil.

Iniciou o Doutorado em Botânica, pela Universidade Federal de Viçosa, Programa de Pós-Graduação em Botânica, em julho de 2017, concluindo em fevereiro de 2022.

“O aspecto mais impressionante do mundo vivo é a sua diversidade. Não existem dois indivíduos iguais em populações que se reproduzem sexuadamente, nem duas populações, espécies ou táxons mais elevados que sejam iguais. Para onde quer que olhemos na natureza, encontramos singularidade”.

(Ernst Mayr)

RESUMO

MIRANDA, Cecília Vieira, D.Sc., Universidade Federal de Viçosa, fevereiro de 2022. **Estudos taxonômicos e filogenéticos em *Oleandra* Cav. (Oleandraceae, Polypodiopsida) para a região Neotropical**. Orientador: Pedro Bond Schwartsburd.

No presente trabalho, 23 espécies de *Oleandra* são reconhecidas para a região Neotropical, com um total de 8 táxons sendo novos à ciência, principalmente pela observação de um complexo de espécies pilosas dentro do gênero, o complexo *Oleandra pilosa*. Foram propostos três grupos morfológicos: 1) espécies com escamas do rizoma adpressas e filopódios tipo-rizoma; 2) espécies com escamas do rizoma adpressas e filopódios tipo-pecíolo; e 3) espécies com escamas do rizoma patentes e filopódios tipo-pecíolo. Das 23 espécies reconhecidas, 13 são endêmicas. Os estudos filogenéticos não apresentaram muitas resoluções, principalmente entre as espécies da Floresta Atlântica, porém a filogenia nos mostrou que os grupos morfológicos propostos são artificais, apesar de úteis para o reconhecimento das espécies. Clados geográficos foram bem definidos, e a evolução dos caracteres reforçaram que o gênero possui evolução muito recente, com muitas homoplasias. O trabalho inclui chave de identificação para as espécies neotropicais de *Oleandra*, descrições dos táxons, sinonímias, tipificações, ilustrações, materiais examinados, comentários taxonômicos, além de árvore filogenética e árvores de evolução dos caracteres.

Palavras-chave: Taxonomia. Samambaias. Biologia Molecular.

ABSTRACT

MIRANDA, Cecília Vieira, D.Sc., Universidade Federal de Viçosa, February, 2022. **Taxonomic and molecular studies in *Oleandra* Cav. (Oleandraceae, Polypodiopsida) to the Neotropics**. Adviser: Pedro Bond Schwartsburd.

In the present work, 23 species of *Oleandra* are recognized for the Neotropical region, with a total of 8 taxa being new to science, mainly due to the observation of a complex of hairy species within the genus, the *Oleandra pilosa* complex. Three morphological groups were proposed: 1) species with adpressed stem scales and stem-like phyllopodia; 2) species with adpressed stem scales and stipe-like phyllopodia; and 3) species with squarrose stem scales and stipe-like phyllopodia. Among the 23 recognized species, 13 are endemic. Phylogenetic studies did not present many resolutions, especially among Atlantic Forest species, but phylogeny showed us that the proposed morphological groups are artificial, despite being useful for species recognition. Geographic clades were well defined, and the evolution of characters reinforced that the genus has a very recent evolution, with many homoplasies. The work includes an identification key for the Neotropical species of *Oleandra*, descriptions of the taxa, synonyms, typifications, illustrations, examined materials, taxonomic comments, as well as a phylogenetic tree and trees of character evolution.

Keywords: Taxonomy. Ferns. Molecular Biology.

SUMÁRIO

INTRODUÇÃO GERAL

Pode-se dizer que o gênero *Oleandra* Cav. era, até o presente momento, um dos grupos mais defasados em estudos taxonômicos dentro das samambaias. Como abordado nos capítulos subsequentes desta tese, apenas dois estudos taxonômicos com caráter revisional haviam sido conduzidos com o gênero para as espécies neotropicais, sendo estes dois estudos muito antagônicos. Maxon (1914) apresenta uma revisão mais ampla, com a descrição de diversas novas espécies, enquanto Tryon (1997) adota uma abordagem muito mais restritiva, considerando pouquíssimas espécies e sinonimizando várias das espécies de Maxon (1914). Portanto, um novo estudo taxonômico se fazia necessário com o gênero, levando em consideração estes dois principais trabalhos, mas também analisando novamente as coleções, inclusive, com muitos materiais posteriores à Maxon (1914). O gênero *Oleandra* apresenta uma distribuição pantropical, e somando-se os resultados desta tese com o trabalho de Roux (2009) para a África, e de Hovenkamp & Ho (2012) para a Ásia, têm-se hoje entre 35-40 espécies de *Oleandra* para o mundo.

Ao longo dos trabalhos realizados com o gênero *Oleandra*, desde 2016, viemos observando dentro do gênero a existência de complexos de espécies, com nomes comumente muito utilizados nas identificações de herbários representando várias espécies diferentes. Foi o que aconteceu no trabalho de Schwartsburd et al. (2016) com a espécie *Oleandra articulata* (Sw.) C. Presl. Neste trabalho, dentro do nome *Oleandra articulata*, descreveu-se outras três espécies novas e um possível híbrido, e observou-se que a espécie mais amplamente distribuída para a Floresta Atlântica se tratava de *Oleandra brasiliana* Schwartsb & J. Prado, e não *Oleandra articulata* como se pensava.

Já no trabalho mais recente, de revisão do gênero para o neotrópico, Miranda & Schwartsburd (2021, *in press*) notaram que o mesmo acontecia com *Oleandra pilosa* Hook. Vários espécimes pilosos e diferentes eram observados nos herbários, todos identificados como *Oleandra pilosa*. Porém, através da diferença nos filopódios, no tamanho e textura da lâmina, e nas partes da planta que apresentam a pilosidade, conseguimos firmar a espécie *Oleandra pilosa s.str.* além de descrevermos outras 5 espécies novas.

Outro ponto muito trabalhado nesta tese relacionado à morfologia do gênero *Oleandra* foi a presença de grupos morfológicos dentro do gênero. Miranda et al. (2021) modificaram as concepções de Maxon (1914), que acreditava na existência de dois grupos morfológicos bem distintos, e propuseram a existência de três grupos morfológicos, com um grupo intermediário entre os dois grupos de Maxon (1914). Estes grupos morfológicos se apresentam como uma ótima ferramenta na identificação das espécies de *Oleandra*, porém, com a filogenia molecular preliminar e evolução de caracteres apresentada nesta tese, podemos concluir que estes grupos não são monofiléticos, mas ainda assim são úteis para a taxonomia do gênero.

Em relação a estudos moleculares com o gênero *Oleandra*, estes são ainda mais escassos do que os estudos morfológicos, apenas existindo algumas espécies incluídas em estudos mais abrangentes. Nesta tese, apresenta-se uma filogenia molecular preliminar para o gênero, com a inclusão de espécies neotropicais e paleotropicias, além de uma evolução de caracteres.

Durante a tese, além dos trabalhos específicos com o gênero *Oleandra*, houveram outras produções com outros grupos de pteridófitas:

1. Avaliação do gênero *Salvinia* para a lista da flora ameaçada de extinção no ES, disponível no livro: Fraga et al. (orgs.) (2019) Fauna e flora ameaçadas de extinção no estado do Espírito Santo. ISBN 978-65-81414-01-6.

2. Monografias de *Salvinia*, *Azolla* e *Pellaea* para a Flora do Brasil 2020. Disponível em:http://floradobrasil.jbrj.gov.br/reflora/listaBrasil/PrincipalUC/PrincipalUC.do?lingua=pt#CondicaoTaxonCP

3. Pena, N.T.L & Miranda, C.V. (2020) Ferns and lycophytes from a forest associated with quartzitic rocky outcrops in southern Espírito Santo, Brazil. Heringeriana 14(1): 33−48. Este artigo trata da lista de samambaias e licófitas associadas a quartzitos em uma localidade do ES. Ele se encontra em anexo ao final da Tese.

REFERÊNCIAS BIBLIOGRÁFICAS

Hovenkamp P, Ho B-C (2012) A revision of the fern genus *Oleandra* (Oleandraceae) in Asia. Phytokeys 11:1–37.

Maxon WR (1914) The American species of *Oleandra*. Contributions from the United States National Herbarium 17:392–398.

Miranda CV, Schwartsburd PB, Labiak PH, Prado J (2021) Three new species of *Oleandra* (Oleandraceae, Polypodiopsida) from the Neotropics, and notes on the morphological groups among the Neotropical species. Brittonia 73(2): 1–9.

Roux JP (2009) Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar, and neighbouring islands. Strelitzia 23:1–296.

Schwartsburd PB, Miranda CV, Prado J (2016) *Oleandra* (Oleandraceae) in the Brazilian Atlantic Forest. American Fern Journal 106(3): 191–205.

Tryon RM (1997) Systematic notes on *Oleandra*. Rhodora 99 (900): 335–343.

ARTIGOS CIENTÍFICOS

Este estudo encontra-se organizado sob a forma de artigos científicos, como disposto nas normas de redação de teses da Universidade Federal de Viçosa. Cada artigo segue as normas da revista a que foi ou será submetido.

Capítulo I. Miranda, C. V., P. B. Schwartsburd, P. H. Labiak & J. Prado. Three new species of *Oleandra* (Oleandraceae, Polypodiopsida) from the Neotropics, and notes on the morphological groups among the Neotropical species. Brittonia 73: 143–151.

Capítulo II. Miranda, C. V. & P. B. Schwartsburd. A taxonomic revision of the Neotropical species of *Oleandra* (Oleandraceae, Polypodiopsida). – Submetido ao periódico American Fern Journal.

Capítulo III. Miranda, C. V. & P. B. Schwartsburd. Uma filogenia preliminar de *Oleandra* (Oleandraceae, Polypodiopsida) – Periódico ainda a ser definido.

Anexo I. Pena, N.T.L & Miranda, C.V. (2020) Ferns and lycophytes from a forest associated with quartzitic rocky outcrops in southern Espírito Santo, Brazil. Heringeriana 14(1): 33−48.

Capítulo I. Miranda, C. V., P. B. Schwartsburd, P. H. Labiak & J. Prado. Three new species of *Oleandra* (Oleandraceae, Polypodiopsida) from the Neotropics, and notes on the morphological groups among the Neotropical species. Brittonia 73: 143–151.

Three new species of *Oleandra* (Oleandraceae, Polypodiopsida) from the Neotropics, and notes on the morphological groups among the Neotropical species

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Abstract: Three new species of *Oleandra* from the Neotropics are described, illustrated, and compared to similar species. ***Oleandra amazonica*** and ***O. steyermarkii*** are endemic to the Guiana Shield, whereas ***O. hovenkampii*** has an apparent disjunct distribution, being known from Peru and Costa Rica. We also re-define the informal, morphological groups of Neotropical *Oleandra:* 1. Species with slender, creeping stems clothed with squarrose, spreading scales, and forming stipe-like phyllopodia, with alternate and spaced phyllotaxy; 2. An intermediate group between groups 1 and 3, composed of species with mostly slender, creeping stems clothed with appressed scales, and forming stipe-like phyllopodia, with mixed phylotaxy (alternate in some species, tending to verticilate in others); and 3. Species with stout, climbing to ascending stems clothed with appressed scales, and forming stem-like phyllopodia, with verticillate phyllotaxy. In total, we recognize 21 valid species for the Neotropics, and tentatively accommodate them in those three groups, each one with 9, 5, and 7 species, respectively.

Keywords: Amazon, biodiversity, endemism, ferns, high elevations, Mount Roraima.

Resumo (Português): Três espécies novas de *Oleandra* (Oleandraceae) da região neotropical são descritas, ilustradas e comparadas a espécies similares. ***Oleandra amazonica*** e ***O. steyermarkii*** são endêmicas ao Escudo das Guianas, e ***O. hovenkampii***, com uma aparente distribuição disjunta, é conhecida até o momento para o Peru e Costa Rica. É também proposta uma redefinição dos grupos morfológicos informais de *Oleandra* da região Neotropical: 1. Espécies com caules delgados, rastejantes, vestidos por escamas esquarrosas e patentes, formando filopódios do tipo "peciolar", e com filotaxia alterna e esparsa; 2. Um grupo intermediário entre os grupos 1 e 3 – espécies principalmente com caules delgados, rastejantes, vestidos por escamas adpressas, formando filopódios do tipo "peciolar", e com filotaxia mista (alterna em algumas espécies, tendendo a verticilada em outras); e 3. Espécies com caules grossos, trepadores a ascendentes, vestidos por escamas adpressas, formando filopódios do tipo "caulinar", e com filotaxia verticilada. No total, são reconhecidas 21 espécies válidas para a região Neotropical e elas são acomodadas nos três grupos, com 9, 5 e 7 espécies, respectivamente.

Oleandra Cav. is a monophyletic fern genus of Pantropical distribution, belonging to the monogeneric family Oleandraceae (sensu PPG I, 2016). It comprises 30–35 species worldwide (Maxon, 1914; Pichi-Sermolli, 1965; Murillo-Pullido et al., 2008; Hovenkamp & Ho, 2012;

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Schwartsburd et al., 2016). The number of Neotropical species has been subject to debate. Whereas Tryon (1997) recognized only four species, Maxon (1914) and more recent authors (e.g., Palacios-Ríos, 1995; Smith, 1995; Murillo-Pullido et al., 2008; Schwartsburd et al., 2016) recognized at most only 19.

Oleandra is characterized by long-creeping stems clothed with peltate scales, bearing long roots often named "rhizophores" because of their superficial resemblance to the rhizophores of Selaginellaceae (Wetter, 1951). The phyllopodia are conspicuous, articulate to the stipe, and support a simple leaf. Additionally, the leaves are monomorphic (in Neotropical species), the veins are typically free, and the sori are rounded and protected by reniform or cordiform indusia (Smith et al., 2008; Hovenkamp & Ho 2012). Two groups of Neotropical species were recognized by Maxon (1914). The first consisted of species with creeping, slender stems bearing squarrose scales (i.e., the bases of the scales are appressed but the apices are patent). The second group consists of species with stouter, ascending to climbing stems bearing appressed scales. Another interesting aspect of *Oleandra* is that some species might have specificity to substrates (Schwartsburd et al., 2016). This is the case in *O. quartziticola* Schwartsb. & J. Prado, for example, which appears to occur exclusively on quartz boulders.

In a review of the Brazilian Atlantic Forest species, Schwartsburd et al. (2016), demonstrated that the widely used name *Oleandra articulata* (Sw.) C. Presl was not correctly applied to the species in that region. Rather, they recognized it as a species-complex. In this paper we continue our studies on Neotropical *Oleandra*, describing two new species from the *Oleandra pilosa*--complex: *O. steyermarkii* Lellinger ex C. V. Miranda & Labiak and *O. hovenkampii* C. V. Miranda & Schwartsb. Additionally, we describe the glabrescent *O. amazonica* C. V. Miranda & J. Prado.

Methods

We analyzed about 650 specimens of *Oleandra* (including types) from the following herbaria: BHCB, CEPEC, CESJ, EAC, GH, HAS, HBRA, HEPH, HRCB, HUEFS, INPA, MBM, NY, OUPR, RB, SJRP, SP, UFP, UPCB, UPRRP, US, VIC, and VT (acronyms following Thiers, 2020). We also analyzed specimens and types from online resources, such as JSTOR Global Plants (https://plants.jstor.org/), Royal Botanic Gardens, Kew (https://apps.kew.org/herbcat/navigator.do), Royal Botanic Garden, Edinburgh (https://data.rbge.org.uk/search/herbarium), and SpeciesLink (http://www.splink.org.br/index).

We also consulted the two taxonomic revisions for the Neotropics (Maxon, 1914; Tryon, 1997) and the most relevant local floras, such as Scamman (1961), Tryon and Stolze (1991), Palacios-Ríos (1995), Smith (1995), Murillo-Pulido et al. (2008), Schwartsburd et al. (2016), and Kessler and Smith (2018). Morphological terms follow Lellinger (2002) and Hovenkamp and Ho (2012).

The distribution map was drawn using the software DIVA-GIS v.7.5 (Hijmans, 2013). We estimated locations through searches in Google Earth (http://www.google.com.br/intl/pt-PT/earth/), since the collections had no coordinate data. We used a layer containing administrative borders at country level, available from DIVA-GIS website (www.diva-gis.org), plus a grid of 10 × 10 degrees.

Results and discussion

NOTES ON THE MORPHOLOGICAL GROUPS OF NEOTROPICAL SPECIES

Maxon (1914) recognized two morphological groups among the Neotropical species of *Oleandra:* one with creeping, slender stems bearing squarrose, spreading scales, and another with stouter, ascending to climbing stems bearing appressed scales. In the first group, he placed *O. articulata* (Sw.) C. Presl*, O. bradei* Christ, and *O. hirta* Brack. In the second group, he included *O. costaricensis* Maxon*, O. decurrens* Maxon*, O. guatemalensis* Maxon*, O. lehmannii* Maxon, *O. panamensis* Maxon*, O. pilosa* Hook.*, O. trinitensis* Maxon, and *O. trujillensis* H. Karst. In the next couplet of his key, Maxon (1914: page 393) presented an important character that further segregated the second group into two sub-groups: the size and shape of the phyllopodia.

After analyzing the types of all described taxa of *Oleandra* from the Neotropics, and about 650 specimens, we feel it best to recognize three morphological groups instead of two. These informal groups need to be evaluated by molecular phylogenetic studies, but for now, they facilitate understanding the morphology and habit of the Neotropical species.

In our judgment, 21 Neotropical species of *Oleandra* can be recognized. Of these, 18 were previously described, and three are described here as new. These 21 species are assigned to the following three morphological groups:

Group 1.—Those species with slender, creeping stems clothed with squarrose, spreading scales, and forming stipe-like phyllopodia, with alternate and spaced phylotaxy. They are: *Oleandra articulata* s. str., *O. australis* Schwartsb. & J. Prado, *O. baetae* Damazio, *O. bradei, O. brasiliana* Schwartsb. & J. Prado*, O. hirta*, *O. hovenkampii*, *O. quartziticola* Schwartsb. & J. Prado, and *O. zapatana* Lellinger. Among them, *O. articulata*, *O. bradei,* and *O. brasiliana* have glabrescent to glabrous laminae, whereas the remaining species have pilose to lanose laminae.

Group 2.—Intermediate group between groups 1 and 3 – Those species with slender, creeping stems (except for *Oleandra lehmanni* and *O. amazonica,* which have stout, climbing to ascending stems) clothed with appressed scales, and forming stipe-like phyllopodia, with mixed phyllotaxy (alternate in some species, tending to verticilate in others). They are: *Oleandra amazonica, O. archeri* Maxon, *O. duidae* A.C. Sm., *O. lehmannii* (with *O. guatemalensis* in synonymy), and *O. steyermarkii.* Among them, only *O. steyermarkii* has lanose laminae; the other species are glabrescent to glabrous.

Group 3.—Those species with stout, climbing to ascending stems clothed with appressed scales, and forming stem-like phyllopodia, with verticilate phylotaxy. They are: *Oleandra costaricensis*, *O. decurrens*, *O. dura* Maxon, *O. panamensis*, *O. pilosa* s. str.*, O. trinitensis*, and *O. trujillensis*. Among them, *O. costaricensis, O. dura,* and *O. trinitensis* have glabrescent to glabrous laminae, whereas the remaining species have pilose to lanose laminae.

New species

Oleandra amazonica C.V. Miranda & J. Prado, **sp. nov.** Type:—Brazil, Amazonas: Santa Isabel do Rio Negro, Parque Nacional do Pico da Neblina, Igarapé Cuiabixi, 2060 m, 20 Sep 2012, *R.C. Forzza, G. Martinelli, D.P. Costa, M. A. Moraes, M. A. Nadruz & M. R. Blind 7192* (holotype: VIC, isotype: RB [RB00770091]) (Figs. 1A–E, 3A, B.)

Diagnosis: Differs from *Oleandra lehmannii* by the longer phyllopodia, 1.5–4.0 cm long (vs. 1.3–2.2 cm), acuminate to cuspidate laminar apices (vs. caudate), and flabelliform midrib scales (vs. deltate to lanceolate).

Plants epiphytic. ***Stems*** stout, 1–3 mm diam., climbing to ascending, dark brown, scaly, pruinose, with grabrescent, rhizophore-like roots; ***scales*** 4–6 mm long, lanceolate, subulate, appressed, imbricate, centrally and in the point of insertion blackish, orange at the margins with hyaline borders, virtually non-ciliate, but with scattered sessile and minute glands, 2 or 3-celled. ***Phyllopodia*** stipe-like, 1.5–4.0 cm long, glabrous. ***Leaves*** 15–25 cm long; ***stipes*** 1–2 cm long, light brown or greenish, glabrous, lustrous; ***laminae*** linear, acute at base, acuminate to cuspidate at apex, 11–22 × 1.7–2.3 cm, glabrescent, fully glabrous at maturity (young leaves sparsely hairy); ***midribs*** abaxially with flabelliform, light brown scales, 0.4–0.6 mm long, glabrescent on both sides; ***veins*** free, furcate, 12–14 per centimeter, glabrescent on both sides; ***laminar tissue between the veins*** glabrescent on both sides; ***margins*** glabrescent (with caduceous hairs, 0.2–0.5 mm long). ***Sori*** inframedial to medial; ***indusia*** orbicular-reniform, bicolorous, dark brown in the center, light brown in the margins, glabrous; ***spores*** monolete, light brown.

Distribution.—Probably endemic to the Guiana Shield; known only from the state of Amazonas in northern Brazil; 2060 m elevation (Fig. 4).

Etymology.—The specific epithet refers to the Amazonian distribution of the species.

Because of its stems with appressed scales and stipe-like phyllopodia (Figs. 1A, 3A), *Oleandra amazonica* belongs to our second, informal morphological group. Among the Neotropical species, it most resembles *O. archeri, O. duidae, O. lehmannii* (with *O. guatemalensis* in synonymy), and *O. steyermarkii.* Because of its linear laminae, scaly midribs, and glabrous laminar tissue between veins (at maturity), *O. amazonica* especially resembles *O. lehmannii*. However, *O. lehmannii* differs in having shorter phyllopodia (1.3–2.2 cm long vs. 1.5–4.0 cm long), lamina apices caudate (vs. acuminate to cuspidate), the laminar bases cuneate to

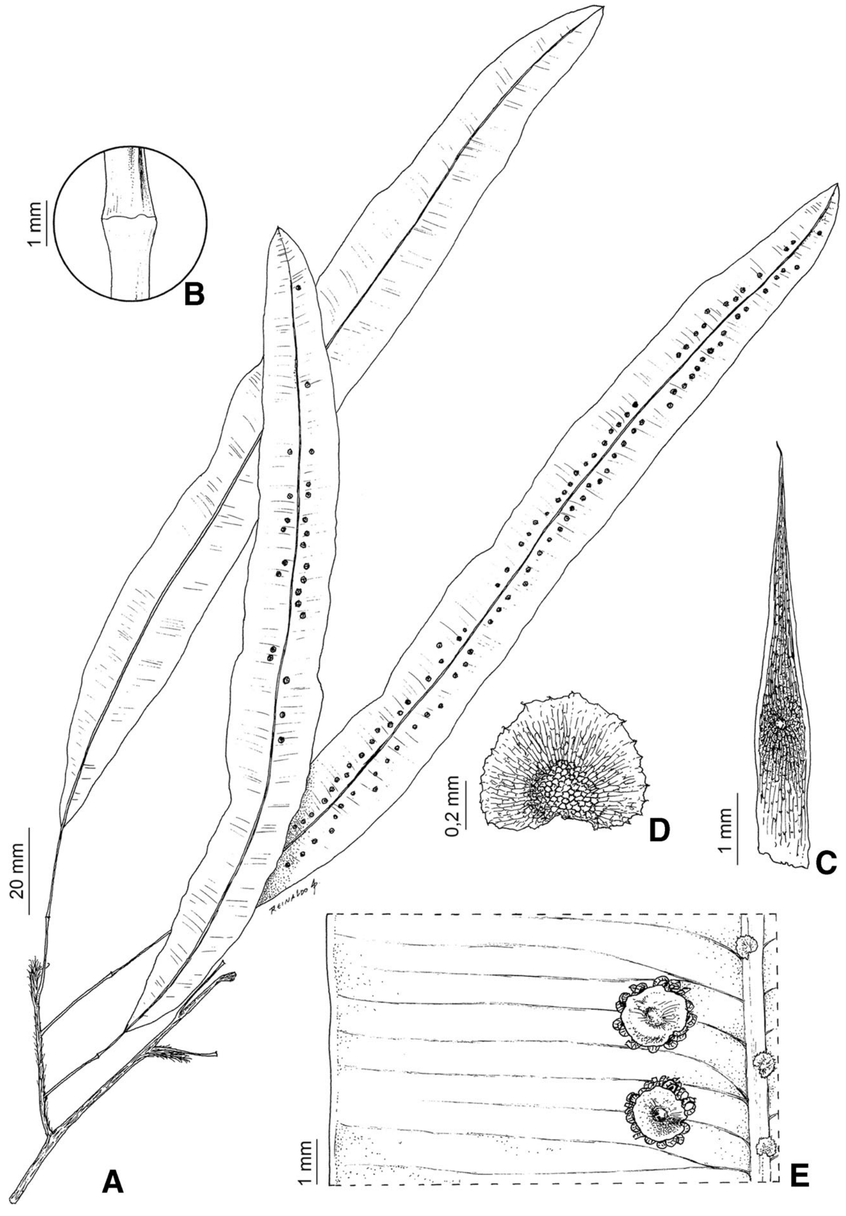

FIG. 1. *Oleandra amazonica*. **A.** Habit. **B.** Detail of the attachment between phyllopodium and stipe. **C.** Stem scale. **D.** Midrib scale, **E.** Lamina, abaxially, showing midrib scales, glabrous veins, laminar tissue, laminar margins, sori, and indusia.

attenuate (vs. acute), midribs with deltate to lanceolate scales (vs. flabelliform), and higher number of veins per centimeter (20–28 vs. 12–14) (Figs. 1A–E, 3A, B).

Oleandra archeri and *O. duidae* are easily distinguished by their elliptical laminae and by the absence of scales on the midribs. *Oleandra steyermarkii* differs by lanose laminae.

Oleandra hovenkampii C. V. Miranda & Schwartsb., **sp. nov.** Type:—Peru, San Martín: Tingo María, 625–1100 m, 30 Oct 1949–19 Feb 1950, *H. A. Allard 21,581* (holotype: US [US01581811]). (Figs. 2A–C, 3C.)

Diagnosis: Differs from *Oleandra baetae* by the acute to obtuse laminar bases (vs. truncate or inequilateral) and lanose, eglandular laminar hairs, 4–5 mm long (vs. laminae

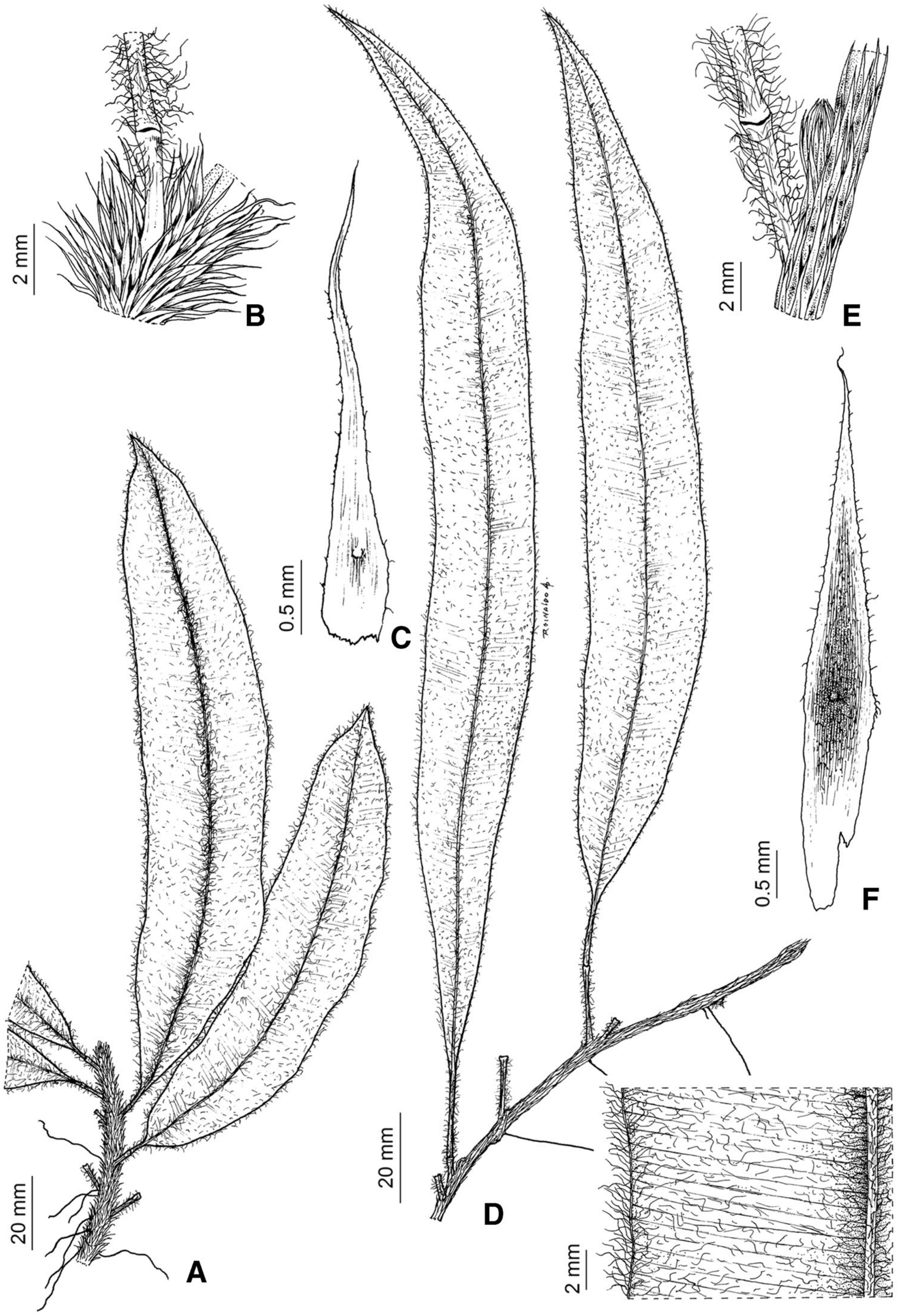

FIG. 2. *Oleandra hovenkampii*. **A.** Habit. **B.** Detail of the stem, phyllopodium and stipe. **C.** Stem scale. **D–G.** *Oleandra steyermarkii*: **D.** Habit. **E.** Detail of the stem, phyllopodium and stipe. **F.** Stem scale. **G.** Lamina, abaxially, showing lanose midrib, veins, laminar tissue, and laminar margins.

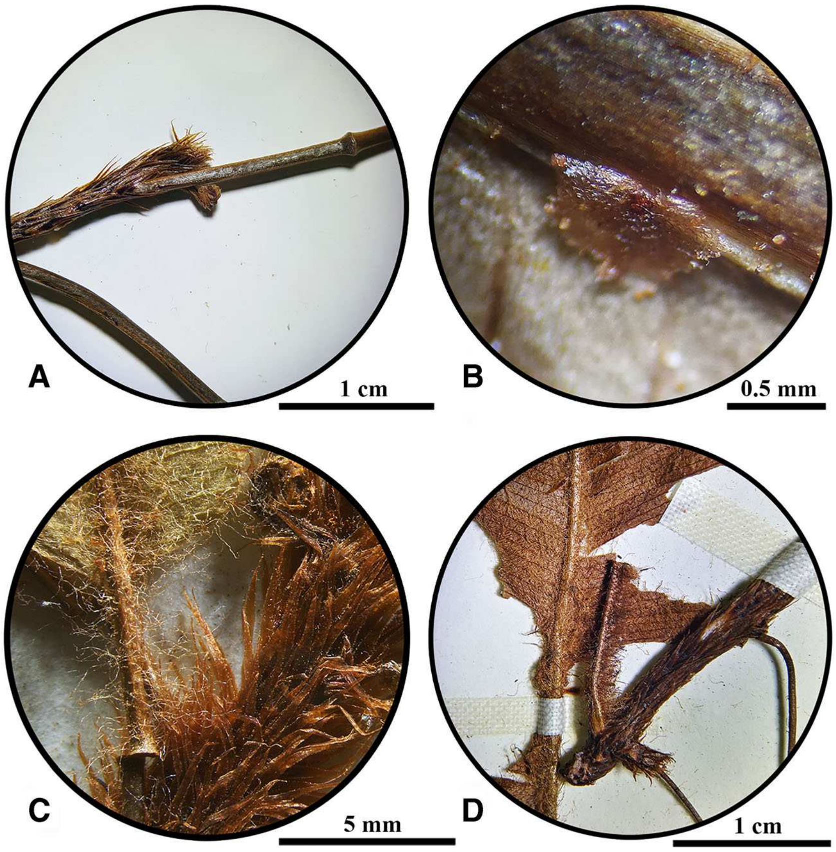

Fig. 3. Morphological details of three species of Neotropical *Oleandra*. **A.** *Oleandra amazonica*, detail of the stem, phyllopodium and stipe. **B.** *Oleandra amazonica*, midrib and midrib scale. **C.** *Oleandra hovenkampii*, detail of the stem, phyllopodium and stipe. **D.** *Oleandra steyermarkii*, detail of the stem, phyllopodium and stipe.

with pilose, glandular hairs, 0.3–0.5 mm long and pilose, eglandular hairs, 0.8–1.2 mm long).

Plants rupestrial. ***Stems*** slender, 2–4 mm diam., creeping, dark brown, scaly, pruinose, with pilose, rhizophore-like roots; ***scales*** 4–6 mm long, lanceolate, squarrose, darker only at the attachment point, orange in the remaining parts, margins with a few glandular cilia. ***Phyllopodia*** short, stipe-like, 3–4 mm long, lanose, the *hairs* eglandular, 4–5 mm long, shiny hyaline. ***Leaves*** 11–17 cm long; ***stipes*** short, 4–5 mm long, light brown, lustrous, lanose, the *hairs* similar to those on the phyllopodia; ***laminae*** elliptical, acute to obtuse at base, acute at the apex, 10.5–16.5 × 2.5–3.5 cm; ***midribs*** lanose on both sides, without scales; ***veins*** free, furcate, 12–14 veins per centimeter, lanose on both sides; ***laminar tissue between the veins*** lanose on both sides, *margins* lanose. ***Sori***, ***indusia***, and ***spores*** not seen.

Distribution.—Apparently with a disjunct distribution, known so far from Peru and Costa Rica (possibly also in other countries of the northern Andes); elevation unknown, probably around 1000–1520 m (Fig. 4).

Etymology.—The specific epithet honors the late pteridologist and professor Peter Hans Hovenkamp (1953–2019). Hovenkamp made several contributions to pteridology, especially from Southeast Asia, including the taxonomic revision of the Asian *Oleandra* (Hovenkamp & Ho, 2012).

Additional specimen examined. COSTA RICA. Cartago: Orosí, ca. 5000 ft., 24–31 Mar 1951, *Scamman 5914* (GH).

Oleandra hovenkampii is included among the species that present slender stems, squarrose stem scales, and stipe-like phyllopodia (our informal group 1). Because of its hairy laminae, it most

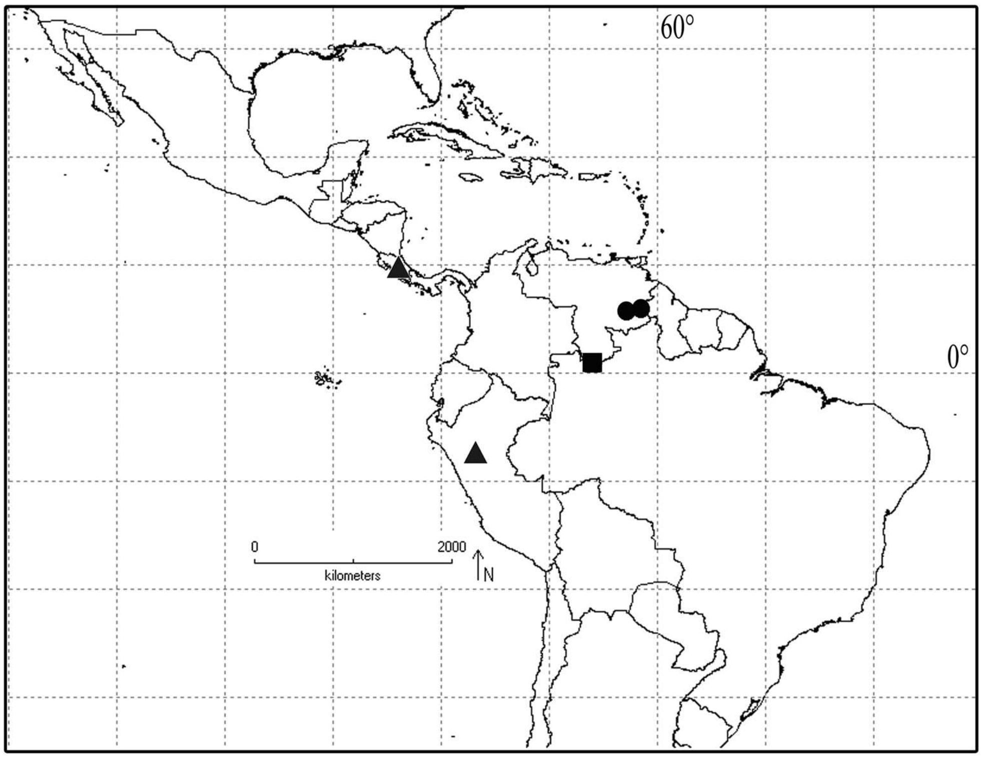

Fig. 4. Geographic distribution of *Oleandra amazonica* (square), *O. hovenkampii* (triangles), and *O. steyermarkii* (circles).

resembles *O. australis*, *O. baetae, O. hirta*, *O. quartziticola,* and *O. zapatana.* From these species, *O. hovenkampii* differs by longer hairs (4–5 mm vs. 0.8–1.2 mm) that impart a lanose aspect (vs. pilose aspect). Compared to *O. hirta*, *O. australis*, *O. quartziticola*, and *O. zapatana*, *O. hovenkampii* differs by the orange stem scales (vs. brown scales). *Oleandra baetae* also has orange stem scales but differs by truncate or inequilateral laminar bases, whereas *O. hovenkampii* has acute to obtuse laminar bases. Another striking difference between these two species is their indument: *O. baetae* is pilose, with glandular hairs 0.3–0.5 mm long and eglandular hairs 0.8–1.2 mm long, whereas *O. hovenkampii* is lanose, with only eglandular hairs 4–5 mm long (compare Figs. 2A–C and 3C with Figs. 1A–D in Schwartsburd et al., 2016:). Additionally, these two species occur at least 3700 km apart. *Oleandra baetae* is endemic to the Brazilian Atlantic Forest, whereas *O. hovenkampii* is known from Peru and Costa Rica (Fig. 4).

Oleandra steyermarkii Lellinger ex C. V. Miranda & Labiak, **sp. nov.** Type:—Venezuela, Bolívar: Cerro Venado, 1100 m, 21 Apr 1960, *J. A. Steyermark & S. Nilsson 442* (holotype: NY [NY00149743]; isotypes: NY [NY00951456], US-*n.v.* [US00799101]). (Figs. 2D–G, 3D.)

Diagnosis: Resembling *Oleandra amazonica*, *O. archeri*, *O. duidae*, and *O. lehmannii* by slender stems with appressed scales and stipe-like phyllopodia, but differing by the densely lanose laminae with hairs 4–5 mm long (vs. glabrescent to glabrous laminae).

Plants rupestrial (sandstone rocks). ***Stems*** slender, 2–3 mm diam., creeping, dark brown, scaly, pruinose, with glabrescent rhizophore-like roots; ***scales*** 3–5 mm long, lanceolate, appressed, imbricate, centrally and in the point of insertion blackish, orange at the margins and borders, with sparse cilia. ***Phyllopodia*** short, stipe-like, 0.5–1.1 cm long, lanose, the *hairs* conspicuous, long, tortuous, eglandular, hyaline with orange cross-wall of the cells, 4–5 mm long, also with a few long-ciliate scales. ***Leaves*** 16–30 cm long; ***stipes*** 1.0–2.2 cm long, light brown, sulcate adaxially, lustrous, lanose on both sides, the *hairs* similar to those on the phyllopodia; ***laminae*** linear, cuneate at base, cuneate at the apex, 15–28 × 1.7–4 cm; ***midribs*** lanose on both sides, without scales; ***veins*** free, furcate, 14–15 per centimeter, lanose on both sides; ***laminar tissue between the veins*** lanose on both sides; ***margins*** lanose. ***Sori***, ***indusia***, and ***spores*** not seen.

Distribution.—Probably endemic to the Guiana Shield, in northeastern Venezuela; 1100–1275 m elevation (Fig. 4).

Etymology.—The epithet honors the late Dr. Julian A. Steyermark, one of the most important collectors of Neotropical plants. He was also the collector of the type and the paratype of this species. This specific epithet was first used on herbarium specimen annotations by David B. Lellinger.

Additional specimens examined. VENEZUELA. Bolívar: Cerro Venado, parte sur-oeste, cerca de los limites con la Guayana Inglesa, 1220–1275 m, 6–7 Jan 1964, *J. A. Steyermark* et al. *92779* (GH, US).

Because of its slender stems, appressed scales, and stipe-like phyllopodia, *Oleandra steyermarkii* belongs to our informal group 2, along with *O. amazonica*, *O. archeri, O. duidae, O. guatemalensis*, and *O. lehmannii.* From these species, *O. steyermarkii* differs by densely lanose laminae with hairs 4–5 mm long. The other species have glabrescent to glabrous laminae.

Oleandra steyermarkii resembles *O. pilosa* s. str. (group 3) and *O. hirta* (group 1) by linear-elongate, hairy laminae. However, it is easy to distinguish *O. steyermarkii* from *O. hirta* due to its appressed stem scales (vs. squarrose) (Figs. 2E, 3D). *Oleandra pilosa* s. str. also has appressed scales on the laminae. However, whereas *O. pilosa* s. str. Has pilose laminae with hairs 1–2 mm long, and cuspidate to acuminate apices and acute bases, *O. steyermarkii* has lanose laminae (hairs 4–5 mm long), with cuneate apices and bases (Figs. 2D–G). *Oleandra steyermarkii* is apparently substrate-specific, occurring on sandstones. Unfortunately, substrate information is not available for *O. hirta* and *O. pilosa* s. str.

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Literature cited

Hijmans, R. J. 2013. DIVA-GIS, a geographic information system for the analysis of biodiversity data, Version 7.5. Available at: http://www.diva.gis.org

Hovenkamp, P. & B-C. Ho. 2012. A revision of the fern genus *Oleandra* (Oleandraceae) in Asia. PhytoKeys 11: 1–37.

Kessler, M. & A. R. Smith. 2018. Prodromus of a fern flora for Bolivia. XXXIX. Oleandraceae. Phytotaxa 344: 280.

Lellinger, D. B. 2002. A modern multilingual glossary for taxonomic pteridology. Pteridologia, vol. 3.

Maxon, W. R. 1914. Studies of tropical American ferns, no. 5. The American species of *Oleandra*. Contributions from the United States National Herbarium 17: 392–398.

Murillo-Pulido, M. T., J. Murillo-Aldana, A. León & L. A. Triana-Moreno. 2008. Los Pteridófitos de Colombia. Biblioteca José Jerónimo Triana No. 18. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.

Palacios-Ríos, M. 1995. *Oleandra* Cav. Pp. 289–290. In: R. C. Moran & R. Riba (volume eds.), Psilotaceae a Salviniaceae. *In:* G. Davidse, M. Sousa & S. Knapp. (general eds.), Flora Mesoamericana, vol. 1. Universidad Nacional Autónoma de México, Mexico City.

Pichi-Sermolli, R. E. G. 1965. Adumbratio Florae Aethiopicae. 11. Oleandraceae. Webbia 20: 745–769.

PPG I. 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 54: 563–603.

Scamman, E. 1961. The genus *Oleandra* of Costa Rica. Rhodora 63: 335–340.

Schwartsburd, P. B., C. V. Miranda & J. Prado. 2016. *Oleandra* (Oleandraceae) in the Brazilian Atlantic Forest. American Fern Journal 106: 191–205.

Smith, A. R. 1995. *Oleandra* Cav. Pp. 113–115. In: P. E. Berry, B. K. Holst, K. Yatskievych (vol. eds.), Pteridophytes, Spermatophytes: Acanthaceae-Araceae, *In:* J. A. Steyermark, P. E. Berry & B. K. Holst (gen. eds.), Flora of the Venezuelan Guayana, vol. 2. Missouri Botanical Garden Press, St. Louis.

Smith, A. R. , K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider & P. G. Wolf. 2008. Fern classification. Pp. 417–467. *In:* T. A. Ranker & C. H. Haufler (eds.), Biology and evolution of ferns and lycophytes. Cambridge University Press, Cambridge, UK.

Tryon, R. M. 1997. Systematic notes on *Oleandra*. Rhodora 99(900): 335–343.

Tryon, R. M. & R. G. Stolze. 1991. Pteridophyta of Peru. Part IV: 17. Dryopteridaceae. Fieldiana: Botany, new series 27: 96–98.

Wetter, C. 1951. Über die Luftwurzeln von *Oleandra*. Planta (Berlin) 39: 471–475.

Capítulo II. Miranda, C. V. & P. B. Schwartsburd. A taxonomic revision of the Neotropical species of *Oleandra* (Oleandraceae, Polypodiopsida). – Submetido ao Periódico American Fern Journal.

A Taxonomic Revision of the Neotropical Species of *Oleandra* (Oleandraceae, Polypodiopsida)

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ABSTRACT.—The present work is a taxonomic revision of the neotropical species of *Oleandra*. The study was mainly based on the analysis of types and regular specimens of herbaria in Brazil and the United States. Twenty three species are here recognized, being 13 of them endemic, and 5 new to science: *Oleandra aequatorialis*, *O. arbuscula*, *O. areniticola*, *O. nigropaleacea* and *O. nigrovenia.* Three informal morphological groups are recognized. The taxonomic treatment includes keys to taxa, synonymies, taxa descriptions, illustrations, examined material, and taxonomic comments.

KEY-WORDS.—Eupolypods, ferns, pteridophytes, South America, taxonomy

RESUMO (PORTUGUESE).—O presente trabalho é uma revisão taxonômica das espécies neotropicais de *Oleandra*. O estudo baseou-se principalmente na análise dos tipos e exsicatas de herbários no Brasil e nos Estados Unidos. Vinte e três espécies são aqui reconhecidas, sendo 13 delas endêmicas e 5 novas para a ciência: *Oleandra aequatorialis*, *O. arbuscula*, *O. areniticola*, *O. nigropaleacea* e *O. nigrovenia*. Três grupos morfológicos informais são reconhecidos. O tratamento taxonômico inclui chave para os táxons, sinonímias, descrições dos táxons, ilustrações, materiais examinados e comentários taxonômicos.

Oleandra Cav. is a monophyletic fern genus of Pantropical distribution, belonging to the monogeneric family Oleandraceae (sensu PPG I, 2016). It comprises 35–40 species worldwide (Hovenkamp and Ho, 2012; Miranda *et al.*, 2021; Roux, 2019). The number of Neotropical species has been subject to debate. Whereas Maxon (1914) recognized 11 species, Tryon (1997) recognized only four species, and Miranda *et al.* (2021) recognized 19 species.

Morphologically, the genus is well delimited and easy to recognize. *Oleandra* is characterized by long-creeping stems clothed with peltate scales, bearing long roots often named "rhizophores" [because of their resemblance to the rhizophores of Selaginellaceae, but they are real roots, according to Wetter (1951)], and conspicuous phyllopodia from which a simple leaf is attached, forming an articulated stipe. Additionally, the leaves are monomorphic (in Neotropical species), the veins are typically free, and the sori are rounded and protected by a reniform or cordiform indusium (Hovenkamp and Ho, 2012; Smith *et al.*, 2008). Spores of *Oleandra* are also distinct for being columelated between the exine and perine (Liew, 1977). Another observed feature by Nayar, Bjapai, and Chandra (1968) refers to the distal part of the pedicels of the sporangia: these have glandular hairs or projections.

Two informal groups of Neotropical species were recognized by Maxon (1914): 1) species with creeping, slender stems bearing squarrose, spreading scales (*i.e.*, scales that are peltately attached, but the apexes are patent); and 2) species with stouter, ascending to climbing stems bearing appressed scales. However, Miranda *et al.* (2021) noted that some species did not fit into the two groups proposed by Maxon (1914), and so they proposed a third one: being an intermediate between the other two. However, molecular studies (Miranda and Schwartsburd, in prep.) are showing that the informal morphological groups, both from Maxon (1914) and from Miranda *et al.* (2021) conceptions, are not monophyletic, as they are not supported by phylogenetic trees.

An interesting aspect of *Oleandra,* pointed out by Schwartsburd, Miranda, and Prado (2016), is that some species might have specificity to substrates where they occur. This is the case of *O. quartziticola* Schwartsb. & J. Prado, for example, which appears to occur exclusively in quartz boulders.

Taxonomic history of the genus.—Oleandra was originally described by Cavanilles (1799), based on *Oleandra neriiformis* Cav. The name was derived from *Nerium oleander* L. (Apocynaceae), due to the resemblance of their leaves. Since then, the genus was included in several taxonomic categories within different families. Swartz (1801, 1806) did not recognize *Oleandra* as a valid genus, including its species within the broad genus *Aspidium* (Aspidiaceae/Dryopteridaceae). Presl (1836) and Smith (1841, 1842) reestablished the genus and, since then, its validity was no longer questioned, with the exception of Splitgerber (1840), who recognized *Oleandra* as a subgenus of *Aspidium*. Several authors (*e.g.*, Baker, 1870; Fée, 1852; Hooker, 1840) considered *Oleandra* as a member of the tribe Aspidieae (Polypodiaceae). However, Smith (1866), created a new independent tribe within the family Polypodiaceae, the tribe Oleandreae. In 1938, while Ogura (1938) suggested an independent family, Christensen (1938) placed *Oleandra* in Polypodiaceae subfam. Oleandroideae. Ching (1940) followed Ogura's opinion, and attempted to established the new family Oleandraceae, but the name was not validly published bescause it lacked a Latin diagnosis. Holttum (1947) also considered *Oleandra* within the subfamily Oleandroideae, but in the family Dennstaedtiaceae. Other subsequent authors considered *Oleandra* in the family Davalliaceae (Alston, 1959; Copeland, 1947; Tardieu-Blot 1958, 1964). Tindale (1961) also included *Oleandra* in Davalliaceae, but within the subfamily Oleandroideae. Finally, Pichi-Sermolli (1965) validated the family Oleandraceae.

Despite the validation of the family Oleandraceae, the genus position continued to vary a lot over the years, mainly among the families Dryopteridaceae and Davalliaceae, mostly associated with genera *Nephrolepis* Schott and *Arthropteris* J. Sm., but molecular studies indicated that the three genera do not form a clade. The monophyly of Oleandraceae and its positioning as sister group of Davalliaceae and Polypodiaceae are supported by phylogenetic studies based on chloroplast DNA sequences (Hasebe *et al.*, 1995; Schuettpelz and Pryer, 2007; Smith *et al.*, 2008; Tsutsumi and Kato, 2006).

Oleandraceae previously consisted of two others genera, in addition to *Oleandra*: *Arthropteris* and *Psammiosorus* C. Chr. (Kramer, 1990), in a classification based only on morphological data. Nevertheless, by means of molecular studies these two genera were not supported as sister group of *Oleandra*, showing them closer to the Tectariaceaese (Christenhusz, Zhang, and Schneider, 2011; Kuo *et al.*, 2011; Schuettpelz and Pryer, 2007; Smith *et al.*, 2008). Therefore, the family Oleandraceae was recircumscribed, being composed, then, solely by *Oleandra*.

MATERIAL AND METHODS

We analyzed ca. 650 specimens of *Oleandra* (including types) from the following herbaria: A, BHCB, CEPEC, CESJ, EAC, GH, HAS, HBRA, HEPH, HRCB, HUEFS, INPA, MBM, NY, OUPR, RB, SJRP, SP, UFP, UPCB, UPRRP, US, VIC, and VT (acronyms following Thiers 2020).

We also analyzed specimens and types from online resources, such as JSTOR Global Plants (https://plants.jstor.org/), Royal Botanic Gardens, Kew (https://apps.kew.org/herbcat/navigator.do), Royal Botanic Garden, Edinburgh (https://data.rbge.org.uk/search/herbarium), and SpeciesLink (http://www.splink.org.br/index).

Morphological terms follow Lellinger (2002), Hovenkamp and Ho (2012), Schwartsburd, Miranda, and Prado (2016), and Miranda *et al*. (2021). As pointed out by Schwartsburd, Miranda, and Prado (2016), some *Oleandra* spp. may bear both catenate and catenate-glandular hairs. Nevertheless, the gland (the globose tip of the hair) can only be seen under magnification of at least 80×, which is uncommon in regular stereoscopes. Thus, in this work we opted for not detailing the hairs, giving information only about the general indumentum (*i.e.*, the hairiness appearance) and general size of hairs. Roughly, we categorized the leaves into four states: glabrous, glabrescent, pilose (with hairs up to 1.5 mm long), and lanose (with 4–5 mm long hairs). Reinaldo Pinto prepared the illustrations.

RESULTS AND DISCUSSION

Diversity and distribuition.—We recognize a total of 23 taxa of *Oleandra* for the Neotropics, five species new to science and four names newly synonymized. Schwartsburd, Miranda, and Prado (2016) concluded that the widely used name *Oleandra articulata* (Sw.) C. Presl had been wrongly applied for the Brazilian Atlantic Forest species, and so they dismembered it into five endemic species and one putative hybrid. Here, we concluded that the same occurred with the widely applied name *Oleandra pilosa* Hook. *Oleandra pilosa s.l.*, a species already consolidated with the characteristics of a stem with appressed scales and stem-like phyllopodia, in fact has a mix of stipe-like and stem-like phyllopodia (Fig. 8E), being included into the informal morphological group 2, and not in group 3 (see in subsection

Morphological Groups). Therefore, the most part of plants identified as *Oleandra pilosa* are misidentified and refer to three different species of group 3, which present appressed scales, stem-like phyllopodia and some pilosity. *Oleandra pilosa s.str.* occurs in Central America, the Guyanas, and in the north region of Brazil.

Among the 23 species recognized in this work, 13 are endemic, being five species endemic to Brazil (*O. amazonica* C.V. Miranda & J. Prado, *O. australis* Schwartsb. & J. Prado, *O. baetae* Damazio, *O. hirta* Brack. and *O. quartziticola*), three endemic to Venezuela (*O. areniticola* C.V. Miranda & Schwartsb., *sp. nov.*, *O. nigrovenia* C.V. Miranda & Schwartsb., *sp. nov.* and *O. steyermarkii* Lellinger ex C. V. Miranda & Labiak), two endemic to Colombia (*O. nigropaleacea* Labiak, *sp. nov.* and *O. zapatana* Lellinger), one endemic to Ecuador (*O. aequatorialis* C.V. Miranda & Schwartsb., *sp. nov.*), *O. bradei* Christ (Costa Rica), and *O. trinitensis* Maxon (Trinidad). The other species are more widely distributed, especially *O. articulata*, *O. brasiliana* Schwartsb. & J. Prado, *O. pilosa,* and *O. costaricensis* Maxon.

We also observed in this work that in addition to *O. quartziticola*, another species apparently demonstrate an affinity with quartzite environments: *O. arbuscula* C.V. Miranda & Schwartsb., *sp. nov.* Already *O. areniticola*, *O. nigrovenia,* and *O. steyermarkii* are found in sandstone environments.

Morphological Groups.—In our judgment, 23 Neotropical species of *Oleandra* can be recognized: 15 previously described, plus three described in Miranda *et al.* (2021) and another five described here. These 23 species are also could be readily split into the three morphological, informal groups established by Miranda *et al.* (2021), with some updates. Although these groups are not monophyletic (Miranda & Schwartsburd, in prep.), they are still usefull for the taxonomy of the species.

Group 1. Those species with slender, creeping stems clothed with squarrose, spreading scales, and forming stipe-like phyllopodia, with alternate and spaced phylotaxy. They are: *Oleandra aequatorialis*, *O. articulata* s. str., *O. australis*, *O. baetae*, *O. bradei, O. brasiliana, O. hirta*, *O. hovenkampii* C.V. Miranda & Schwartsb., *O. quartziticola,* and *O. zapatana*. Among them, *O. articulata*, *O. bradei,* and *O. brasiliana* have glabrescent to glabrous laminae, whereas the remaining species have pilose to lanose laminae.

Group 2. Intermediate group between groups 1 and 3 – Those species with slender (except for *Oleandra lehmannii* Maxon and *O. amazonica,* which have stout stems), creeping or climbing to ascending stems clothed with appressed scales, and forming stipe-like phyllopodia (except *O. pilosa s. str.*, which have a mix of stipe-like and stem-like phyllopodia – Fig.8E), with mixed phyllotaxy (alternate in some species, tending to verticilate in others). They are: *Oleandra amazonica*, *O. duidae* A.C. Sm. , *O. lehmannii, O. nigrovenia, O. pilosa* and *O. steyermarkii.* Among them, *O. steyermarkii* has lanose laminae and *O. pilosa* and *O. nigrovenia* have pilose laminae; the other species are glabrescent to glabrous.

Group 3. Those species with stout, climbing to ascending stems clothed with appressed scales, and forming stem-like phyllopodia, with verticillate phylotaxy. They are: *Oleandra arbuscula*, *O. areniticola*, *O. costaricensis*, *O. decurrens* Maxon, *O. nigropaleacea*, *O. trinitensis*, and *O. trujillensis* Karst. Among them, *O. costaricensis* and *O. trinitensis* have glabrescent to glabrous laminae; the remaining species have pilose or lanose laminae.

TAXONOMIC TREATMENT

Oleandra Cav., Anales Hist. Nat. 2:115. 1799. *Aspidium* subg. *Oleandra* (Cav.) Splitg., Tijdschr. Natuurl. Gesch. Physiol. 7:411. 1840. Type: *Oleandra neriiformis* Cav. (as ‘‘*neriformis*’’). Figs. 1, 2.

Plants epiphytic or rupestrial. Stems long-creeping or ascending to climbing, dorsiventral, light brown to blackish (commonly greenish *in vivo*), pruinose or not, 1–5 mm diam., with glabrous, glabrescent or pilose rhizophore-like roots; peltate scales, squarrose or appressed, bicolorous at base (darker only at the attachment point, orange in the remaining parts) or entirely bicolorous (centrally blackish, orange at the margins), sparsely to densely glandular-ciliate. Phyllopodia 1–55 mm long, stipe-like or stem-like, glabrous/glabrescent, pilose or lanose, scaly or not. Leaves sparse or subfasciculate/fasciculate, monomorphic (in Neotropical taxa), articulated to phyllopodia, 8.5–55 cm long; stipes 0.3–7(–15) cm long, stramineous to dark brown, or greenish, scaly or not, glabrous, pilose or lanose; laminae simple, linear, lanceolate, oblong or elliptical; midribs with catenate and/or glandular hairs, glabrescent or glabrous, scaly or not; veins free or rarely partly anastomosing, with or without catenate and/or glandular hairs; laminar tissue between the veins with or without catenate and/or glandular hairs; laminar margins cartilagineous, with or without catenate and/or glandular hairs; sori infra-medial to medial, in one irregular row between midribs and laminar margins; indusia reniform or orbicular-reniform, glabrous or pilose; spores monolete, ellipsoid, non-green, columellate between the exospore and perispore.

KEY TO NEOTROPICAL SPECIES OF *OLEANDRA*

1. Phyllopodia stipe-like; stem scales appressed or squarrose

2. Stem scales squarrose..3

3. Plants glabrous or glabrescent

4.Stems pruinose.. *Oleandra bradei*

4.Stems not pruinose..5

5. Midribs with conspicuous and persistent deltoid/cordate reddish scales, midribs without hairs...*Oleandra articulata*

5. Midribs without scales or with caducous lanceolate light brown scales, midribs with sparse hairs ....*Oleandra brasiliana*

3. Plants pilose or lanose

6. Stem scales orange...7

7. Plants pilose, with hairs up to 2 mm long; lamina bases truncate or inequilateral..*Oleandra baetae*

7. Plants lanose, with hairs 4–5 mm long; lamina bases acute to obtuse ....*Oleandra hovenkampii*

6. Stem scales brown or orange only at the margins..8

8. Laminae linear, veins partly anastomosing.........................*Oleandra hirta*

8. Laminae linear-lanceolate or elliptical, veins free......................................9

9. Indusia pilose..*Oleandra zapatana*

9. Indusia glabrous...10

10. Laminar tissue beetwen the veins adaxially pilose...*Oleandra quartziticola*

10. Laminar tissue beetwen the veins adaxially glabrous or glabrescent..11

11. Laminae linear-lanceolate; laminar tissue beetwen the veins adaxially glabrescent; midribs abaxially with lanceolate scales..*Oleandra aequatorialis*

11. Laminae elliptical; laminar tissue between the veins adaxially glabrous; midribs lacking scales........................... *Oleandra australis*

2. Stem scales appressed..12

12. Plants pilose or lanose...13

13. Plants lanose, with hairs 4–5 mm long; stem scales orange... *Oleandra steyermarkii*

13. Plants pilose, with hairs up to 2 mm long; stem scales brown...14

14. Veins brown; laminae linear-oblong with entire margins.. *Oleandra pilosa*

14. Veins black; laminae filiformis, with crenate margins...*Oleandra nigrovenia*

12. Plants glabrous or glabrescent...15

15. Midribs with caduceous lanceolate or lacking scales; laminae oblong to elliptical...*Oleandra duidae*

15. Midribs with persistent scales; laminae linear......................................16

16. Midribs scales deltoid to slightly lanceolate; laminar apices caudate..*Oleandra lehmannii*

16. Midribs scales flabeliform; laminar apices acuminate to cuspidate ....*Oleandra amazonica*

1. Phyllopodia stem-like; stem scales appressed..17

17. Plants glabrous or glabrescent..18

18. Stem scales deltoid to slightly lanceolate and strongly fimbriate..*Oleandra costaricensis*

18. Stem scales elongated, tapered at the tips, with few cilia..*Oleandra trinitensis*

17. Plants pilose...19

19. Plants with stipes 0.3–0.4 cm long or absent…………….....*Oleandra decurrens*

19. Plants with stipes more than 0.4 cm long..20

20. Midribs with black, fimbriate scales...........................*Oleandra nigropaleacea*

20. Midribs with brown, non fimbriate scales..21

21. Laminae pilose with conspicuous hairs on the stipes, laminae, midribs and margins, glandular hairs on the laminar tissue between the veins.. *Oleandra arbuscula*

21. Laminae pilose only at margins or pilose at margins and midribs...22

22. Laminae pilose only at margins.................................*Oleandra areniticola*

22. Laminae pilose at margins and midribs.......................*Oleandra trujillensis*

Oleandra aequatorialis C.V. Miranda & Schwartsb., ***sp. nov.*** TYPE:—ECUADOR. Prov. Napo-Pastaza: Mera, Elev. 1100 m, 2 Mar 1956, *E. Asplund 19562* (holotype: NY!, barcode 04163311; isotype: US!, barcode 2652606). Figs.5A–D.

Diagnosis.—Differs from *Oleandra autralis* by the laminae linear/lanceolate (*vs*. elliptical) and by the presence of scales on midribs.

Stems slender, 2–3 mm diam., long-creeping, light brown, scaly, not pruinose, with glabrescent, rhizophore-like roots; ***scales*** 3.5–5 mm long, linear/lanceolate, squarrose, centrally dark brown to blackish, light brown at the margins, moderate do densely ciliate. ***Phyllopodia*** stipe-like, sparse, 1–4 cm long, olivaceous to light brown, lustrous, glabrous, not scaly. ***Leaves*** 12–30 cm long; ***stipes*** 2–6.5 cm long, olivaceous to light brown, lustrous, sulcate, glabrous, not scaly; ***laminae*** linear to lanceolate, acute to cuneate at base, attenuate to long-acuminate at apex, 10–24 × 1–3.5 cm; ***midribs*** abaxially with linear/lanceolate, light brown, not ciliate scales, 2.5–3 mm long, pilose on both sides, ***veins*** free, furcate, 20–30 per centimenter, abaxially pilose, adaxially glabrescent; ***laminar tissue between the veins*** abaxially glabrous, adaxially glabrescent, ***laminar margins*** pilose; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, bicolorous, blackish in the middle, dark brown at the margins, glabrous; ***spores*** monolete, light brown.

Etymology.—The specific epithet refers to the type locality of the species, in Ecuador.

Distribution and ecology.—Plants epiphytic, on tree trunk in pasture, 1,100 m alt.; Endemic to Ecuador.

Oleandra aequatorialis fits in our informal morphological group 1, which comprises the species with squarrose stem scales (Fig.5B) and stipe-like phyllopodia (Fig.5B). The species is already easily separated from *O. articulata* and *O. brasiliana* for pilosity, these two species being glabrous/glabrescent. Among the species of the group with pilosity, *O. aequatorialis* is closer to *O. australis*, due to the pilose veins and glabrous laminar tissue between the veins (Fig.5C,D). However, the two species are distinguished by the laminae shape (linear/lanceolate in *O. aequatorialis* and elliptical in *O. australis*) and by the presence of midribs scales (Fig.5C) in *O. aequatorialis*, absent in *O. australis*. Other pilose species in the group are *O. hirta, O. quartziticola* and *O. zapatana*. *Oleandra quartziticola* is rupestrial, whereas *O. aequatorialis* is epiphyte. In addition, *O. quartziticola* has the laminar tissue between the veins adaxially pilose and laminae elliptical (*vs.* laminar tissue beetwen the veins adaxially glabrescent and laminae linear/lanceolate) (Fig.5A,D). *Oleandra hirta* has the veins partly anastomosing (Fig.3L), laminar tissue between the veins pilose and pilose indusia (*vs.* veins free, laminar tissue beetwen the veins glabrous and glabrous indusia). *Oleandra zapatana* doesn't have midribs scales, has the laminar tissue between the veins pilose and pilose indusia (Fig.10G,H) (*vs.* presence of midribs scales, laminar tissue beetwen the veins glabrous and glabrous indusia) (Fig.5C,D).

Oleandra amazonica C.V. Miranda & J. Prado *in* Miranda *et al.*, Brittonia 73: 145, figs. 1A–E, 3A, B. 2021**.** Type:—**BRAZIL. Amazonas**: Santa Isabel do Rio Negro. Parque Nacional do Pico da Neblina. Igarapé Cuiabixi, 2060 m, 20 Sep 2012, *R.C. Forzza, G. Martinelli, D.P. Costa, M. A. Moraes, M. A. Nadruz & M. R. Blind 7192* (holotype: VIC!; isotype: RB, barcode RB00770091, image!). **Figs.1A–E.**

Stems stout, 1–3 mm diam., climbing to ascending, dark brown, scaly, pruinose, with grabrescent, rhizophore-like roots; ***scales*** 4–6 mm long, lanceolate, appressed, imbricate, centrally and in the point of insertion blackish, orange at the margins with hyaline borders, sparsely glandular-ciliate. ***Phyllopodia*** stipe-like, sparse, 1.5–4 cm long, olivaceous to light brown, lustrous, glabrous, not scaly. ***Leaves*** 15–25 cm long; ***stipes*** 1–2 cm long, light brown or greenish, lustrous, sulcate, glabrous, not scaly; ***laminae*** linear, acute at base, acuminate to cuspidate at apex, 11–22 × 1.7–2.3 cm, glabrescent, fully glabrous at maturity (young leaves sparsely hairy); ***midribs*** abaxially with flabelliform, light brown scales, 0.4–0.6 mm long, glabrescent on both sides; ***veins*** free, furcate, 12–14 per centimeter, glabrescent on both sides;

laminar tissue between the veins glabrescent on both sides; ***margins*** glabrescent (with caducous hairs, 0.2–0.5 mm long). ***Sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, bicolorous, dark brown in the middle, light brown in the margins, glabrous; ***spores*** monolete, light brown.

Distribution and ecology.—Plants epiphytic; ca. 2,060 m.; Probably endemic to the Guiana Shield; known only from the type, wich was collected at Pico da Neblina, Amazonas, Brazil.

Due to the stems with appressed scales and stipe-like phyllopodia, *Oleandra amazonica* belongs to our informal morphological group 2. Therefore, it is morphologically more similar to *O. duidae* (with *O. archeri* in synonymy)*, O. lehmannii* and *O. steyermarkii*, among the Neotropical species. Due to the linear laminae, the scaly midribs, and the glabrous laminar tissue between veins (at maturity) (Fig.1A,D,E), *O. amazonica* is especially similar to *O. lehmanii*. However, *O. lehmanii* differs in having shorter phyllopodia, 1.3–2.2 cm long (Fig.9G) (*vs* 1.5–4.0 cm long) (Fig.1B), the laminar apices caudate (*vs.* acuminate to cuspidate), the laminar bases cuneate to attenuate (Fig.9F) (*vs.* acute) (Fig,1A), the midribs with deltoid to slightly lanceolate scales (Fig.9H) (*vs.* flabelliform) (Fig.1D), and by the higher number of veins per centimeter 20–28 (*vs.* 12–14).

Oleandra duidae is easily distinguished by its elliptical laminae and by the absence (or rare presence) of scales on the midribs; *O. steyermarkii* differs by its lanose laminae.

Oleandra arbuscula C.V. Miranda & Schwartsb., ***sp. nov.*** TYPE:—COLOMBIA. Yapoboda: Comisaria del Vaupes, Rio Kuduyari (tributary of Rio Vaupes), 900–1000 ft., 4 Sep 1956, *A.S. Barclay, R.E. Schultes & I. Cabrera 524* (holotype NY!, barcode 04163496). Figs.5E–H.

Diagnosis.—Differs from *Oleandra pilosa* by the stem-like phyllopodia (Fig.5F) (*vs.* mix of stipe-like and stem-like phyllopodia) (Fig.8E), coriaceous laminae (*vs.* membranaceous laminae) and by the smaller laminae, both in length and width.

Stems stout, 3–5 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent, rhizophore-like roots; ***scales*** 2.5–6 mm long, lanceolate, appressed, imbricate, in the point of insertion blackish, light brown to orange at the margins and centrally, moderate to densely ciliate. ***Phyllopodia*** stem-like, subfasciculate, 1–8 mm long, dark brown, glabrous, scaly at base. ***Leaves*** 8.5–18 cm long; ***stipes*** 0.5–0.7 cm long, light brown, sulcate, glabrescent, scaly; ***laminae*** linear/lanceolate, acute to cuneate at base, attenuate to long-acuminate at apex, 8–17.3 × 0.9–2 cm; ***midribs*** abaxially with linear/lanceolate, light brown, with few cilia at margins scales, 1–2 mm long, pilose on both sides; ***veins*** free, furcate, 26–32 per centimenter, pilose on both sides; ***laminar tissue beetwen the veins*** pilose on both sides; ***laminar margins*** pilose; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, dark brown, pilose; ***spores*** monolete, light brown.

Etymology.—The specific epithet was chosen for its robust stems, similar to tree trunks.

Distribution and ecology.—The species has affinity with quartizite rocks; high elevations, 270–1,500 m alt. (Mount Roraima); Colombia and Brazil (Mount Roraima), probably also in Venezuela.

Additional examined material.—BRAZIL. **Roraima:** Amajari, Serra do Tepequém, 19 Apr 2017, *P. M. Campos, s.n.* (VIC-48238); Upper plateau and summit of Serra Tepequem, 1500 m, 16 Feb 1967, *G. T. Prance et al. 4422* (INPA). **Amazonas:** Upper slopes of Central Massif of Serra Aracá at base of cliff face, 0°50'N, 63°17'W, 800–900 m, 15 Jul 1985, *G. T. Prance & J. Guedes 29549* (INPA). **Bahia:** Igrapiúna: Reserva Ecológica das plantações Michelin da Bahia, Fragmento Pacangé, 13°48'8"S, 39°10'3"W, 35 m, 4 Jul 2008, *J. L. Paixão 1457* (CEPEC).

Oleandra arbuscula belongs to the informal morphological group 3, which is characterized by species with stem scales appressed and stem-like phyllopodia. This already differentiates the species from *O. pilosa*, a very similar species, but which belongs to the informal morphological group 2 for presenting stipe-like phyllopodia (Fig.8E), in addition to the species also differentiating themselves by the texture of the laminae (membranaceous in *O. pilosa* vs. coriaceous in *O. arbuscula*) and by the laminae size (*O. arbuscula* has smaller laminae, both in length and width). Within the informal morphological group 3, we can compare *Oleandra arbuscula* to the other hairy species included in it: *Oleandra areniticola, O. decurrens, O. nigropaleacea, O. panamensis* and *O. trujillensis*. Among these species, we can differentiate *O. arbuscula* from *O. decurrens* by the stipe. *Oleandra decurrens* is almost without stipe ou with absent stipe (Fig.9B) (*vs.* stipes 0.5–0.7 cm long in *Oleandra arbuscula*) (Fig.5E). *Oleandra areniticola* is pilose only to the laminar margins (Fig.6C), while *O. arbuscula* has a entirely pilose laminae, with catenate hairs in the veins and glandular hairs in the laminar tissue between the veins (Fig.5G,H). *Oleandra nigropaleacea* has a pilose laminae only in the midribs, in addition to the dark and strongly fimbriate scales in this same region (Fig.7G) (*vs.* laminae entirely pilose and linear/lanceolate, light brown scales, with few cilia at margins in *O. arbuscula*) (Fig.5G,H). *Oleandra trujillensis* has veins and laminar tissue between the veins glabrous/glabrescent (*vs.* veins and laminar tissue between the veins pilose in *O. arbuscula*).

Oleandra areniticola C.V. Miranda & Schwartsb., ***sp. nov.*** TYPE:—VENEZUELA. Estado Bolivar: Sierra de Lema, Cabeceras de Río Chicanán, 80 km. (en línea recta) al suroeste de El Dorado, 6º5' N, 62º W, 700 m, 29 Aug 1961, *J.A. Steyermark 89628* (holotype: NY!, barcode 04163413; isotype: US!, barcode 2419642). Figs.6A–D.

Diagnosis.—Differs from *Oleandra trujillensis* by the laminae pilose only at the margins (*O. trujillensis* has laminae pilose at margins and midribs).

Stems stout, 3–4.5 mm diam., climbing to ascending, light brown, scaly, pruinose, rhizophore-like roots not seen; ***scales*** 4–5.5 mm long, lanceolate, appressed, imbricate, centrally and in the point of insertion blackish, light brown to orange at the margins, moderate to densely ciliate. ***Phyllopodia*** stem-like, subfasciculate, 1–6 mm long, light brown, lustrous, glabrous, scaly. ***Leaves*** 12–20 cm long; ***stipes*** 0.7–1.7 cm long, light brown, lustrous, sulcate, glabrous, scaly; ***laminae*** linear/lanceolate, cuneate to acute at base, long-acuminate at apex, 10–17 × 1.0–2.1 cm; ***midribs*** abaxially with deltoid to lanceolate, dark brown scales, with few cilia at margins, 0.7–1.5 mm long, glabrescent in both sides; ***veins*** free, furcate, 32–45 per centimenter, abaxially glabrescent, adaxially glabrous; ***laminar tissue beetwen the veins*** glabrous in both sides; ***laminar margins*** pilose; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, dark brown, pilose; ***spores*** monolete, light brown.

Etymology.—The specific epithet refers to the type of substrate that the species apparently has affinity (sandstones).

Distribution and ecology.—Forested summit, sandstone bluffs of waterfall of headwaters; 700 m alt; Endemic to Venezuela.

Oleandra areniticola is a species that differs from the others species included in the informal morphological group 3 by the pilosity limited only to the laminar margins (Fig.6C). Among the species of this group, *Oleandra decurrens* differs by decurrent laminae with absent or very short stipe (Fig.9B). *Oleandra arbuscula* and *O. pilosa* (included in this work in informal morphological group 2) have hairs on the entire laminae. *Oleandra nigropaleacea* concentrates its pilosity only on the midribs, and has characteristic dark and fimbriate scales in the same region (Fig.7G). *Oleandra trujillensis* is the most similar species, as both species are not entirely pilose and have brown scales on the midribs. However, *O. areniticola* has only pilose margins, whereas *O. trujillensis* has pilose margins and also pilose midribs.

Oleandra articulata (Sw.) C. Presl., Tent. Pterid. 78. 1836. *Aspidium articulatum* Sw., J. Bot. (Schrader) 1800(2): 30. 1801. *Polypodium articulatum* (Sw.) Juss. ex Poir., Encycl. [J. Lamarck & al.] 5 : 514. 1804. *Hypopeltis articulata* (Sw.) Bory, Voy., Indes Or. [Bélanger] 2: 64. 1833. LECTOTYPE (designated by Maxon 1914: 394): Martinique, *Plumier*, Traité Foug. Amér. t. 136! 1705. **Figs.6E–H.**

Aspidium nodosum Willd. Sp. PI. ed. 4 [Willdenow] 5: 211. 1810, *nom. superfl. Oleandra nodosa* (Wiild.) C. Presl, Tent. Pterid. 78. 1836. LECTOTYPE (designated by Tryon 1997: 338): Martinique, *Plumier*, Traité Foug. Amér. t. 136! 1705.

Stems slender, 2–3 mm diam., long-creeping, brown, scaly, not pruinose, with glabrescent, rhizophore-like roots; ***scales*** 3.5–5 mm long, lanceolate, subulate, squarrose, centrally and in the point of insertion blackish, light brown at the margins, sparsely ciliate. ***Phyllopodia*** stipe-like, sparse, 0.6–5.5 cm long, light brown to greenish-brown, lustrous, glabrous, not scaly. ***Leaves*** 25–50 cm long; ***stipes*** 1–15 cm long, light brown to greenish-brown, lustrous, glabrous, not scaly; ***laminae*** linear-oblong to elliptical, acute/acuminate at base, long acuminate at apex, 18–30 × 2.2–6 cm, glabrous; ***midribs*** abaxially with deltoid/cordate, dark brown/reddish scales, 0.5–3 mm long, glabrous on both sides; ***veins*** free, furcate, glabrous on both sides, 15–19 (20–23) veins per centimeter; ***laminar tissue between the veins*** glabrous on both surfaces; ***laminar margins*** glabrous; ***sori*** inframedial in an irregular row; ***indusia*** orbicular-reniform, dark brown, glabrous; ***spores*** monolete, light brown.

Distribution and ecology.— Plants epiphytic; elevation very variable, up to 2,000 m alt.; Mexico, Mesoamerica, Antilles and South America (Venezuela, Colombia and north region of Brazil).

Specimens examined.—MÉXICO. **Veracruz:** Mpio. Hidalgotitlán, 17º14’ N, 94º31’ O, 350 m, 16 Apr 1982, *T. Wendt et al. 3846* (NY). **Chiapas:** Municipio of Ocozocoautla de Espinosa, 900 m, 09 Jan 1972, *D. E. Breedlove 23583 & E. McClintock* (NY).

GUATEMALA. **Izabal:** Livingston, 17 Feb 1905, *C. C. Deam. 456* (NY, GH-on 2 sheets); Moriscos, bordering Lake Izabal, on Playa Dorada, 09 Feb 1968, *E. Contreras 7554* (NY); Sierra del Mico, between Los Amates and Izabal, 2000 ft, 26 Feb 1908, *W. A. Kellerman 7367* (NY); Vicinity Lago Izabal, 15º15'—15º35', 89º0'—89º25', 600 m, 23 Apr 1966, *G. C. Jones et al. 3056* (NY). **Alta Verapaz:** Cubilquitz, 350 m, M. Oct 1903, *H. von Tuerckheim 8632* (NY, GH); Cobán, Parque Nacional las Victorias, 15º28'35"N, 90º22'58"W, 1300 m, 19 Mar 2017, *W. L. Testo 1276* (NY). **Quiché:** Finca Chailá, "zona Reyna" [interpreted], 1300 ft., 30 Nov 1934, *A. F. Skutch 1804* (GH).

HONDURAS. **Atlántida:** Lancetilla, Tela area, 29 Jul 1951, *T. Stevees & P. Ray 366* (GH). **Region Unknown:** Temash River, 100 ft., 03 Aug 1934, *W. A. Schipp 924* (GH).

NICARÁGUA. **Bluefields:** Base Camp 3.6 km, S.E. Cerro San Isidro, Rio Kama, Rio Escondido, 12º05'—12º15', 83º45'—84º20', 65 m, 15 Mar 1966, *G. R. Proctor et al. 27141* (NY).

BELIZE. **Toledo:** Little Quartz Ridge, 4.5 km east of Union Camp, 16º24'02"N, 089º06'40"W, 980–1035 m, 22 Feb 1997, *T. Hawkins 1542* (NY). **Stann Creek:** Maya mtns, upper Angel Falls, 17º02.292', 88º33.812', 480 m, 15 Jun 2017, *R. Seiler 2099* (NY).

COSTA RICA. **Puntarenas:** Cantón de Golfito, P.N. Corcovado, Península de Osa, Cerro Ríncon, Nacientes del Río Tigre, 8º31'00"N, 83º28'00"W, 700–745 m, 28 Jan 1998, *A. Rojas et al. 4183* (NY). **Cocos Island:** Chatham Bay, Isla del Coco, 11 Apr 1965, *A. M. Jiménez 3147* (NY); Locality Unknown, 22 – 24 Feb 1963, *L. R. Holdridge 5132* (GH); Locality Unknown, Mar 1970, *L. D. Gómez P. 3346* (GH). **Limón:** Inundated forest at the northern base of Cerro Coronel, 83º39'30"W, 10º40'30"N, 5 m, 19 Sep 1986, *G. Davidse & G. Herrera 31448* (NY); Guápiles, Rio Santa Clara, 400 m, 18 Sep 1964, *A. M. Jiménez 2370* (NY). **Guanacaste:** Liberia, P.N. Guanacaste, Cuenca del Tempisque, 10:53:21.7785 N, -85:28:32.7824 W, 600 m, 28 Apr 2000, *L. Acosta et al. 979* (NY). **Heredia:** Upstream from Puerto Viejo ca. 4 km at Finca la Selva, 125 m, 16 Aug 1967, *J. T. Mickel 3482* (NY); La Selva, finca of Dr. L. R. Holdridge, on the Río Puerto Viejo, near the junction with Sarapiqui, 300 feet, 28 Mar – 01 Apr 1956, *E. Scamman & L. R. Holdridge 7884* (GH). **Cartago:** San Juan del Norte, 3500 feet, 15 Mar 1955, *E. Scamman 7600* (GH).

PANAMÁ. **Colon:** Teck Cominco Petaquilla mining concession, 08º49'43"N—08º49'32"N, 080º39'37"W—080º39'54"W, 237–330 m, 30 Nov 2007, *H. van der Werff & G. McPherson*

22228 (NY). **Cocle:** Tropical wet forest, La Mesa, 4 km N of El Valle, 875 m, 12 Feb 1974, *M. Nee & M. Hale 9655* (NY); La Mesa, 5 mi n El Valle, 2500', 10 Nov 1965, *E. L. Tyson et al. 2436* (GH). **Panama:** Cerro Campana, west of the Canal Zone, 01 Sep 1940, *H. H. Bartlett & T. Lasser 16915* (GH). In Ishtmo Panama, 1859 – 1861, *Dr. S. Hayes 35* (GH).

TRINIDAD. **Region Unknown:** Locality Unknown, 23 Oct 1877, *A. Fendler 79* (US- on 2 sheets); Forest, four miles east of Arima, 15 Mar 1920, *N. L. Britton et al. 616* (US); Cummento, on palm tree, 16 Aug 1908, *W. E. Broadway 4679* (US).

CUBA. **Baracoa:** El Yunque, Mar 1903, *L. M. Underwood & F. S. Earle 1267* (NY); El Yunque Mt. Baracoa, Mar 1903, *L. M. Underwood & F. S. Earle 1267* (US). **Holguín:** Municipio Mayarí, Sierra de Nipe, Cayo de las Mujeres, Alto de la Torre, 20º31'46"N, 75º45'58"W, 750–790 m, 15 Mar 2011, *W. Greuter & R. Rankin 27335* (US). **Oriente:** Nothern spur of Sierra Maestra west of Río Yao, 300–700 m, 24–30 Oct 1941, *C. V. Morton & J. Acuna 3426* (US, GH); Sierra Nipe, near Woodfred, 450–550 m, 21 Dec 1909, *J. A. Shafer 3249* (US); Pinales de Monte Verde to Falls of Rio Palenque, 16 Feb 1911, *J. A. Shafer 8869* (US, GH); Loma del Gato and, vicinity, Sierra Maestra, Aug 1923, *B. Hioram & B. Clement 6482* (US); Southern Oriente and Pico Turquino, 1300 m, Jul 1922, *F. Leon 1146 & E. L. Ekman* (US); Loma del Gato, 900 m, 1923, *Clement 790* (US); Deciduous woods near base of Loma Menqura, 680 m, 1–3 Feb 1910, *J. A. Shafer 3843* (US); Upper Valey of Rio Navas, 22 Mar 1910, *J. A. Shafer 4397* (GH); Baracoa, Lomas de Cuaba [interpreted], in manacales, 23 Nov 1914, *E. L. Ekman 3601* (GH); Rio Yao, forêt humide, Mar 1943, *F. Marie-Victorin & Clément 60009* (GH). **Santiago:** Vicinity of Baracoa, 1–7 Feb 1902, *C. L. Pollard et al. 238* (US, GH). **Guantánamo:** La Prenda, Dec 1921, *B. Hioram 5003* (GH). **Region Unknown:** Pinal de Sta. Ana, 800 m, Apr 1889, *Eggers 414* (US); Prope, villam [illegible text], Cuba Orientali, Cubenses [interpreted], 1859, *C. Wright 836* (US-on 2 sheets, GH-on 2 sheets).

PORTO RICO. **Fajardo:** Luquillo, Jul 1902, *P. Wilson 358* (NY); Sierra Naguabo, Loma Icaco, 210–675 m, 24 Jul 1914, *J. A. Shafer 3459* (US); Sierra Naguabo, Barrio de Maizales, 650 m, 08 Mar 1914, *N. L. Britton & J. F. Cowell 2204* (US); Sierra Luquillo, N side, in deep wet woods, 2000 ft., 13 Apr 1899, *Mr. & Mrs. A. A. Heller 1072* (US); Naguabo, 8o. Rio Blanco, Caribbean National Forest, along 1.5 km stretch up Rio Sabana S of closed portion of Rt 191, 480–600 m, 29 Feb 1991, *F. Axelrod 4141 & P. Chavez* (UPRRP). **Region Unknown:** Maricao, 19 May 1935, *F. H. Sargent 604* (US); Cerro de Las Pinas, near Las

Cruces, 18º09’15”N, 66º05’09”W, 600–720 m, 29 Mar 1922, *N. L. Britton et al. 6863* (US); Alto de la Bandera, near Adjuntas, 14 Mar 1913, *N. L. Britton & J. A. Shafer 2060* (US). **Río Grande:** Bosque Nacional El Yunque, El Verde, quebrada Sonadora, 364 m, N 18º19.318’ W 65º49.056’, 3 Oct 2009, *F. Areces et al. 55* (UPRRP); Luquillo Experimental Forest, El Verde Field Station at 18º18’N, 65º47’W, 350–500 m, 23 Jun 2011, *J. Ackerman & W. Reyes 5* (UPRRP); Near the top of El Yunque Peak, 1065 m, 12 Jan 1992, *J. L. Vivaldi 72–22* (UPRRP); Sierra de Luquillo, Caribbean National Forest; South of Road 930, 660 m, 15 Mar 1986, *E. N. Dávila et al. 36* (UPRRP); El Yunque National Forest, 18.3238ºN -65.8196ºW, 303 m, 14 May 2011, *M. A. Vincent et al. 15349* (UPRRP); El Verde Research Station, rte 186 at the rio Sonadora, 18º20’N, 65º50’W, 350 m, 7 Jun 1994, *C. M. Taylor & R. Gereau 11864* (UPRRP). **Canovanas:** Caribbean National Forest, along 3 km stretch of trail to El Toro Peak, 750 m, 17 Nov 1985, *F. Axelrod 282 & J. Ackerman* (UPRRP); West end of El Toro Trail about Highway 186 between 600–700 m, 02 Jan 1997, *J. F. Barcelona et al. 1080* (UPRRP); Río Grande/Canóvanas: Bo. Guzmán Arriba/Bo. Cubuy, Caribbean National Forest, El Toro Trail from Rt. 186, 18º16.90’N, 65º50.63’W, 750–800 m, 1 Mar 2004, *F. Axelrod 12824 & M. Christenhusz* (UPRRP). **Central Region:** Guayama, Sierra de Cayey, Cerro de La Santa, Vereda Estación Barrio Carite, Sector Palma Sola, 29 Sep 2001, *J. D. Ackerman 3498* (UPRRP); San Lorenzo, Sierra de Cayey, Carite Forest Reserve, 800 m, 12 Jan 1986, *F. Axelrod 379 & G. Proctor* (UPRRP); Cayey, Guavate, Cerro La Santa, Carite Forest Reserve, 18º06’53”N, 66º03’10”W, 903 m, 28 Dec 2006, *O. Monsegur 857 & B. Sanchez* (UPRRP). **San German:** 8o. Minillas, Maricao Forest Reserve, about 2 km down disused Rt. 362, 18º08.00’N, 67º58.00’W, 575 m, 15 Jan 1996, *F. Axelrod 9583 & O. Potter* (UPRRP). **Arecibo:** 8o. Río Arriba, along S end of proposed Rt 10, 18º20.33’N, 66º40.67’W, 225–250 m, 6 Aug 1994, *F. Axelrod 8198 & A. Axelrod* (UPRRP); 8o. Río Arriba, area to N of temporary S end of new Rt 10, 18º20.12’N, 66º40.58’W, 28 Oct 1995, *F. Axelrod 9318* (UPRRP). **Bayamón:** Cerro La Peña, Barrio Guaraguao Arriba, uppee slopes & summit peak, 500–552 m, 2 Sep 1989, *J. A. Carrasquillo 58 with scouts Troop 327 B. S. A.* (UPRRP).

ISLAND OF MARGARITA. Juan Griego trail, 300 m, 29 Jul 1903, *J. R. Johnston 189* (US, GH, NY).

SAINT LUCIA. **Forestry:** Castries: Piton Flore, upper trail, 13º57.790’N, 60º56.467’W, 300 m, 9 Dec 2006, *R. Graveson 2408* (UPRRP).

JAMAICA. **Portland:** E. slope of John Crow Mtns., Mar 1951, *E. Robertsen 4170* (NY); Seamen's Valley, 150–250 m, 14 Feb 1920, *W. R. Maxon & E. P. Killip 15* (GH); Valley of Trafalgar River, near Jumbe Spring, 800 m, 06 Mar 1920, *W. R. Maxon & E. P. Killip 787* (GH). **Region Unknown:** Mansfield and adjoining properties, near Bath, 300–500 m, 04 Jun 1904, *W. R. Maxon 2487* (NY); Locatility Unknown, 1885, *ex herb. Bot, Gard. s.n.* (US-091358); Vinegar Hill [interpreted], 3980 feet, 12–13 Apr 1909, *M. D. Watt 127* (US, GH); Locality Unknown, 1858, *N. Wilson s.n.* (GH). **Clarendon:** Second Breakfest Spring near Tweeside, 2000 ft., 10–13 Apr 1903, *L. M. Underwood 2063* (NY). **St. Thomas:** Moutain trail between House Hill and Cuna Cuna Gap, 550–725 m, 07 Jun 1926, *W. R. Maxon 8946* (US); Sourtheastern slopes of Stone Hole Bump, 600–800 m, 09 Jun 1926, *W. R. Maxon 8995* (GH); Forested ridge east of Cuna Cuna Gap, 750–840 m, 22 Jun 1926, *W. R. Maxon 9457* (GH); Immediate vicinity of Corn Puss Gap, 2100 feet, 12 Jul 1966, *W. R. Anderson & D. C. Sternberg 3140* (GH); Upper Southern slopes of Gossamer Peak, 750–900 m, 14 Jun 1926, *W. R. Maxon 9183* (GH); Blue Mts, 1895, *A. Moore s.n.* (GH); Vicinity of Corn Puss Gap, ca. 3.5 miles (air) north of Bath, St. Thomas Parish, ca. 1800 feet, 01 Jan 1967, *G. Gastony 110* (GH); Blue Mountains, montane rain forest 1–2 miles southeast of Cuna Cuna Pass, 2500–2700 ft., 26 Aug 1954, *K. A. Wilson & W. Murray 636* (GH). **Saint Ann:** Lower eastern slopes of Mount Diabolo, 350 m, 29 Feb 1920, *W. R. Maxon & E. P. Killip 544* (GH). **Hanover Parrish:** Dolphin Head Mountain, NE side of mountain, 544 m, 07 Sep 2001, *P. Acevedo-Rdgz et al. 11954* (UPRRP).

DOMINICAN REPUBLIC. **Sabaneta:** Prov. of Monte Cristy, La Cidra, 5–600 m, 19 Nov 1930, *E. J. Valeur 549* (NY). **Barahona:** Paradis vicinity, 800 m, 28 Jan – 18 Feb 1922, *W. L. Abbott 1667* (US); Cachete, 18º06'16.2"N, 71º11'18.6"W, 21 May 2004, *P. Acevedo-Rdgz et al. 13898* (UPRRP). **Samaná:** Vicinity Laguna, chiefly on the Pilón de Azúcar, 100–500 m, 26 Dec 1920, *W. L. Abbott 432* (US, GH); ibid., 18 Dec 1920, *W. L. Abbott 283* (US). **San Cristobal:** Cordillera Central, Loma Los 7 Picos, entre los limites de Yamasá y Villa Altagracía, 18º45'N, 70º10'W, 580 m, 13 Jun 1984, *M. Mejía et al. 742* (US). **Seibo:** Cordillera Oriental, Seibo-El Jovero road, 300 m, 29 Dec 1964, *G. C. Jones & D. H. Norris 1177* (GH); Cordillera Oriental, 16.5 km al Sur de Míches, em la carretera a El Seibo y Pedro Sánchez, 18º55'N, 69º09'W, 540–560 m, 27 Jun 1990, *T. Zanoní & F. Jiménez 44554* (UPRRP).

HAITI. **Grand'Anse:** Riviere Glace, 750 m, 07 Aug 1945, *L. R. Holdridge 2225* (US). **Unknown Departament:** Summit of Morne Delcour, Montagnes de la hotte, 950 m, 25 Aug 1927, *W. J. Eyerdam 352* (US, GH).

DOMINICA. **Saint Paul:** About 5 miles from Pont Cassé along road to Rosalie, 22 Jul 1964, *R. L. Wilbur et al. 7838* (US). **Sylvania:** Rainforest bordering Imperial Road, 549 m [rainfall 508 cm.], 15 Feb 1940, *W. H. Hodge 1101* (US).

GUADALUPE. **Region Unknown:** Concussin [capesterre], 01 Apr 1943, *A. Questel 3056* (US). **Saint-Claude:** Matouba, ravine Flore, Camp-Jacob (Choisy), Sofaya (Bois Couches), 400–780 m, Jul 1895 – Dec 1895, *P. A. Duss 4161* (US).

GRENADA. **Locality Unknown:** Oct 1890 – May 1891, *R. V. Sherring 73* (US).

MONTSERRAT. **Locality Unknown:** s.d., *F. T. Turner s.n.* (US-428404).

LESSER ANTILLES. **St. Lucia:** Barre de L'isle, c. 950 ft., 27 Oct 1957, *G. R. Proctor 16775* (US); Savanne Edmund district, southeast of Piton Troumassée, 1800–2000 ft., 22–23 Apr 1958, *G. R. Proctor 17719* (GH).

MARTINIQUE. **Fonds Saint Denis:** 14º44'N, 61º5'W, 350–450 m, 21 Mar 2003, *M. J. M. Christenhusz & S. M. Bollendorff 2709* (NY); Route de Fonds St. Denis aux Deux-Choux, 500–700 m, 1884 – 1900, *P. A. Duss 4587* [ou 1569?] (US).

BRITISH GUIANA. **Kamakusa:** Along upper Mazaruni River, 09 Nov 1922, *H. Leng 77* (NY). **Potaro–Siparuni:** Trail from Kaiatuk to Tukeit, 15 May 1944, *B. Maguire & D. B. Fanshawe 23474* (GH).

SURINAME. **Sipaliwini:** Tafelberg (Table Mountain), 390 m, 11 Aug 1944, *B. Maguire 24318* (NY); Tafelberg, shaded walls, gorge above Lisa Falls, 490 m, 15 Aug 1944, *B. Maguire 24366* (GH); Tafelberg, South of Arrowhead basin, about 1–2 km W of Caiman Camp, 3º54'10.6"N, 56º10'26.8"W, 700–750 m, 20 Aug 2013, *J. Aguire-Santoro et al. 1893* (NY). **Brokopondo:** Brownsweg, ad viam ferream prope km 115–116, 06 Jan 1961, *K. U. Kramer & W. H. A. Hekking 2574* (GH).

ECUADOR. Sucumbios: Reserva Faunistica Cuyabeno south of Laguna Grazacocha, 76º11'W, 00º01'S, 265 m, 1 Apr 1989, *H. Balslev et al. 84674* (NY).

BOLIVIA. **La Paz:** Nor-Yungas, Coroico, Estrada del Inca, vizinhanças do Hostal Sol y Luna, ca. 2000 m, 10 Apr 1990, *P. G. Windisch 5660* (ICN, SJRP); Ticunhuaya, 5000 feet, 20–24 Apr 1926, *G. H. H. Tate 1063* (NY).

VENEZUELA. **Bolívar:** Sierra de Lema, Cabeceras de Río Chicanán, 80 km (en línea recta) al suroeste de El Dorado, 6º 5' N, 62º W, 300 m, 30 Aug 1961, *J. A. Steyermark 89659* (US). **Tachira:** Vertientes del valle situado inmediatamente al oeste de Ayari, 200 m, 27 Aug 1966, *J. A. Steyermark & M. Rabe 96648* (GH).

COLOMBIA. **Antioquia:** Urrao, Corregimiento La Encarnación, vereda Clles, Parque Natural Las Orquídeas, 6º32'20"N, 76º14'51"W, 1350–1360 m, 28–29 Jan 2011, *J. Betancur et al. 14778* (NY). **Santander:** Cordillera Oriental, Departamento Norte de Santander, región del Sarare, Hoya del río Cubugón, El Indio, 420–480 m, 13 Nov 1941, *J. Cuatrecasas 13081* (US). **Del Chocó:** Locality Unknown, s.d., *O. Haught 5576* (US).

BRAZIL. **Amazonas:** Distrito Agropecuário, Fazenda Dimona of WWF/INPA MCS project, ca. 72 km N of Manaus, 02º19'S, 60º05'W, 50–125 m, 23 Oct 1988, *B. Boom & M. Pacheco 8524* (INPA, NY); Manaus, Sítio Água Branca, 23 Oct 1981, *P. J Pivetta 248* (HRCB-on 3 sheets); Coarí, Província Petrolífera de Urucu, ramal para o Porto Evandro, ponte da cobra, ca. 4º48'13,8"S-65º02'0,5"W, ca. 58 m, 15 Feb 2008, *M. R. Pietrobom et al. 7665* (HBRA); ibid., 4º51'03.7"S-65º05'15.4"W, 57 m, 15 Feb 2008, *M. R. Pietrobom et al. 7654* (HBRA); ibid., 4º53'37"S-65º10'52"W, 13 Mar 2007, *M. R. Pietrobom 7141* (HBRA); ibid., 4º52'55.6"S-65º19'04"W, 11 Mar 2007, *M. R. Pietrobom 7092* (HBRA); Manaus, ca. 90 km N de Manaus, Distrito Agropecuário da SUFRAMA, Fazenda Dimona, ca. 02º19'S, 60º05'W, 50–125 m alt., 25 Nov 1989, *P. Kukle 110* (INPA); ibid., 12 Feb 1992, *M. Nee 42541* (INPA); Manaus, Reserva Florestal Adolpho Ducke, 2º55'57"S, 59º57'35"W, 76 m, 1 Jul 2015, *P. H. Labiak et al. 6285* (INPA); Manaus, 2º55'S, 59º59'W, 14 Oct 2005, *T. Emilio 40 & F. Costa* (INPA); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, 02º53'S, 59º58'W, 15 Mar 1995, *J. Prado et al. 610* (INPA); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, 02º53'S, 59º58'W, 3 May 1995, *M. A. S. Costa 247 & C. F. da Costa* (INPA). **Roraima:** Summit of Serra da Lua, 2º25-29'N, 60º11-14'W, 1400 m, 24 Jan 1969, *G. T. Prance et al. 9435* (INPA). **Pará:** Santa Bárbara do Pará, Parque Ecológico Gunma, ca. 1º12'15.5"S-48º17'15.8"W, 17 May 2005, *M. R. Pietrobom 5975* (HBRA); Breves, Ilha Macujubim, Comunidade Lauto, ca. 01º23'54.6"S-50º40'44.2"W, 29 Apr 2011, *M. G. C. Souza & M. R. Pietrobom 889* (HBRA).

Oleandra articulata s.l. is certainly the most used name in the identification of Neotropical, non-pilose specimens in herbaria, and also is a name that has been the focus of great debates about its validity. Due to a material found in the Swartz herbarium, Morton (1968) questioned the typification given by Maxon (1914) to *O. articulata.* The specimen found would be from Mauritius, with an annotation of "*Aspidium articulatum*". However, the specimen has only two leaves, without the stem. For Morton (1968), *O. articulata* was then a name applied to a species from Africa, today called *Oleandra distenta* Kunze, and the American species would be better classified as *Oleandra nodosa* C. Presl. Being the specimen of Mauritius very uninformative, Maxon (1914) decided to consider Plumier's plate, which, in addition to being more informative, would be more in line with the Code (de Joncheere, 1969).

Schwartsburd, Miranda and Prado (2016), analyzing the materials of the Brazilian Atlantic Forest, concluded that the speciemens from this region, commonly identified as *O. articulata*, were, in fact, equivalent to three endemic species. They also hypothesized that *O. articulata s. str.* would be restricted to the Antilles, Mesoamerica and Mexico, not occurring in South America. Nevertheless, in this work we recognize the species indeed occurring in the northern and western regions of South America: in the Guyanas, Suriname, Ecuador, Bolivia, Venezuela, and northern Brazil.

Oleandra articulata is among the glabrous/glabrescents species included in our informal morphological group 1, which are: *O. articulata*, *O. brasiliana* and *O. bradei*. The three species have stipe-like phyllopodia, stem scales appressed and ellipitical laminae, although *O. bradei* is easily differentiated by the very pruinose stems (in *O. articulata* and *O. brasiliana* the stems are not pruinose). Already *O. articulata* and *O. brasiliana* are distinguished by the persistent and conspicuous deltoid/cordate, dark brown/reddish midribs scales presents in *O. articulata* (Fig.6G) (*vs.* rare caducous lanceolate light brown scales in *O. brasiliana*), in addition to the glabrescent midribs in *O. brasiliana* (*vs.* absence of any kind of hairs in *O. articulata*).

Oleandra australis Schwartsb. & J. Prado, Amer. Fern J. 106: 191, figs. 2C–F. 2016. TYPE.—BRAZIL. Paraná: Antonina, Reserva Natural do Cachoeira, SPVS, 25º14'28''S, 48º40'23''W, 350 m, 25 Jun 2007, *P.H. Labiak & F.B. Matos 3941* (holotype: UPCB!; isotypes: MBM!, NY, image!, SP!, VIC!). Figs.4C–F.

Stems slender, 1–2 mm diam., long-creeping, light brown, scaly, not pruinose, with glabrescent, rhizophore-like roots; ***scales*** 4–6 mm long, linear/lanceolate, squarrose, bicolorous, centrally dark brown, orange at the margins, densely glandularciliate. ***Phyllopodia*** stipe-like, sparse, (8–)10–35 mm long, light brown, lustrous, glabrescent, scaly only at base. ***Leaves*** 12–20 cm long; ***stipes*** 1.0–4.0 cm long, light brown, sulcate, lustrous, glabrescent, not scaly; ***laminae*** elliptical, cuneate at base, aristate at apex, 11–18 × 2.5–4.5 cm; ***midribs*** pilose on both sides, not scaly; ***veins*** free, furcate, 17–21 per centimenter, glabrescent on both sides; ***laminar tissue between the veins*** glabrous on both sides; ***laminar margins*** pilose; ***sori*** inframedial to medial in a irregular row; ***indusia*** orbicular-reniform, bicolorous, dark brown in the middle, light brown in the margins, glabrous; ***spores*** monolete, light brown.

Distribution and ecology.—Plants terrestrial or epiphytic, ca. 300–350 m alt.; Endemic to the state of Paraná, southern Brazil.

Specimens examined.—BRAZIL. **Paraná:** Antonina, Reserva Natural Guaricica (antiga Reserva Natural Rio Cachoeira, SPVS), Morro do Queimado, próximo ao cume, 25º23’29”S, 48º41’39”W, 303 m, 12 Jun 2019, *F. B. Matos et al. 2635* (UPCB, VIC).

Oleandra australis is the southernmost species of *Oleandra* in the Americas and it is characterized by entirely bicolorous stem scales, elliptical laminae, laminae pilose on both sides of midribs and laminar margins, glabrous laminar tissue between the veins, and bicolorous indusia. It is very similar to *O. aequatorialis* (see the differences in taxonomic comments of *O. aequatorialis*).

Oleandra baetae Damazio, Bull. Herb. Boissier, ser. 2, 6:892. 1906. TYPE.—BRAZIL. Minas Gerais: Serra do Frasão, 1906, *A. Baeta 258* (holotype: OUPR!-10824 [ex Herb. Damazio 460]; isotypes: P-00630964, image!, P-00630965, image!). Figs.3A–D.

Oleandra nodosa var. *magalhaesii* Christ *in* Schwacke, Pl. Nov. Mineir. 2: 29. 1900 [as ‘‘*Magalhaesi*’’]. Type.—BRAZIL. Minas Gerais: Serra do Ibitipoca, Sep 1897, *H. Magalhães 2259* (holotype: P-00630963, image!).

Stems slender, 2–4 mm diam., long-creeping, dark brown, scaly, pruinose, with glabrescent, rhizophore-like roots; ***scales*** 5–7 mm long, linear/lanceolate, squarrose, bicolorous at base (darker only at the attachment point, orange in the remaining parts), sparsely glandular-ciliate.

Phyllopodia stipe-like, sparse, 5–15 mm long, stramineous, lustrous, pilose, scaly. ***Leaves*** 9–15(22) cm long; ***stipes*** 3–5 mm long, stramineous, lustrous, pilose, scaly (caduceous scales); ***laminae*** elliptical, truncate or inequilateral at base, acute or obtuse at apex, 8–14(21) × 3.0–4.5 cm; ***midribs*** with with linear/lanceolate, brown, caduceous scales, pilose on both sides; ***veins*** free, furcate, 18–20 per centimenter, pilose on both sides; ***laminar tissue between the veins*** pilose on both sides; ***laminar margins*** pilose; ***sori*** infra-medial in a irregular row; ***indusia*** orbicular-reniform, light brown, with sparse hairs or glabrescent; ***spores*** reddish-brown to dark brown.

Distribution and ecology.—Plants rupestrial, in quartizite rocks, ca. 1,000– 1,500 m alt.; Endemic to the state of Minas Gerais, southeastern Brazil.

Specimens Examined.—BRAZIL. **Minas Gerais:** Campo Grande, 1942, *J. Badini 4106* (OUPR); Campo Grande, 19 May 1975, *J. Badini 22321* (OUPR); Lima Duarte, Conceição do Ibitipoca, Parque Estadual Florestal do Ibitipoca, 5 Dec 1992, *J.E.Z. Oliveira 8* (CESJ); Lima Duarte, Conceição do Ibitipoca, Parque Estadual Florestal do Ibitipoca, 1 May 1993, *R.F. Novelino et al. 1020* (CESJ); Lima Duarte, Conceição do Iibitpoca, Parque Estadual do Ibitipoca, próximo à Cachoeira dos Macacos, 1,200 m, 21º43'47"S, 43º53'38,38"W, 09 Jul 2019, *J. N. Fregonezi & A. R. Fregonezi s.n.* (VIC-48239); Lima Duarte, Conceição do Ibitipoca, Parque Estadual Florestal do Ibitipoca, 15 May 1993, *J.E.Z. Oliveira et al. 267* (CESJ); Lima Duarte, Conceição do Ibitipoca, Parque Estadual Florestal do Ibitipoca, 1,360 m, 29 May 1993, *J.E.Z. Oliveira et al. 296* (CESJ); Lima Duarte, Conceição do Ibitipoca, 21°42'S, 43º53'W, 1,300 m, 9 Aug 2015, *P.B. Schwartsburd & R. Santana Milagres 3515* (SP, VIC); Lima Duarte, Serra Negra, 21°55' 49.9''S, 43º46' 43.1''W, 986 m, 15 Nov 2008, *F.R.G. Salimena & P.H. Nobre 2757* (CESJ, UPCB); Ouro Preto, Andorinhas, 21 Jun 1974, *J. Badini 21702* (OUPR); Ouro Preto, Cachoeira Andorinhas, 1940, *E.V. Miranda 63* (CESJ, SPF); Ouro Preto, Camarinhas, 9 May 1974, *J. Badini 22058* (OUPR); Ouro Preto, 19 Sep 1989, *L. Krieger 24551* (CESJ); Rio Preto, Ribeirão Santana, 22 Mar 1997, *R.B. Tostes* (CESJ-29779, VIC-47056); São João del Rei, Serra do Lenheiro, 11 Jan 1999, *J. Prado et al. 996* (NY, SP); São Thomé das Letras, 13 Jul 1950, *A.C. Brade & A.P. Duarte 20465* (P, RB); São Thomé das Letras, 1,250 m, 13 Jul 1950, *A.C. Brade 3451* (CESJ); São Thomé das Letras, 14 Jul 1954, *A.P. Duarte 3834* (RB-on 2 sheets, VIC); São Thomé das Letras, 13 Oct 1984, *L. Krieger & A. Pavan 20641* (CESJ); São Thomé das Letras, 1300 m, 1 Jul 1987, *L.S. Kinoshita-Gouvêa et al. 19126* (SP, UEC, VIC); São Thomé das Letras, Gruta São Tome, 21º43'23''S, 44º59'09''W, 1278 m, 11 Jan 2016, *P.S.P. Sampaio & A.F.P. Sampaio 1355*

(HUSC, VIC); Baependi, em São Thomé das Letras, 20 Jun 1962, *J. Mattos 10363 & H. D. Bicalho* (HAS); Serra do Frasão, 1942, *J. Badini 4104* (OUPR); Serra de Ouro Preto, Mar 1907, *L. Damazio 380* (OUPR [on 2 sheets]); Serra de Ouro Preto, 9 May 1917 [or 1907?], *L. Damazio s.n.* (RB-36235 [on 2 sheets]); Serra de Ouro Preto, s.d., *J. Badini 2610* (CESJ); Serra do Frasão, 12 Mar 1907, *L. Damazio s.n.* (RB-171642); Tiradentes, Serra de São José, 21º5'S, 44º10'W, 1,250 m, 24 Sep 1989, *R.J. Válka Alves & J. Holbek 700* (SP, SPF); Locality unknown, s.d., L. *Krieger 20931* (CESJ); Iguarapé, Pico Itatiaiuçu/C1, 20º7'17"S, 44º21'43,8"W, 1340 m, 10 May 2008, *F. F. Carmo 2996* (BHCB); Tiradentes, Serra de São José, 22 Sep 1984, *R. Alves & J. Holbels 700* (SJRP).

In the protologue of *Oleandra nodosa* var. *magalhaesii,* Christ (1900) stated that the type was collected at ''Serra do Itatiaia.'' A detailed examination of the label of the type (Magalhães 2259 [P-00630963]) lead us to conclude he misread the locality. The correct type locality is Serra do Ibitipoca, Minas Gerais, Brazil.

Oleandra baetae is endemic to the state of Minas Gerais, especially in the mountain regions of the south and southeast. It is characterized by stem scales bicolorous at base (darker only at the attachment point, orange in the remaining parts), short stipes (3–5 mm long), elliptical laminae, which are truncate or inequilateral at the base, laminae pilose in all regions, and light brown pilose indusia (Fig.3A–D).

Besides not overlapping in geographic range, *Oleandra baetae* differs from *O. hirta* by having fronds 9–15(22) cm long (vs. 50–55 cm long), phyllopodia 5–15 mm long (vs. 25–42 mm), elliptical laminae (vs. linear), with truncate or inequilateral base (vs. long-attenuate base), and free veins (vs. partly anastomosing) (see Brackenridge, 1854:t. 29).

Other species recently published, *O. hovenkampii*, is very close to *O. baetae*, due to the orange stem scales. However, *O. baetae* has a truncate or inequilateral laminar bases (Fig.3A), while *O. hovenkampii* has acute to obtuse laminar bases (Fig.2A), in addition to the pilose laminae of *O. baetae*, (vs. lanone laminae of *O. hovenkampii).* Additionally, these two species occur at least 3,700 km apart: *O. baetae* is endemic to the Brazilian Atlantic Forests, while *O. hovenkampii* is known from Peru and Costa Rica.

Oleandra bradei Christ, Bull. Soc. Bot. Genève ser. 2, 1: 231. 1909. LECTOTYPE (designated by Tryon 1997: 339).—COSTA RICA. La Palma: 1300 m, 17 Mar 1908, *A. C. Brade* (P-*n.v.*; isolectotypes: NY!, UC-*n.v.*, US!, US!). Fig.9A.

Oleandra nodosa var. *caudata* Christ, Bull. Herb. Boissier ser. 2, 4: 964. 1904. Type.—COSTA RICA. Talamanca, Haut Uren, 1000 m, 1898, *H. Pittier 12669* (holotype: P-*n.v.*).

Stems slender, 1–3 mm diam., long-creeping, light brown, scaly, strongly pruinose, with glabrescent, rhizophore-like roots; ***scales*** 3.5–6 mm long, lanceolate, squarrose, more laxly spreading, not bicolorous, light brown to reddish brown, sparsely ciliate. ***Phyllopodia*** stipe-like, sparse, 5–30 mm long, light brown, lustrous, glabrous, scaly at base. ***Leaves*** 14–30 cm long; ***stipes*** 3–14 cm long, light brown, lustrous, sulcate, glabrous, not scaly; ***laminae*** elliptical, cuneate at base, long-acuminate to attenuate at apex, 11–27 × 3–4(7) cm; ***midribs*** abaxially with rare caduceous scales at base, glabrous on both sides; ***veins*** free, furcate, 16–20 per centimenter, glabrous on both sides; ***laminar tissue between the veins*** glabrous on both sides; ***laminar margins*** glabrous; ***sori*** inframedial to medial; ***indusia*** orbicular-reniform, not bicolorous, dark brown, glabrous; ***spores*** light brown.

Distribution and ecology.—Plants epiphytic, found in high elevations, ca. 1,000–2,500 m; Endemic to Costa Rica.

Specimens Examined.—COSTA RICA. **Puntarenas:** Cantón de Monte Verde, 200 m from comedor of Monteverde Biological Station on Sendero El Camino, 10º18'12"N, 84º47'30"W, 1550 m, 09 Jul 2000, *B. Boyle 5800 & R. Spicer* (=Spicer 6) (GH). **Alajuela:** Los Angeles de San Ramon, 21 Jul 1932, *A. M. Brenes 16146* (NY); ibid., 02 Aug 1932, *A. M. Brenes 16245* (NY); La Palma de San Ramon, 08 Mar 1930, *A, M. Brenes 11901* (NY); ibid., 24 Nov 1926, *A. M. Brenes 5113* (NY, US); ibid., XI 1926, *A. Brenes 5113* (US); 11 km N of San Ramón, 1000 m, 28 Jul 1967, *J. T. Mickel 2924* (NY, US); 8 km N of San Ramón and 4 km W on side road, 1300 m, 22 Jun 1967, *J. T. Mickel 3632* (NY); 10 km N of San Ramón, on continental divide, above Piedades Norte, Finca Numancia, 1300 m, 24 Nov 1966, *R. L. Hauke 329* (NY-2 sheets); Ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Sta Cloud forest, 1100 m, 17 Jul 1983, *R. C. Moran 3226* (GH); Região dos Rios São Lourenço e Balsa, ca. 3 km ao norte de Balsa de San Ramón, 11 Apr 1976, *Windinsch 1111* (GH); 12 km N of San Ramón, 27 Jul 1967, *D. B. Lellinger 731* (US); N of San Ramón, ca. 4 km N of Balsa along road to Colonia Palmareña, 23 Jul 1970, *D. B. Lellinger 1223 & J. J. White* (US). **Cartago:** Turrialba, P.N. Barbilla, Cuenca del Matina, Sendero Barthon, Cerro Tigre, 9:55:15.0000 N, -83:23:55.0000 W, 1600 m, 10 Mar 2001, *E. Mora 1911* (NY); Cantón de Paraíso, P.N. Tapantí, Cuenca del Reventazón, Parque Nacional Tapanti, 9º 44' 53" N, 83º 46' 55" W, 1600 m, 01 Apr 1997, *A. Rodríguez et al. 2072* (NY); About 10 km south of Tapantí along the new road, on the east slope above the Rio Grande de Orosí 9º 42' N, 83º 47' W, 1400–1600 m, 10–24 Jun 1968, *W. C. Burger 5645 & R. G. Stolze* (NY, GH); ibid., 10–24 Jun 1968, *W. C. Burger 5691 & R. G. Stolze* (NY, GH, US); About 15 km south of Tapantí along the new road, on the east slope above the Rio Grande de Orosí, 9º 42' N, 83º 47' W, 1500 m, 12, 14, 17 Dec 1969, *W. C Burger 6856 & R L. Liesner* (NY, GH); Tapantí, 1300 m, 13 Aug 1969, *L. D. Gómez 2323* (NY, GH); About 5 km SW of Tapanti, 1500 m, 17 Aug 1967, *R. J. Taylor 4483* (NY), ibid., 17 Aug 1967, *R. J. Taylor 4469* (NY); Refugio Nacional de Vida Silvestre Tapantí, 1300 m, 01 Mar 1991, *F Almeda et al. 6866* (NY); Rio Grande de Orosí, Tapanti, 07 Apr 1976, *Windinsch 1015* (GH); Taucito de Orosi, 1400 m, 05 Oct 1982, *B. Pérez-García & L. D. Gómez 174* (GH); Above San Isidro, about 1700 m, 21 Aug 1961, *C. Weber 6010* (GH, US); SE of Orosí, ca. 2.2 km SSE of Purisil, above Finca la Concordia, ca. 1800–2300 m, 9 and 11 Aug 1970, *D. B. Lellinger 1538 & J. J. White* (US). **San José:** La Palma (Rte 220?) rd. to La Hondura, 12 Mar 1977, *J. Beitel 77118* (NY); La Palma area, northeast of San Jeronimo, above de La Hondura valley, 10° 2' N, 84º 0' W, 1500 m, 27 May, 01 Jun 1868, *W. C. Burger 5350 & R. G. Stolze* (NY, GH, US); About 3 km NW of Cascajal, 1750 m, 30 Jul 1972, *J. & C. Taylor 11338* (NY); Between La Palma and La Hondura, 1500 m, 09 Jul 1967, *J. T, Mickel 2534* (NY); Vicinity of La Palma, 1450–1550 m, 6–8 May 1906, *W. R. Maxon 389* (NY, US); ibid., 6–8 May 1906, *W. R. Maxon 404* (NY, US); ibid., 1500–1700 m, 17–18 Jul 1923, *W. R. Maxon 7904 & A. D. Harvey* (GH, US); La Palma rd. to La Hondura, 19 Nov 1977, *W. H. Wagner 77593 & F. S. Wagner* (NY); Las Nubes, 5000 feet, 18 Feb 1956, *E. Scamman & L. R. Holdridge 7885* (GH); La Palma on the road to La Hondura, 4700–4800 feet, 5–6 Mar 1955, *E. Scamman 7601* (GH, US); Along the road to La Hondura, 4700–4800 feet, 08 Apr 1956, *E. Scamman & L. R. Holdridge 7886* (GH); La Palma, 2500 m, Apr 1912, *H. Bertolini 608* (US). **Limón:** Limón, Z.P. Rio Banano, Cuenca del Banano, Valle de la Estrella, 09:48:56.4120 N, -83:09:49.3560 W, 1200 m, 26 Oct 2007, *D. Solano et al. 4730* (NY).

Oleandra bradei is very similar with *O. articulata* and *O. brasiliana*, because they are species with squarrose stem scales, stipe-like phyllopodia and elliptical and glabrous laminae. Although, *O. bradei* has a strongly pruinose stem, in addition to more laxly spreading stem scales (Fig.9A). *Oleandra articulata* and *O. brasiliana* have non pruinose stems. *Oleandra* *bradei* rarely has midribs scales (apparently the scales are caduceous). *Oleandra articulata* has a lot persistent midribs scales and *O. brasiliana* has rarely caducous scales at base in young leaves.

Oleandra brasiliana Schwartsb. & J.Prado, Amer. Fern J. 106: 199, figs. 1E–J. 2016. TYPE.—BRAZIL. Bahia: Arataca, Serra do Peito de Mo¸ca, RPPN Caminho das Pedras, 15810025''S, 39820030''W, 950 m, 6 Aug 2006, *P.H. Labiak et al. 3652* (holotype: SP!; isotypes: NY, image!, UPCB!). Figs.3E–J.

Stems light brown to blackish, not pruinose, 1.5–2.5 mm diam.; ***scales*** 4–6 mm long, lanceolate, squarrose, bicolorous, centrally black, orange at the margins, moderate to densely glandular-ciliate. ***Phyllopodia*** stipe-like, sparse, 10–40 mm long, light brown to greenish-brown, lustrous, glabrous, not scaly. ***Leaves*** 12–35 cm long; ***stipes*** 3–7(10) cm long, light brown to greenish-brown, lustrous, glabrous, not scaly; ***laminae*** generally obovate, rarely elliptical, cuneate at base, aristate at apex, 10–303(2–)4.5–7 cm; ***midribs*** glabrescent on both sides, sometimes seeming glabrous, with caduceous scales at base in young leaves; ***veins*** free, furcate, 15–18 per centimenter, glabrous on both sides; ***laminar tissue between the veins*** abaxially glabrous, adaxially glabrescent; ***laminar margins*** glabrescent, hairs especially common at the laminar apices; ***sori*** infra-medial to medial; ***indusia*** orbicular-reniform, dark brown, glabrous; ***spores*** light brown.

Distribution and ecology.—Plants rupestrial or epiphytic, from 600 to 1,200 m elev.; Widespread along the Brazilian Atlantic Forest, from Bahia to São Paulo, with a disjunct population in Ceará.

Specimens examined.—BRAZIL. **Bahia.** Arataca, 15º10'25''S, 39º20'30''W, 1,000 m, 20 Jan 2007, *A.M. Amorim et al. 6701* (UPCB, RB); Arataca, 15º10'25''S, 39º20'30''W, 1,000 m, 13 Apr 2007, *F.B. Matos et al. 1355* (CEPEC, SP, UPCB); Arataca, 15º10'12''S, 39º20'17''W, 940 m, 13 Nov 2011, *L. Daneu et al. 581* (RB); Barro Preto, 14º46'13''S, 39º12'10''W, 600–900 m, 8 Feb 2005, *F.B. Matos et al. 377* (MBM, UPCB); Camacã, 15º23'30''S, 39º33'55''W, 835 m, 13 Feb 2005, *F.B. Matos et al. 440* (UPCB); Camacã, 15º23'30''S, 39º33'55''W, 835 m, 9 Jul 2005, *F.B. Matos et al. 628* (UPCB); Camacã, 15º23'35''S, 39º33'53''W, 850 m, 11 Aug 2006, *P.H. Labiak et al. 3710* (SP, UPCB); Camacã, RPPN Serra Bonita, 15º23'30"S, 39º33'55"W, 25 May 2012, L. *J. Olenscki 60 & J.*

L. Paixão (CEPEC); Camacã, RPPN Serra Bonita, 15º23’30”S, 39º33’55”W, 25 Oct 2012, L. *J. Olenscki 61 & J. L. Paixão* (CEPEC); Camacã, RPPN Serra Bonita, 15º23’30”S, 39º33’55”W, 30 Mar 2007, *F. B. Matos et al. 1336* (CEPEC); Lençois, 12º34’S, 41º23’W, 900–1000 m, 3 Apr 1980, *L. R. Noblick 1760* (CEPEC, HEPH-25154). **Ceará:** Maranguape, 3º54’05’’S, 38º43’ 12’’W, 900 m, 10 Apr 2011, *P.B. Schwartsburd & J.A.P. Araújo 2516* (EAC, NY, SP, VIC); Maranguape, Serra de Maranguape, Pedra Chorona, 20 May 2001, *E. L. Paula-Zárate s.n.* (EAC-51577); Maranguape, Serra de Maranguape, 4 Oct 1992, *L. P. Felix s.n.* (EAC-18962). **Espírito Santo:** Cachoeiro do Itapemirim, Vargem Alta, Morro de Sal, 21 Aug 1948, *A.C. Brade 19324* (RB-on 2 sheets); Cachoeiro do Itapemirim, Vargem Alta, Morro de Sal, 21 Aug 1948, *A.C. Brade 3452* (CESJ); Cachoeiro do Itapemirim, Vargem Alta, 3 May 1966, *A.P. Duarte 9767* (MBM, RB-on 2 sheets, VIC). **Minas Gerais:** Mariana, Serra do Frasão, km 7, 19 Sep 1989, *R.F. Novelino et al. s.n.* (CESJ-24127, VIC-47057); Serra do Frasão, 1904, *Schwacke 14340* (BHCB); Serra do Frasão, 1937, *J. Badini 258* (BHCB); Monte Verde de Cima, Serra Negra, 9 Mar 1991, *M. Brugger & H.G. Souza s.n.* (CESJ-24711 [on 2 sheets], VIC-47054); Santa Bárbara do Monte Verde, 21º57’55’’S, 43º49’51’’W, 1,200 m, 24 Apr 2004, *J.P.S. Condack 135* (RB, VIC); Rio Preto, Serra Negra, 17 Mar 2007, *N.L. Abreu et al. 151* (CESJ, MBM); Rio Preto, Serra Negra, Sep 2011, *R.J.V. Alves & N.L. Abreu 8751* (CESJ, VIC); Rio Preto, Vilarejo do Funil, 21 May 2004, *F.R.G. Salimena et al. 1286* (CESJ); Rio Preto, Gruta do Funil, Jul 1989, J. *S. M. & M. M. N. Braga 330* (BHCB); Rio Preto, Cânion do Funil, 10 Nov 2005, *F. S. Souza et al. 104* (BHCB); Santa Rita do Jacutinga, 17 Apr 1992, *L. Krieger s.n.* (CESJ-29460, VIC-47055); Santo Antônio do Itambé, Serra do Espinhaço, 18.45475º S, 43.33445ºW, 865 m, 14 Jan 2010, *E. Schuettpelz et al. 1415* (MO, SP); Serra do Capanema, 1943, *J. Badini 4239* (OUPR); Serra do Frasão, 1906, *A. Baeta 259* (OUPR); Serra do Frasão, 26 Mar 1907, *L. Damazio et al. 381* (OUPR-on 2 sheets); Serra do Frasão, 1907, *L. Damazio s.n.* (RB36236); Serra do Frasão, 1934, *J. Badini & P. Lisboa e Costa s.n.* (OUPR-10833 [on 2 sheets]); Serra do Frasão, 1934, *J. Badini 253* (RB); Serra do Frasão, 1943, J. *Badini 4238* (OUPR); Serra do Frasão, 19 Sep 1989, *R.F. Novelino et al. 706* (OUPR); Porteirinha, Cachoeira do Cerrado, 15 Apr 2007, *O. S. Ribas & J. M. Silva 7670* (MBM-332162, RB); Conceição do Mato Dentro, *s.d.*, *W. S. Costa 14* (VIC); Conceição do Mato Dentro, *s.d.*, *W. S. Costa 15* (VIC). **Rio de Janeiro:** Serra do Couto, s.d., *A. Glaziou 2153* (RB-30604 [on 2 sheets]); Serra do Couto, s.d., A. *Glaziou 3450* (CESJ). **São Paulo:** Salesópolis, Boracéia, 4 Mar 1962, *O. Travassos 336* (RB-on 2 sheets); Serra de Paranapiacaba, Sep 1925, *A.C. Brade 8402* (MBM, RB-on 2 sheets); São Luiz do Paraitinga, Parque Estadual Serra do Mar, Núcleo de Santa Virgínia, 23º19’27.2”S, 45º05’19.2”W, entre 800–900 m, 9 Aug 2001, *A. Salino et al. 7380* (BHCB).

Oleandra brasiliana is the most widespread species in the Brazilian Atlantic Forest, occurring from the state of Bahia southwards to São Paulo. Disjunct populations in the state of Ceará are in the Baturité and Maranguape regions, which are ‘‘islands’’ of wet forest within the Brazilian semi-arid vegetation (Caatinga biome), presenting many species in common with the Atlantic Forest (Brade, 1940; Freitas and Matias, 2010).

Oleandra brasiliana has glabrescent laminae: *i.e.*, hairs are found in juvenile fronds, but they fall off in older ones. Most specimens seen appear to have fully glabrous laminae, but a detailed examination reveals hairs on both sides of the midribs, adaxially on the laminar tissue between the veins, and on the laminar margins (especially on the laminar apices). The other Brazilian Atlantic Forest species all have pubescent laminae (each with a different pattern of indument), and the laminae remain pubescent as they age.

Among the Neotropical species, *Oleandra brasiliana* is the most similar to *O. articulata* and *O. bradei*. *Oleandra brasiliana* differs from *O. articulata* by glabrescent midribs (*vs.* glabrous midribs), and by the caduceous lanceolate light brown scales, whereas in *O. articulata* the midribs present persistent and conspicuous cordate reddish scales abaxially (Fig.6G), and lack any kind of hairs. *Oleandra bradei* is strongly pruinose and has more laxly spreading stem scales (Fig.9A).

Oleandra costaricensis Maxon, Contrib. U. S. Natl. Herb. 17: 397. 1914. TYPE.—COSTA RICA. La Palma: 1459 m, 8 Sep 1898, *A. Tonduz 12551* (holotype: US!, no. 366014; isotypes: US!, MO-*n.v.*). Figs.7A–D.

Oleandra dura Maxon, Amer. Fern J. 35: 21. 1945. TYPE. —COLOMBIA. Santander: *Haught 1329* (holotype: US!; isotypes: GH!, K-*n.v.*).

Stems stout, 2.5–4.5 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent, rhizophore-like roots; ***scales*** 4–5.5 mm long, lanceolate, subulate, appressed, imbricate, bicolorous, centrally dark brown to blackish, light brown at the margins, densely fimbriate. ***Phyllopodia*** stem-like, subfasciculate, 1–3 mm long, glabrous, scaly. ***Leaves*** 19–27 cm long; ***stipes*** 0.7–2 cm long, light brown, glabrous, scaly, scales fimbriate, deciduosly;

laminae linear-oblong, cuneate at base, aristate at apex, 18–25 × 1.5–4 cm; ***midribs*** abaxially with deltoid/lanceolate, reddish brown, strongly fimbriate scales, 0.5–1.5 mm long, glabrous on both sides; ***veins*** free, furcate, 18–24 per centimenter, glabrous on both sides; ***laminar tissue between the veins*** minutely pubescent abaxially, but soon glabrous on both sides; ***laminar margins*** glabrous; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, dark brown, glabrous; ***spores*** monolete, light brown.

Distribution and ecology.—Plants epiphytic; ca. 700–1,800 m alt.; Costa Rica, Panama, Colombia, Ecuador, and north region of Brazil.

Specimens examined. —COSTA RICA. **Cartago:** Tapantí, 1300 m, 13 Aug 1969, *L. D. Gómez P. 2324* (NY); ibid., 1150 m, 03 Jul 1967, *J. T. Mickel 2321* (NY); ibid., in Valley of Río Revantizón, 3700 feet, 18 Mar 1956, *E. Scamman & L. R. Holdridge 7887* (GH); Orosi, 3.900 ft, 28 Feb 1981, *F. Almeda 4647 & K. Nakai* (NY); Orosi, Tapanti, 1380 m, 23 Mar 1924, *R. T. Rojas 185* (US); Orosi, finca del Dr. Valverde [interpreted], 1400 m, s.d., A. *Brade s.n.* (US-575271); Turrialba, 1200 m, 09 Aug 1924, *A. Alfaro s.n.* (NY-04163287, US-1205850, GH); Ca. 22 km E of Turrialba, 1200–1450 m, 22 Aug 1967, *J. T. Mickel 3443* (NY-2 sheets); La Cangreja, 1800 m, 18 Jan 1965, *A. Jiménez M. 2754* (NY, US); Paraíso, 9:44:05.0000N, 83:46:42.0004W, 1500 m, 14 Mar 2000, *L. Acosta 633 & V. Ramírez* (NY); Vicinity of Quebrada Casa Blanca, 9°47’N, 83°48’W, ca. 1350 m, 30 Sep 1984, *M. Grayum 3951* (US); Finca la Esperanza, 1200–1300 m, 13 Jul 1970, *D. B. Lellinger 1112 & J. J. White* (US); Along old cartroad in the hills east of San Isidro de Cartago, 18 Mar 1952, *H. E. Stork 4529* (US); Cerro Jucosal, 5350 feet, 03 Mar 1928, *H. E. Stork 1098* (US, GH); ibid., 5350 feet, s.d., *H. E. Stork s.n.* (US-2421769); Hills of the Navarro Valley, 6000 feet, 01 May 1928, *H. E. Stork 1721* (US); La Estrella, 26-27 Mar 1924, *P. C. Standley 39393* (US); ibid., 26–27 Mar 1924, *P. C. Standley 39259* (US, GH); El Muñeco, on the Río Navarro, 1400–1500 m, 6–7 Mar 1926, *P. C. Standley & R. Torres R. 50994* (US); Juan Viñas, Reventazon Valley, 1000 m, 22 Apr 1903, *O. F. Cook & C. B. Doyle 222* (US); Juan Viñas, Gebiet des Rio Chis, 1200 m, 30 Mar 1910, *Alfred & A. C. Brade 667* (GH); Juan Vinas [interpreted], s.d., *Berger 26* (US); Cartago, 1400 m, s.d., *Beyer s.n.* (US-2577856A); Cartago, ca. 1800 m, 30 Jan 1965, *R. K. Godfrey 66111* (GH); Entre Rio Navarro y Rio Sombrero, 1300 m, 26 Jan 1964, *A. Jiménez M. 1646* (GH). **San José:** Vicinity of El General, 975 m, Aug 1936, *A. F. Skutch 2817* (NY, US); ibid., 1500 m, Dec 1936, *A. F. Skutch 2961* (NY, US, GH); Between La Palma and La Hondura, 1500 m, 09 Jul 1967, *J. T. Mickel 2533* (NY); La Hondura, 1300–1700 m, 2–4 Mar 1924, *P. C. Standley 36210* (US); La Palma on the road to La Hondura, 4700–4800 feet, 5–6 Mar 1955, *E. Scamman 7602* (US, GH); La Palma, 1600 m, 17 Mar 1924, *P. C. Standley 38229* (US-2 sheets). **Heredia:** Canton Santo Domingo, Virgen del Socorro, 10º16’11”N, 84º09’59”W, 800–850 m, 29 Dec 2016, *W. L. Testo 1238* (NY); Cinchona, above the Upper Sarapaquí Valley, ca. 4000 feet, 20 Mar 1955, *E. Scamman 7604* (GH). **Alajuela:** Base of Cerro Congo, ca. 10º16’N, 84º15’W, ca. 1200 m, 22 Jan 1986, *A. R. Smith et al. 1893* (NY); Area of Balsa da San Ramon, 900 m, 29 Dec 1974, *J. Taylor 17754* (NY); Los Angeles de San Ramon, 24 Jul 1934, *A. M. Brenes 19273* (NY); N of San Ramón, ca. 1300 m, 23 Jul 1970, *D. B. Lellinger 1250 & J. J. White* (US); La Fortuna, entre bervantes et Pacayas, 1400 m, Mar 1906, *P. Biolley s.n.* (US-578603). **Puntarenas:** Vicinity of biological field station at Finca Wilson, 1200–1400 m, 04 Aug 1967, *J. T. Mickel 3101* (NY); ibid., 04 Aug 1967, *J. T. Mickel 3124* (NY); Monte Verde área, valley of Rio San Luis, 10º16’N, 84º48’W, 1000–1200 m, 18 Jun 1985, *B. Hammel & W. Haber 13909* (NY); Helechales du General, valle du Diguis, 700 m, 02 Feb 1898, *H. F. Pittier s.n.* (US-828690); Coto Brus., San Vito, Camino a Cerro Paraguas, Finca de la família Gamboa, 08º47’05”N, 82º59’17”W, 1500 m, 16 Jan 2013, *F. B. Matos et al. 2089* (UPCB). **Guanacaste:** La Tejona, North of Tilarán, 600–700 m, 25 Jan 1926, *P. C. Standley & J. Valerio* 45928 (US); El Silencio, 750 m, 13 Jan 1926, *P. C. Standley & J. Valerio 44702* (US). **Limón:** Rainforest area on hills near Morairai, 1300 m, 07 Apr 1949, *L. O. Willians 16181* (US, GH).

PANAMA. **Chiquirí**: Propriedade del Irhe, NE del campamento Fortuna (Hornito), 1000–1200 m, 15 Aug 1976, *M. D. Correa A. et al. 2499* (NY, US); Distrito de Gualaca, Reserva Florestal de Fortuna, 22 Jan 2003, *B. Araúz et al. 757* (NY). **Cocle:** 08 Jul 1970, *P. Armond 404* (NY); Between Cerro Pilón and El Valle de Antón, 700–900 m, 15 Aug 1967, J. A. Duke & J. D. Dwyer 13962 (GH). **Darien:** Elfin forest at top of W peak of Cerro Tacarcuna massif, 1800–1850 m, 28 Jan 1975, *A. Gentry & S. Mori 13977* (US).

COLOMBIA. **Magdalena:** Alto Rio Buritaca, Alto de Mira, 11º05’N, 73º48’W, 1100–1500 m, 16 Jul 1989, *S. Madriñán & C. E. Barbosa 306* (NY); **Antioquia:** Mun. Guatapé, Vereda Santa Rita, 1850 m, 09 May 1985, *A. Uribe & J. Vallejo 5192* (NY); ibid., 6º15’N, 75º10’W, 1850 m, 20 Mar 1990, *N. Contreras & D. L. Echeverri 257* (NY); Mun. Frontino, Parque Nacional Natural Las Orquídeas, 6º33’1.3”N, 76º18’54.3”W, 1240–1280 m, 25 Jul 2011, *D. Sanín et al. 5200* (NY); ibid., 6º32’6.8”N, 76º18’46.3”W, 880–920 m, 29 Jul 2011, *D. Sanín et al. 5107* (NY).

ECUADOR. **Morona-Santiago:** Bomboiza, 3º27’S, 78º34’W, 750 m, 23 Jul 1985, *W. Palacios 549* (NY).

BRAZIL. **Amazonas:** Barcelos, Parque Estadual da Serra de Aracá, tepuí do Aracá, formações campestres, igarapé Preto, acima da Cachoeira do Eldorado, 0º52’23”N, 63º20’29”W, 960 m, 16 Aug 2011, *G. Martinelli et al. 17010* (INPA).

Tryon (1997) synonymized *O. costaricensis* with *Oleandra lehmannii* Maxon, however the two species are easily distinguished. *Oleandra lehmannii* has stipe-like phyllopodia (Fig.9G) (*vs.* stem-like phyllopodia of *O. costaricensis*) (Fig.7B). *Oleandra costaricensis* is also considered close to *O. decurrens* and *O. trinitensis*, however *O. decurrens* differs easily from all other recognized species of *Oleandra* by the almost sessile leaves (Fig.9B), with stipes that do not exceed 5 mm, in addition to being a pilose species (Fig.9C). *Oleandra trinitensis* is a glabrous plant, but the marked difference between the species and *O. costaricensis* is in the midribs scales. While *O. costaricensis* has deltoid and very fimbriate scales (Fig.7C), *O. trinitensis* has lanceolate scales without much cilia (Fig.10B).

We personally examined the types of *O. costaricensis* and *O. dura*, and concluded that they belong to the same species, thus being synonyms.

Oleandra decurrens Maxon, Contrib. U. S. Natl. Herb. 17: 396. 1914. TYPE.—COSTA RICA. El General: Jan 1897, *H. Pittier 10649* (holotype: US!, no. 828702). Figs.9B–C.

Stems stout, 2–3 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent, rhizophore-like roots; ***scales*** 3–5 mm long, lanceolate, appressed, imbricate, bicolorous, centrally dark brown to blackish, light brown to orange at the margins, densely glandularciliate. ***Phyllopodia*** stem-like, subfasciculate to fasciculate, 1–1.5 mm long, light brown, glabrous, scaly. ***Leaves*** 15–25 cm long; ***stipes*** 0.3–0.4 cm long or absent, light brown, glabrous, scaly; ***laminae*** linear-oblong, narrowly cuneate at base, long-acuminate to attenuate at apex, 15–25 × 2.5–3.5 cm; ***midribs*** abaxially with linear/lanceolate, light brown, sparsely ciliate scales, 1.5–2 mm long, pilose on both sides; ***veins*** free, furcate, 22–26 per centimenter, adaxially glabrescent, abaxially pilose; ***laminar tissue between the veins*** adaxially glabrous, abaxially pilose; ***laminar margins*** pilose; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, light brown, pilose; ***spores*** monolete, light brown.

Distribution and ecology.— Plants epiphytic; ca. 700–1,500 m alt.; Costa Rica and Panamá.

Specimens examined.—COSTA RICA. **Puntarenas:** Parque Nacional Corcovado Cerro Rincón, Dos Brazos de Rio Tigre, 8º 31' 30" N, 83º 28' 00" W, 745 m, 02 Aug 1990, *G. Herrera 4091* (NY); Forested area near the airfield about 4 miles west of Rincon de Osa, Osa Peninsula, 8º42'N, 83º31'W, 30 m, 4–7 Jun 1968, *W. C. Burger 5475 & R. G. Stolze* (GH, US). **San José:** San Isidro del General, 2200 feet, 25 Jul 1940, *M. A. Chrysler & W. E. Roever 5229* (NY). **Alajuela:** Pentes occidentales des collines de Piedades prés San Ramón, 1100 m, 30 May 1901, *A. M. Brenes 14240* (GH); San Isidro de San Ramón, 10º 04' 46" N, 84º 26' 30" W, 1259 m, 22 Oct 1986, *G. Herrera 101* (US); Along straight gravel road on ridge SW of Quebrada Zapote, 1100–1500 m, 14 Jul 1987, *A. M. Evans & D. B. Lellinger 275* (US).

PANAMA. **Veraguas:** Distrito de Montijo, Isla Coiba, 30 Aug 1995, *B. Araúz et al. 204* (NY, US). **Coclé:** Cloud Forest, El Valle, 800–1000 m, 28 Jun 1967, *J. A. Duke 13172 (3)* (US); Ell Valle, at edge of road above valley 29 Aug 1960, *J. E. Ebinger 1110* (US). **Panamá:** Cerro Jefe, 11 miles S. from Goofy Lake (Cerro Azul), 16 Sep 1967, *M. D. Correa A. & R. L. Dressler 268* (US).

The types of *O. decurrens* and *O. costaricensis* ate from the same locality, but these species are very distinct from each other. *Oleandra decurrens*, besides having a decurrent laminae, with almost absent or absent stipe (Fig.9B), which already differentiates it from all others species of *Oleandra*, is a pilose plant. *Oleandra costaricensis* has stipes with more than 0.4 mm, and is a glabrous/glabrescent plant.

Within the informal morphological group 3, which *O. decurrens* is part, the species differs by the decurrent laminae, with almost absent or absent stipe (Fig.9B).

Oleandra duidae A.C. Smith, Bull. Torrey Bot. Club 58: 301. 1931. TYPE.—VENEZUELA. Mount Duida: Central Camp, 4900 ft, 1928–1929, *Tate 580* (holotype: NY!). Figs.9D–E.

Oleandra archeri Maxon, Amer. Fern J. 24: 74. 1934. Type.—COLOMBIA. Choco: Between La Oveja & Quibdo, 1 Apr 1931, *W. A. Archer 1669* (holotype: US!).

Stems slender, 1–3 mm diam., climbing to ascending, dark brown, scaly, pruinose, with glabrous, rhizophore-like roots; ***scales*** 6–8 mm long, lanceolate, appressed, imbricate, bicolorous, centrally dark brown, orange at the margins, with a hyaline border, sparse to moderately ciliate. ***Phyllopodia*** stipe-like, sparse, 1.4–2.7 cm long, light brown to greenish-brown, lustrous, glabrous, not scaly. ***Leaves*** 22–24 cm long; ***stipes*** 3–5.2 cm long, light brown to greenish-brown, lustrous, sulcate, glabrous, not scaly; ***laminae*** elliptical to elliptical-oblong, cuneate at base, long-acuminate at apex, 17–30 × 4–5 cm; ***midribs*** abaxially with rare lanceolate, brown, caduceous scales at base, glabrous on both sides; ***veins*** free, furcate, 13–17 per centimenter, glabrous on both sides; ***laminar tissue between the veins*** glabrous on both sides; ***laminar margins*** glabrous; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, bicolorous, dark brown in the middle, light brown in the margins, glabrous; ***spores*** light brown.

Distribution and ecology.—Plants rupestrial or epiphytic, ca. 1,500 m alt.; Venezuela and Colombia.

Specimens examined.—VENEZUELA. **Rio Negro:** Cerro Aracamuni, summit. Proa camp. Medium height, 01º32'N, 65º49'W, 1400 m, 2 Nov 1987, *R. Liesner & G. Carnevali 22723* (NY).

COLOMBIA. **Chocó:** Area of Baudó, On the right side of Rio Baudo, about 19 km upstream from the estuary, 11 Feb – 29 Mar 1967, *H. P. Fuchs & L. Zanella 22370* (US).

Oleandra duidae is within the species of *Oleandra* that have stem scales appressed, imbricate and stipe-like phyllopodia (informal morphological group 2) (Fig.9E). Due to these characteristics, Tryon (1997) synonymized the species with *O. lehmannii*. However, *O. lehmannii* has several persistent midribs scales (Fig.9H) (hardly found in *O. duidae*), in addition to the laminae more linear (Fig.9F) (*vs.* laminae more elliptical of *O. duidae*) (Fig.9D). In the original description of *O. archeri*, Maxon (1934) differed the species from *O. duidae* by the size of leaves (*O. archeri* would be a bigger plant), by the stem scales up to 8 mm, and only 13–16 veins per centimenter in the laminae. However, personally analyzing the types of the two species, in addition to finding more than 20 veins per cetimenter in the laminae of the type of *O. archeri*, we also did not see these big differences in the sizes of the leaves and the stem scales.

Oleandra hirta Brack., U.S. Expl. Exped., Filic. 16:214, t. 29. 1854. *Oleandra neriiformis* Cav. var. *hirta* (Brack.) Baker, Fl. Bras. [Martius] 1(2):495. 1870. LECTOTYPE (designated by Maxon, 1914: 394).—BRAZIL. Rio de Janeiro: Organ Mountains, near Rio de Janeiro, 1838–

1842, Herb. U.S. South Pacific Expl. Exped, *Capt. Wilkes s.n.* (US! barcode 00810702; isolectotype: K barcode 000590573, image!). Figs.3K–L.

Stems dark brown, pruinose, ca. 2 mm diam.; ***scales*** not seen. ***Phyllopodia*** 25–42 mm long. ***Leaves*** 50–55 cm long; ***stipes*** 2.5–4 cm long, brown; ***laminae*** linear, long-attenuate at base, acuminate to slightly aristate at apex, 45–50 3 3–3.2 cm; ***midribs*** pilose on both sides and fimbriate scales; ***veins*** partly anastomosing, pilose on both sides; ***laminar tissue between the veins*** pilose on both sides; ***laminar margins*** pilose; ***sori*** infra-medial in an irregular row; ***indusia*** reniform, dark brown, pilose; ***spores*** not seen.

Distribution and ecology.—Plants epiphytic or rupestrial; elevation unknown (probably ca. 1,000–1,500 m); Endemic to the state of Rio de Janeiro.

Oleandra hirta is known only from the type collection, which was made by the United States Exploring Expedition in the mid 19th century. The linear laminae (Fig.3K) make *O. hirta* more similar to Old World species, such as *O. neriiformis* Cav. and *O. mollis* C.Presl, and the partly anastomosing veins (Fig.3L) are unique in the genus. Further collections are needed to better understand this species and to propose conservation actions.

Oleandra hovenkampii C. V. Miranda & Schwartsb., Brittonia 73: 146, Figs. 2 A–C, 3C. 2021. TYPE:—PERU. Dept. San Martín: Tingo María, 625–1100 m, 30 Oct 1949–19 Feb 1950, *H. A. Allard 21581* (holotype: US! barcode US01581811). Figs.2A–C.

Stems slender, 2–4 mm diam., long-creeping, dark brown, scaly, pruinose, with pilose, rhizophore-like roots; ***scales*** 4–6 mm long, lanceolate, squarrose, darker only at the attachment point, orange in the remaining parts, margins with a few glandular cilia. ***Phyllopodia*** short, stipe-like, 3–4 mm long, lanose, the hairs shiny hyaline. ***Leaves*** 11–17 cm long; ***stipes*** short, 4–5 mm long, light brown, lustrous, lanose, the hairs similar to those from the phyllopodia; ***laminae*** elliptical, acute to obtuse at base, acute at the apex, 10.5–16.5 × 2.5–3.5 cm; ***midribs*** lanose on both sides, without scales; ***veins*** free, furcate, 12–14 veins per centimeter, lanose on both sides; ***laminar tissue between the veins*** lanose on both sides, ***laminar margins*** lanose. ***Sori***, ***indusia***, and ***spores*** not seen.

Distribution and ecology.—Plants rupestrial, elevation unknown, probably around 1,000–1,520 m; Apparently with a disjunct distribution, known so far from Peru and Costa Rica (possibly also in other countries of the northern Andes).

Additional specimens examined. COSTA RICA. **Cartago:** Orosí, ca. 5000 ft., 24–31 Mar 1951, *Scamman 5914* (GH).

Oleandra hovenkampii is included among the species that present slender stems, squarrose stem scales, and stipe-like phyllopodia (Fig.2B) (our informal morphological group 1). Due to the hairy lamina, it is more similar to *O. australis*, *O. baetae, O. hirta*, *O. quartziticola,* and *O. zapatana.*

Oleandra hovenkampii easily differs from all these species by the lanose laminae (*vs.* pilose laminae). Also compared to *O. hirta*, *O. australis*, *O. quartziticola*, and *O. zapatana*, *O. hovenkampii* differs by the orange color of their stem scales (*vs.* brown scales). This brings *O. baetae* closer, which also has orange stem scales. However, *O. baetae* has a truncate or inequilateral laminar bases (Fig.3A), while *O. hovenkampii* has acute to obtuse laminar bases (Fig.2A). Additionally, these two species occur at least 3,700 km apart: *O. baetae* is endemic to the Brazilian Atlantic Forests, while *O. hovenkampii* is known from Peru and Costa Rica.

Oleandra lehmannii Maxon, Contrib. U. S. Natl. Herb. 17: 395. 1914. TYPE.—COLÔMBIA. Amalfi: 2000 m, Oct 1884, *F.C. Lehmann XLII* (holotype: US! no. 828705). Figs.9F–H.

Oleandra guatemalensis Maxon, Contrib. U. S. Natl. Herb. 17: 395. 1914. Type.—GUATEMALA. Alta Verapaz: Senahú to Actalá, 17 Jan 1905, *W.R. Maxon & R. Hay 3333* (holotype: US! no. 473315).

Stems stout, 2–3.5 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent, rhizophore-like roots; ***scales*** 2–4 mm long, lanceolate, appressed, imbricate, bicolorous, centrally dark brown, orange at the margins, moderately ciliate. ***Phyllopodia*** stipe-like, subfasciculate, 12–22 mm long, glabrous, scaly at base. ***Leaves*** 11–40 cm long; ***stipes*** 1–4 cm long, light brown, lustrous, glabrous, not scaly; ***laminae*** linear/oblong, cuneate to attenuate at base, caudate at apex, 10–36 × 1.2–3 cm; ***midribs*** abaxially with deltoid, light brown, sparsely ciliate scales, glabrous on both sides; ***veins*** free, furcate, 20–22 per centimenter, glabrous on both sides; ***laminar tissue between the veins*** glabrous on both sides;

laminar margins glabrous; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, light brown, glabrous; ***spores*** light brown.

Distribution and ecology.—Plants epiphytic; high elevations, ca. 1,300–2,200 m alt.; Colombia, Venezuela, Peru, Ecuador, Guatemala and Hispaniola.

Specimens Examined.—COLOMBIA. "**El Valle" [Valle del Cauca]:** Buenaventura, 0–10 m, 5–10 Oct 1922, *E. P. Killip 11738* (NY); Agua Clara, along highway from Buenaventura to Cali, 100 m, 06 Jun 1944, *E. P. Killip & J. Cuatrecasas 38920* (US); Río Calima (región del Chocó), La Trojita, 5–50 m, 19 Feb – 10 Mar 1944, *J. Cuatrecasas 16597* (US). **Antioquia:** Mpio. Betania, Vereda Pedral arriba, Alto de las Flores, 05º44'49.33" N, 76º00'18.66" W, 2100–2200 m, 06 Nov 2004, *W. D. Rodríguez et al. 4619* (NY); "El Santuario", Jul 1934, *Bro. Daniel 14* (US). **Chocó:** Area of Baudó, on the right side of Rio Baudo, about 19 km upstream from the estuary, 11 Feb – 29 Mar 1967, *H. P. Fuchs & L. Zanella 22370* (US-2 sheets); Dense forest south of Rio Condoto, between Quebrada Guarapo and Mandinga, 120–180 m, 22, 28 Apr 1939, *E. P. Killip 35438* (US). Departament unknown: Locality unknown, s.d., *Herbarium Lehmannianum collection 5165* (US). **Chocó-Antioquia:** At and on both sides of the principal ridge W of La Mansa, at ca. Km. 105.5 of the Ciudad Bolivar-Quibdo Road, 2100–2200 m, 04 Apr 1971, *D. B. Lellinger & E. R. de la Sota 943* (US). **Huila:** Pass between Garzon and Florencia, west slope of Cordillera Oriental, 2300 m, 19 Feb 1949, *H. L. Mason 13923* (GH).

VENEZUELA. **Bolivar:** Distrito Piar, Macizo del Chimantá, aprox. 5º 18' N, 62º 09' W, +2000 m, 26–29 Jan 1983, *J. A. Steyermark et al. 128207* (NY); ibid., 26–29 Jan 1983, *Otto Huber & J. A. Steyermark 6928* (NY); Ptari-tepuí, on forested south-facing slopes overlying sandstone, on "Cave Rock" above "Cave Camp", 1810 m, 29 Oct 1944, *J. A. Steyermark 59495* (NY, US); Talus cloud forest, nothwest slopes of Churi-tepuí (Muru-tepuí), 2050 m, 25 Jan 1953, *J. J. Wurdack 34199* (NY, US). **Amazonas:** Cerro Sipapo (Paráque), 5000', 20 Jan 1949, *B. Maguire & L. Politi 28467* (NY, US); Cerro Marahuaca, 1000 m, 03 May 1949, *B. Maguire & B. Maguire Jr. 29173* (NY); Cerro de la Neblina, Río Yatua, 1700–1750 m, 27 Dec 1953, *B. Maguire et al. 36941* (NY).

PERU. **Pasco:** Oxapampa, Dist. Villa Rica, Parque Nacional Yanachaga-Chemillén, 10º39'57"S, 075º10'41"W, 1760–1850 m, 29 May 2005, *E. Ortiz V. et al. 667* (NY); Pass before La Suiza, 20 km W of Oxapampa, 75º 33' W, 10º 35' S, 2100–2150 m, 27 Dec 1983, *D. N. Smith 5395* (NY, GH); Oxapampa, La Suiza Nova, 10º 33' 44" S, 075º 27' 22" W, 2210 m, 06 May 2005, *H. van der Werff et al. 19739* (NY); Oxapampa, La Suiza Vieja, 10º33’ S, 075º27’ W, 2200 m, 23 Jun 2003, *H. van der Werff et al. 17737* (NY); Chontabamba, Abra la Suiza, ca. 2500 m, 23 Jun 1986, *B. León et al. 968* (GH). **Junín:** Pichis Trail, Dos de Mayo, 1700–1900 m, *E. P. Killip & A. C. Smith 25870* (NY, US, GH). **Huanuco:** Southwestern slope of the Rio Llullapichis watershed, on the ascent of Cerros del Sira, 9º25’ S, 74º44’ W, 1850 m, 31 Jul 1969, *T. R. Dudley 13554* (US, GH); ibid, 9º25’ S, 74º42’ W. 2100 m, 30 Jul 1969, *T. R. Dudley 13453* (GH); ibid., 9º25’ S, 74º43’ W, 2000 m, 30 Jul 1969, *T. R. Dudley 13489* (GH); ibid., 9º26’ S, 74º45’ W, 1480 m, 26 Jul 1969, *T. R. Dudley 13306B* (GH).

ECUADOR. **Morona-Santiago:** Cordillera de Cutucú, western slopes, along a trail from Longroño to Yaupi, 2º46’ S × 78º06’ W, 2000 m, Nov 1976, *M. T. Madison et al. 3557* (GH).

GUATEMALA. **Alta Verapaz:** Cobán, 4300 pp., Aug 1886, *H. von Türckheim 983* (US-2 sheets, GH-paratype). **Quetzaltenango:** Trail from Esperanza to Purulá [interpreted], 19 Jan 1905, *W. R. Maxon 3361 & R. Hay* (US).

HISPANIOLA. **Haiti:** Massif de la Hotte, western group, Torbec, slope of Morne Formand, 1550 m, 29 Dec 1926, *E. L. Ekman H7459* (US-2 sheets).

Maxon (1914) differs *O. lehmannii* from *O. guatemalensis* by the midribs scales (cordate-ovate or deltoid-ovate, acuminate in *O. lehmannii* and orbicular-cordate to cordate, acute or acutish in *O. guatemalensis*) and by the number of veins per centimenter in the leaves (20 to 28 in *O. lehmannii* and 14 to 18 in *O. guatemalensis*). Although, analizyng the holotypes of the two species, we observe that the scales are very similar (deltoid to lanceolate), in addition to the number of veins per centimenter being equal, approximately 21 veins per centimenter.

Difference of *O. lehmannii* with *O. amazonica* and *O duidae*, see in the comments of these species.

Oleandra nigropaleacea Labiak, ***sp. nov.*** TYPE:—COLOMBIA. Departament of El Cauca: “La Gallera.” Micay Valley, Cordillera Occidental, 1500–1800 m, 1 Jul 1922, *E.P. Killip 7893* (holotype NY!, barcode 04163495). Figs.7E–H.

Diagnosis.—Differs from *Oleandra trujillensis* by the deltoid/lanceolate, blackish and fimbriate midribs scales (*vs.* linear/lanceolate, light brown and not much fimbriate).

Stems stout, 1.0–3.5 mm diam., climbing to ascending, light brown, scaly, pruinose, rhizophore-like roots not seen; ***scales*** 3–5 mm long, lanceolate, appressed, imbricate, centrally and in the point of insertion blackish, light brown to orange at the margins, with few cilia in the margins. ***Phyllopodia*** stem-like, subfasciculate, 1–3 mm long, glabrous, scaly. ***Leaves*** 18–25 cm long; ***stipes*** 1.2–2.0 cm long, light brown, sulcate, glabrous, scaly; ***laminae*** linear/lanceolate, cuneate at base, long-acuminate at apex, 16–23 × 0.8–1.0 cm; ***midribs*** abaxially with lanceolate to deltoid, blackish, strongly ciliate scales, abaxially pilose, adaxially glabrescent; ***veins*** free, furcate, 20–28 per centimenter, glabrous on both sides; ***laminar tissue between the veins*** abaxially glabrous, adaxially glabrescent; ***laminar margins*** glabrous; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, light brown, pilose; ***spores*** monolete, light brown.

Etymology.—The specific epithet refers to the blackish midribs scales presents only in this species.

Distribution and ecology.—Plants epiphytic, climbing shrub, 1,500–1,800 m alt.; Endemic to Colombia.

Oleandra nigropaleacea differs from the others species of the informal morphological group 3 by its pilosity restricted to the midribs, in addition to also having blackish and fimbriate midribs scales, very characteristic (Fig.7G). Others species of the group have the laminae entirely pilose (*O. arbuscula*) or pilosity restricted to the laminar margins (*O. areniticola*). *Oleandra decurrens* is a decurrent species, with stipe almost absent or absent (Fig.9B). *Oleandra trujillensis* is very similar to *O. nigropaleacea* by the pilose indusia and pilose midribs, but the two species easily differs by the midribs scales (deltoid/lanceolate, blackish and fimbriate in *O. nigropaleacea* vs. linear/lanceolate, light brown and not much fimbriate in *O. trujillensis*). *Oleandra trinitensis* and *O. costaricensis* have glabrous indusia.

Oleandra nigrovenia C.V. Miranda & Schwartsb., ***sp. nov.*** TYPE:—VENEZUELA. Atabapo: Falda del extremo norte del Cerro Duida, 6 Feb 1982, *J. Steyermark s.n., M. Guariglia, N. Holmgren, J. Luteyn & S. Mori* (holotype NY!, barcode 04163486). Figs.8A–C.

Diagnosis.—Differs from all others species of *Oleandra* by the laminae extremely afilate/filiformis with crenate laminar margins and by the black veins.

Stems slender, 1–3 mm diam., long-creeping, dark brown, not pruinose, with glabrescent, rhizophore-like roots, scaly; ***scales*** 3–4.5 mm long, lanceolate, subulate, appressed, imbricate, centrally and in the point of insertion blackish, orange at the margins, densely ciliate. ***Phyllopodia*** stipe-like, sparse to subfasciculate, 0.2–0.6 cm long, light brown, pilose, scaly. ***Leaves*** 9–15 cm long; ***stipes*** 0.3–1.5 cm long, light brown, lustrous, pilose, scaly; ***laminae*** linear/filiformis, narrowly cuneate at base, acuminate at apex, 8.5–14.5 × 0.4–0.8 cm, pilose, crenate margins; ***midribs*** abaxially with lanceolate, dark brown scales, 2–3 mm long, abaxially; ***veins*** free, furcate, pilose on both sides, 18–26 veins per centimeter; ***laminar tissue between the veins*** pilose on both sides; ***laminar margins*** pilose. ***Sori***, ***indusia*** and ***spores*** not seen.

Etymology.—The specific ephitet refers to the well-marked black veins, unique to the species.

Distribution and ecology.—Plants rupestrial, in rock crevices, 800–900 m, sandstones; Endemic to Venezuela.

Oleandra nigrovenia differs easily from all others species of *Oleandra* by the laminae extremely afilate/filiformis with crenate laminar margins (Fig.8A) and by the unique black veins (Fig.8C).

There is another material from Venezuela, Liesner 16086 (NY-04163417), with darker veins such as in *O. nigrovenia*, but the laminae and the stem scales are diferent. The laminae of this material is not afilate/filiformis with crenate margins, but lanceolate, with entire margins. The stem scales are dark in the center and at the point of insertion, with brown margins with few cilia. In *O. nigrovenia*, the stem scales are dark only at point of insertion, and densely ciliate. So, there are doubts about this material, being needed more studies of this plants in Venezuela.

Oleandra pilosa Hook., Gen. Fil. [Hooker] t. 45B and text. 1840. LECTOTYPE (designated by Tryon 1997: 340).—BRITISH GUIANA. Berbice: *Schomburgk 416* (holotype: K-*n.v.*; isotypes: B-image!, E-image!, L-*n.v.*). Figs.8D–G.

Stems stout, 2–5 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent, rhizophore-like roots; ***scales*** 2.5–4.5 mm long, lanceolate, appressed, imbricate, bicolorous at base, dark brown to blackish at the attachment point, light brown at the margins, moderate to densely ciliate. ***Phyllopodia*** stipe-like (mixed with stem-like in some points), sparse to subfasciculate, 3.5–20 mm long, light brown to olivaceous, lustrous, pilose, not scaly. ***Leaves*** 10.5–30 cm long; ***stipes*** 0.6–2 cm long, light brown to olivaceous, lustrous, pilose (or glabrescent, in marurity), not scaly; ***laminae*** linear-oblong, cuneate at base, acuminate to long-acuminate at apex, 10–29 × 2–4.5 cm; ***midribs*** abaxially with lanceolate, light brown, sparsely ciliate scales, 1–2.5 mm, pilose on both sides; ***veins*** free, furcate, 16–20 per centimenter, pilose on both sides; ***laminar tissue between the veins*** glabrous on both sides; ***laminar margins*** pilose; ***sori*** inframedial to medial in an irregular row; ***indusia*** orbicular-reniform, dark brown, pilose; ***spores*** monolete, light brown.

Distribution and ecology.—Plants epiphytic or rupestrial; elevation unknown, probably around 700–1,250 m alt.; Central America, Guyanas and north region of Brazil.

Specimens Examined.—GUYANE FRANÇAISE. **Savane:** Crique Gabaret: Bassin de l’Oyapock, Em aval de saut Merignan, Long. 51º48’, Lat. 3º55, 10 m, 13 Apr 1988, *G. Cremers 9917* (INPA).

BRAZIL. **Pará:** Canaã dos Carajás, Floresta Nacional de Carajás, Seera Sul, Corpo A, 6º19’43”S, 50º27’18”W, 737 m, 15 Feb 2010, *T. E. Almeida et al. 2201* (BHCB); Mato Grosso: R. Juruena, Cachoeira Lavarinto, 22 Mai 1977, *N. A. Rosa & M. R. Santos 1979* (RB); Breves, Comunidade São Pedro, ca. 01º33’33,2”S-50º26’45,9”W, 4 May 2011, *M. G. C. Souza & M. R. Pietrobom 1053* (HBRA). **Amazonas:** Igarapé da Lage, quilômetro 115 estrada Manaus – Boa Vista, 23 Jul 1981, *P. J. Pivetta 1521* (HRCB); Presidente Figueiredo, Estrada de Balbina: Margem da estrada de acesso a Balbina, 26 Jan 1998, *C. A. A. Freitas et al. 607* (INPA); Coari, Base da Petrobrás: Rio Urucu, 27 May 1991, *C. A. A. Freitas 342 & C. D. A. da Mota* (INPA); Reserva Florestal A. Ducke, sector baixo acará-Manaus, 1 Nov 1995, *M. Flores Arévalo & J. Lima 823* (INPA); Barcelos, Platô da Serra de Aracá, parte SE da Serra Norte. 0º51N, 63º22’W, 1150 a 1250 msm, 13 Feb 1984, *I. L. Amaral 1533* (INPA); Manaus, km 138 da estrada Manaus – Itacoatiara, 8 Jun 1972, *O. Pires & J. Lima 58* (INPA); Campus da Universidade – Manaus, 21 Sep 1995, *M. Flores Arévalo 792* (INPA). **Roraima:** Caracaraí, Parque Nacional do Viruá: Grade do PPBio do PARNA do Viruá, 1º28’07”N, 61º00’27”W, 71 m, 23 Oct 2011, *N. F. O. Mota et al. 2424* (INPA).

The original description of *Oleandra pilosa* by Hooker (1840) is very brief, in just two lines. The author just describes the articulated stipes, the pubescent-hirsute leaves and the pilose phyllopodia. Due to the very brief description, all pilose specimens of *Oleandra*, with appressed stem scales and stem-like phyllopodia, has been identified as *Oleandra pilosa* in herbaria.

However, in this work we noted that there are many pilose plants with these characteristics, but different species, and analizing the type of *Oleandra pilosa*, we concluded that *Oleandra pilosa* s. str. has no stem-like phyllopodia, but a mix of stipe-like and stem-like phyllopodia (Fig.8E) and is more distributed in Central America, Guyanas and north region of Brazil.

Oleandra quartziticola Schwartsb. & J.Prado, Am. Fern J. 106(3): 202, Figs. 2G–J. 2016. TYPE.—BRAZIL. Espírito Santo: Vargem Alta, Morro Branco, 20º39’28’’S, 41º00’18’’W, 640 m, 17 Sep 2015, *P.B. Schwartsburd & C.V. Miranda 3522* (holotype: SP!; isotypes: FI!, NY!, RB!, UC!, UPCB!, VIC!-on 2 sheets). Figs.4G–J.

Stems slender, 1–3.5 mm diam., long-creeping, light brown, scaly, not pruinose, with glabrescent rhizophore-like roots; ***scales*** 4–4.5 mm long, lanceolate, squarrose, bicolorous, centrally black, orange at the margins, densely glandular-ciliate. ***Phyllopodia*** stipe-like, 15–20 mm long, pilose in young leaves, glabrescent in maturity, scaly. ***Leaves*** 18–30 cm long; ***stipes*** (2–)3–5.5 cm long, stramineous to brown, sulcate, pilose in young leaves, glabrescent in maturity, scaly; ***laminae*** elliptical, cuneate at base, acuminate or aristate at apex, 15–25 3 2–4.2 cm; ***midribs*** abaxially with a few linear/lanceolate, brown scales, pilose on both sides; ***veins*** free, furcate, pilose on both sides, 17–19 veins per centimeter; ***laminar tissue between the veins*** abaxially glabrous, adaxially glabrescent; ***laminar margins*** pilose. ***Sori*** infra-medial in an irregular row; ***indusia*** orbicular-reniform, bicolorous, centrally dark brown, light brown at the margins, glabrous; ***spores*** light brown.

Distribution and ecology.—Plants rupestrial, ca. 600–700 m alt., growing on quartz boulders; Endemic to the state of Espírito Santo, southeastern Brazil.

Specimens Examined.—BRAZIL. **Espírito Santo:** Vargem Alta, ES-164, no km 332, 20º39’ 26.7’’S, 41º00’20.0’’W, 663 m, 23 Jan 2011, *J.R. Pirani et al. 6209* (SP, SPF); Vargem Alta, Morro Branco, 20º39’26’’S, 41º00’19’’W, 660 m, 17 Sep 2015, P.B. *Schwartsburd & C.V. Miranda 3525* (SP, VIC); ibid, 22 Sep 2018, C. V. Miranda et. al. 59 (VIC); Vargem Alta, Sítio Morro Branco, 24 Sep 2018, *C. V. Miranda et al. 88* (VIC); ibid., 24 Sep 2018, *C. V. Miranda et al. 89* (VIC); ibid., 24 Sep 2018, *C. V. Miranda et al. 90* (VIC); ibid., 24 Sep

2018, *C. V. Miranda et al. 91* (VIC); ibid., 24 Sep 2018, *C. V. Miranda et al. 92* (VIC); ibid., 24 Sep 2018, *C. V. Miranda et al. 93* (VIC); ibid., 24 Sep 2018, *C. V. Miranda et al. 94* (VIC); ibid., 24 Sep 2018, *C. V. Miranda et al. 95* (VIC).

Oleandra quartziticola is endemic to the state of Espírito Santo, and it is characterized by bicolorous stem scales, elliptical laminae (Fig.4G), midribs pilose on both sides, veins, and laminar margins, glabrous laminar tissue between the veins (abaxially), and bicolorous indusia (Fig.4I). Besides having different geographical ranges, *O. quartziticola* differs from *O. baetae* by longer fronds, 18–30 cm long (vs. 9–15(22) cm), longer stipes, (2–)3–5.5 cm long (vs. 3–5 mm), laminae proximally cuneate (vs. truncate or inequilateral), and laminar tissue between the veins abaxially glabrous (vs. with catenate and glandular hairs) (Figs.3A–D; 4G–J).

Oleandra steyermarkii Lellinger ex C. V. Miranda & Labiak, Brittonia 73: 149, figs. 2D–G, 3D. 2021. TYPE:—VENEZUELA. Estado Bolívar: Cerro Venado, 1100 m, 21 Apr 1960, *J. A. Steyermark & S. Nilsson 442* (holotype: NY! Barcode 00149743; isotypes: NY! barcode 00951456, US-*n.v.* barcode 00799101). Figs.2D–G.

Stems slender, 2–3 mm diam., creeping, dark brown, scaly, pruinose, with glabrescent rhizophore-like roots; ***scales*** 3–5 mm long, lanceolate, appressed, imbricate, centrally and in the point of insertion blackish, orange at the margins and borders, with sparse cilia. ***Phyllopodia*** short, stipe-like, 0.5–1.1 cm long, lanose, the hairs conspicuous, long, tortuous, hyaline with orange cross-wall of the cells, also with a few long-ciliate scales. ***Leaves*** 16–30 cm long; ***stipes*** 1.0–2.2 cm long, light brown, sulcate adaxially, lustrous, lanose on both sides, the hairs similar to those from the phyllopodia; ***laminae*** linear, cuneate at base, cuneate at the apex, 15–28 × 1.7–4 cm; ***midribs*** lanose on both sides, without scales; ***veins*** free, furcate, 14–15 per centimeter, lanose on both sides; ***laminar tissue*** between the veins lanose on both sides; ***laminar margins*** lanose. ***Sori***, ***indusia***, and ***spores*** not seen.

Distribution and ecology.—Plants rupestrial (sandstone rocks); 1,100–1,275 m alt.; Probably endemic to the Guiana Shield, in northeastern Venezuela.

Additional specimens examined. VENEZUELA. **Bolívar**: Cerro Venado, parte Sur-Oeste, cerca de los limites con la Guayana Inglesa, 1220–1275 m, 6–7 Jan 1964, *J. A. Steyermark et al. 92779* (GH, US).

Due to the slender stems, appressed scales, and stipe-like phyllopodia, *Oleandra steyermarkii* falls in our informal group 2, along with *O. amazonica*, *O. archeri, O. duidae, O. guatemalensis*, and *O. lehmannii. Oleandra steyermarkii* differs from all these other species due to its densely lanose laminae (Fig.2G). The other species have glabrescent to glabrous laminae.

Oleandra steyermarkii resembles *O. pilosa* s. str. (group 3) and *O. hirta* (group 1) by linear-elongate, hairy laminae. However, it is easy to distinguish *O. steyermarkii* from *O. hirta* due to its appressed stem scales (vs. squarrose) (Figs.2E, 3K). *Oleandra pilosa* s. str. also has appressed scales on the laminae. However, whereas *O. pilosa* s. str. has pilose laminae, and cuspidate to acuminate apices and acute bases (Fig.8D), *O. steyermarkii* has lanose laminae, with cuneate apices and bases (Fig.2D). *Oleandra steyermarkii* is apparently substrate-specific, occurring on sandstones – the substrate information is not available for *O. hirta,* nor *O. pilosa* s. str.

Oleandra trinitensis Maxon, Contrib. U. S. Natl. Herb. 17: 397. 1914. TYPE.—TRINIDAD: 1877–78, *A. Fendler 114* (holotype: US!, isotypes: US!, GH!, K-*n.v.*). Figs.10A–B.

Stems stout, 3–4 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent rhizophore-like roots; ***scales*** 4–6 mm long, lanceolate, appressed, imbricate, centrally and at the point of insertion blackish, light brown at the margins and borders, glandularciliate. ***Phyllopodia*** stem-like, 1–5 mm long, glabrous, scaly. ***Leaves*** 17–40 cm long; ***stipes*** 1–3 cm long, light brown to olivaceous, lustrous, sulcate, glabrous, scaly; ***laminae*** linear/lanceolate, acute at base, acuminate to attenuate at the apex, 15–28 × 2.5–4 cm; ***midribs*** abaxially with long-lanceolate, brown, sparsely ciliate scales; adaxially glabrous, abaxially glabrescent; ***veins*** free, furcate, glabrous on both sides, 19–23 veins per centimeter; ***laminar tissue between the veins*** glabrous on both sides, ***laminar margins*** glabrous or glabrescent. ***Sori*** inframedial to medial in an irregular row, ***indusia*** orbicular-reniform, light brown, glabrous; ***spores*** light brown.

Distribution and ecology.—Plants epiphytic; ca. 940 m (height of Cerro del Aripo); Endemic to Trinidad.

Specimens Examined.—TRINIDAD. **Arima:** Heights of Aripo, *s.d.*, *collector unknown 333* (NY-4163482). **Region Unknown:** Locality Unknown, *s.d.*, *collector unspecified s.n.* (NY-4163481).

Oleandra trinitensis is very close to *O. costaricensis* by the habit, stem-like phyllopodia, stem scales appressed (Fig.10A) and laminae glabrous, although the main feature that differentiates these two species are the midribs scales. Whereas in *O. costaricensis* the midribs scales are smaller and deeply ciliate (Fig.7C), in *O. trinitensis* the midribs scales are much more elongated, tapering at the tips and almost without cilia (Fig.10B). In the original description Maxon (1914) cited that the species also differs from *O. costaricens* by the strap-like shape of its leaves.

Tryon (1997) synonymized *Oleandra trinitensis* with *O. lehmannii*, but the two species are very different. *Oleandra lehmannii* has stipe-like phyllopodia (Fig.9G), whereas *O. trinitensis* has stem-like phyllopodia (Fig.10A). The midribs scales of *O. lehmannii* are also different from the midribs scales of *O. trinitensis*. The scales of *O. lehmannii* are deltoid and shorter (Fig.9H), whereas the scales of *O. trinitensis* are lanceolate and very elongated, with thin tips (Fig.10B).

Oleandra trujillensis Karst., Fl. Columb. 1: 147, t. 73. 1861. TYPE.—VENEZUELA. Escuque: Cordillera Meridensi, 1000 m, *Karsten s.n.* (holotype: LE-image!, barcode 00008190). Figs.10C–D.

Oleandra panamensis Maxon, Contrib. U. S. Natl. Herb. 17: 396. 1914. Type.—PANAMA: Cerro Vaca, eastern Chiriqui, 25–28 Dec 1911, *H. Pittier 5322* (US!).

Stems stout, 2–4 mm diam., climbing to ascending, light brown, scaly, pruinose, with glabrescent rhizophore-like roots; ***scales*** 3–5 mm long, lanceolate, appressed, imbricate, centrally and in the point of insertion dark brown, light brown at the margins and borders, with sparse cilia. ***Phyllopodia*** stem-like, 1–3 mm long, glabrous, scaly. ***Leaves*** 27–40 cm long; ***stipes*** 1–1.5 cm long, light brown, sulcate, glabrous, scaly; ***laminae*** linear/lanceolate, cuneate at base, long-acuminate at the apex, 25.5–38.5 × 2.5–3.5 cm; ***midribs*** abaxially with deltoid to lanceolate, light brown, strongly fimbriate scales, adaxially glabrescent, abaxially pilose; ***veins*** free, furcate, glabrous on both sides, 16–17 veins per centimeter; ***laminar tissue between the veins*** adaxially glabrous, abaxially glabrescent, ***laminar margins*** pilose or with sparse hairs in maturity. ***Sori*** inframedial to medial in an irregular row, ***indusia*** orbicular-reniform, dark brown, pilose, and ***spores*** light brown.

Distribution and ecology.—Plants epiphytic, 900–1,150 m alt.; Venezuela, Panama, Colombia and Ecuador.

Specimens Examined.—**COLOMBIA. El Cauca:** "La Gallera", Micay Valley, Cordillera Ocidental, 1500–1800 m, 01 Jul 1922, *E. P. Killip 7893* (NY). **Del Meta:** Sierra de la Macarena, Vereda El Tablazo, Morro Bello, Meseta Sur, 1200 m, 28 May 1973, *M. L. Chaparro et al. 52* (NY); Sierra de la Macarena, Central Mountains Approach Ridge, 1200 m, 23 Dec 1949, *W. R. Philipson & J. M. Idobro 1896* (NY). **Caqueta:** Sierra de Chiribiquete, Campamento Sur, Al SW del campamento, 0º55'N, 72º45'W, 450 m s.n.a., 11 Dec 1990, *J. Fuertes et al. 1127* (NY).

ECUADOR. Carchi: Tulcán, Chical, along path from the village of Chical towards na área known locally as "Crystal", walked along Rio Blanca via the Cordillera Gualchan, 00°53'49"N, 078º12'33.9" W, 1200–1800 m, 07 Dec 2001, *J. L. Clark et al. 6338* (NY).

Oleandra trujillensis is part of informal morphological group 3, species with stem scales appressed and phyllopodia stem-like (Fig.10D). Maxon (1914), separates this species of *O. panamensis* and *O. pilosa* in key step "indusia ciliate" and "indusia not ciliate", including the species within species with "indusia not ciliate", together *O. trinitensis* and *O. costaricensis*. However, in the original description the indusia is described as pilose and in the detailed illustration of Karsten's type this feature is clearly seen. Therefore, with the pilose/ciliate indusia, *O. trujillensis* and *O. panamensis* are the same species and are synonymized here.

Besides the Maxon's mistake by including the species in the key as "indusia not ciliate", in the species comments the author makes it clear that no specimen of this species was seen by him, in addition to quote: "…and will doubtless be found in Colombia and eastern Panama".

O. trujillensis differs from others species of informal morphological group 3 with pilose indusia by the pilosity and midribs scales. Whereas *O. trujillensis* has midribs and margins pilose, *O. areniticola* is pilose only at margins and *O. arbuscula* is entirely pilose. *O. nigropaleacea* has only midribs pilose and dark scales at midribs, whereas *O. trujillensis* has brown scales at midribs.

Oleandra zapatana Lell., Proc. Biol. Soc. Wash. 89: 719, f. 3. 1977. TYPE.—COLOMBIA. Chocó: ca. 1450–1750 m, *D. Lellinger & E.R. de la Sota 300* (holotype: US!, isotype: COL-*n.v.*, LP-*n.v.*). Figs.10E–H.

Stems slender, 2.–3.5 mm diam., long-creeping, dark brown, scaly, pruinose, with glabrescent rhizophore-like roots; ***scales*** 4–7 mm long, linear/lanceolate, squarrose, in the point of insertion dark brown, light brown at the margins and borders, with sparse cilia. ***Phyllopodia*** stipe-like, 11–22 mm long, glabrous, not scaly. ***Leaves*** 20–34 cm long; ***stipes*** (2.5)5–7 cm long, light brown, sulcate, glabrous, not scaly; ***laminae*** elliptical, acute to cuneate at base, long-acuminate at the apex, 18–29 × 4–7 cm; ***midribs*** pilose on both sides, not scaly; ***veins*** free, furcate, glabrous on both sides, 12–14 veins per centimeter; ***laminar tissue between the veins*** pilose on both sides, ***laminar margins*** pilose. ***Sori*** inframedial in an irregular row, ***indusia*** orbicular-reniform, dark brown, pilose, and ***spores*** light brown.

Distribution and ecology.—Plants epiphytic; ca. 850–1,750 m alt.; Disjunct distribution in Colombia and Bolivia. Perhaps present in Ecuador, Peru and north region of Brazil.

Specimens Examined.—COLOMBIA. **Chocó:** Río Mutatá ca. 3 km above its junction with the Río El Valle. NW of Alto del Buey. Primary montane forest on hillside, 850 m, 7 Feb 1971, *D. B. Lellinger & E. R. de la Sota 195* (paratype: US!, isoparatype: LP-*n.v.*).

BOLIVIA. **La Paz:** Chuquini, 3000 feet, 17–19 Apr 1926, *G. H. H. Tate 1152* (NY).

Tryon (1997) synonymized *O. zapatana* with *O. articulata*, probably due to the two species having stipe-like phyllopodia, stem scales squarrose and laminae elliptical. Although, the two species are easily distinguished by the pilosity. *O. zapatana* is a pilose plant, whereas *O. articulata* is a glabrous plant. In addition, *O. zapatana* doesn't have midribs scales, whereas *O. articulata* has midribs scales.

Within informal morphological group 1, *Oleandra zapatana* is closer to *O. quartziticola* and *O. australis*, due to the elliptical laminae (Fig.10E), some pilosity on the laminae and absence of midribs scales. However, *O. zapatana* has pilose indusia (Fig.10H), whereas *O. quartizicola* and *O. autralis* have glabrous indusia.

PUTATIVE HYBRIDS

Oleandra baetae × *Oleandra brasiliana*

Based on a specimen with intermediate morphological characters between *Oleandra baetae* and *O. brasiliana*, Schwartsburd, Miranda and Prado (2016) considered a hybrid between these two species. In this work, we confirm these intermediate characteristics between the two species, but also believe that it can be treated as only variations in *O. baetae*. Therefore, there is not enough robustness to assert the hybrid, and further studies are needed, cytogenetic or/and molecular, for its proof.

Oleandra pilosa × *Oleandra nigrovenia*

Initially, as mentioned in the taxonomic comments of *Oleandra nigrovenia*, we thought to have found other material (Liesner 16086 [NY- 04163417]) of this species, with dark veins, appressed stem scales, stipe-like phyllopodia and pilose laminae. However, differences were also noted in this material, such as the stem scales and the laminae shape. In this material, the stem scales are dark in the center and in the point of insertion, with brown margins and few cilia. In *O. nigrovenia*, the stem scales are dark only at the point of insertion, in addition to being densely ciliate. The laminae of this material are lancolate, with a much larger width and entire margins. In *O. nigrovenia* the laminae are afilate/filiformis, with crenate margins.

Therefore, joining morphological charateres and geographic distribution, is believed to be a hybrid between *O. nigrovenia* and *O. pilosa*. However, more materials from Venezuela must be colleted and analyzed, in addition to cytogenetic and molecular studies.

DOUBTFUL SPECIES

Oleandra micans Kunze Bot. Zeitung (Berlin) 9: 346. 1851

Oleandra micans had its type material destroyed in Leipzig (LZ), during a bombing in World War II (Thiers, 2022). Mettenius (1856) tried to designate a neotype, using the name and describing a material from Peru – *Lechler 2539* (B-*n.v.*, K-*n.v.*). However, in addition to the lost type material, the description of *Oleandra micans* is very succint and uninformative, being hard to say that they are the same species. Tryon (1997) designated a *Poeppig* lectotype in his work, however this lectotype does not exist, can not be, then, designated. Therefore, for the all reasons mentioned, the species is treated in this work as doubtful.

Oleandra articulata f. eglandulosa Domin, Rozpr. Kral. Ceske Spolecn. Nauk., Tr. Mat.-Prir. n.s., 2: 233. 1929. Holotype: Dominica, *Eggers 1036* (K-*n.v.*).

For *Oleandra articulata f. eglandulosa* we were able to analyze only one paratype – *Eggers 756* (L-image seen) – which seems to be *O. articulata*. The name alludes to a plant without glandular hairs, although *O. articulata* does not have any type of hairs, even. Perhaps, the author saw another material very similar to *O. articulata* and glabrescent, such as *O. brasiliana*, for example, and described the species as an *O. articulata* totally glabrous.

ACKNOWLEDGMENTS

The senior author thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for her Ph.D. fellowship, and Programa de Pós-Graduação em Botânica (Universidade Federal de Viçosa) through CAPES-PROAP for partially funding this work, including a trip to North American herbaria. We thank the curators and herbarium staff by their assistance during our visits or by the loans. We thank Reinaldo Pinto for the illustrations, and Robbin Moran (NY) and Túlio Pena (VIC) for their support. We also thank editors and anonymous reviewers for their contributions to the manuscript.

LITERATURE CITED

ALSTON, A. H. G. 1959. The Ferns and Ferns Allies of West Tropical Africa. Millbank, London.

BAKER, J. G. 1870. Cyatheaceae et Polypodiaceae. In: Martius, C. F. P. and A. G. Eichler (eds) Flora Brasiliensis. Monachii, Lipsiae: Fleischer in Comm. vol. 1(2):306–624.

BRACKENRIDGE, W. D. 1854. United States exploring expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. Vol. 16: botany, Cryptogamia, Filices, including Lycopodiaceae and Hydropterides. C. Sherman, Philadelphia.

BRADE, A. C. 1940. Contribuição para o estudo da flora Pteridophyta da Serra de Baturité, Estado do Ceará. Rodriguésia 4:289–302.

CAVANILLES, A. J. 1799. Nuevos caractéres genéricos de los Helechos por Smith. Anales de Historia Natural 2:108–115.

CHING, R. C. 1940. On natural classification of the family “Polypodiaceae”. Sunyatsenia 5:201–268.

CHRISTENHUSZ, M. J. M., X-C. ZHANG, AND H. SCHNEIDER. 2011. A linear sequence of extant families and genera of lycophytes and ferns. Phytotaxa 19:7–54.

CHRISTENSEN, C. 1938. Filicinae, pp. 522–550. In: Verdoorn, ed., Manual of Pteridology. Nijhoff. The Hague.

COPELAND, E. B. 1947. Genera Filicum. Chronica Botanica, Waltham, Mass, 247 pp.

FÉE, A. L. A. 1852. Genera Filicum. Exposition des genres de la famille des Polypodiacées (Classe des fougères) – 5me Mémoire sur la famille des fougères. J. B. Baillière, Victor Masson, Paris; V. Berger-Levraut et fils, Strasbourg.

FREITAS, R. C. A. AND L. Q. MATIAS. 2010. Situação amostral e riqueza de espécies das Angisopermas do Estado do Ceará, Brasil. Acta Botanica Brasilica 24 (4):964–971.

HASEBE, M., P. G. WOLF, K. M. PRYER, K. UEDA, M. ITO, R. SANO, G. J. GASTONY, J. YOKOYAMA, J. R. MANHART, N. MURAKAMI, E. H. CRANE, C. H. HAUFLER, AND W. D. HAUK. 1995. Fern Phylogeny based on *rbcL* nucleotide sequences. American Fern Journal 85(4):134–181.

HOLTTUM, R. E. 1947. A revised classification of leptosporangiate ferns. Botanical Journal of the Linnean Society. 53:123–158.

HOOKER, W. J. 1840. Genera Filicum. H. G. Bohn. London.

HOVENKAMP, P. AND B-C. HO. 2012. A revision of the fern genus *Oleandra* (Oleandraceae) in Asia. PhytoKeys 11:1–37.

KRAMER, K. U. 1990. Oleandraceae. In:Kramer, K. U., Green PS (Eds) The Families and Genera of Vascular Plants. Springer, New York, 190–193.

KUO, L-Y., F-W. LI, W-L. CHIOU, AND C-N. WANG. 2011. First insights into fern *matK* phylogeny. Molecular Phylogenetics and Evolution 59:556–566.

LELLINGER, D. B. 2002. A modern multilingual glossary for taxonomic pteridology. Pteridologia, vol. 3.

LIEW, F. S. 1977. Scanning eléctron microscopical studies on spores of Pteridophytes. 11. The family Oleandraceae (*Oleandra*, *Nephrolepis* and *Arthropteris*). Gardens' Bulletin. (Singapore) 30:101–110.

MAXON, W. R. 1914. Studies of tropical American ferns, no.5. The American species of *Oleandra*. Contributions from the United States National Herbarium 17:392–398.

MIRANDA, C. V., P. B. SCHWARTSBURD, P. H. LABIAK, AND J. PRADO. 2021. Three new species of *Oleandra* (Oleandraceae, Polypodiopsida) from the Neotropics, and notes on the morphological groups among the Neotropical species. Brittonia 73:143–151.

NAYAR, B. K., N. BJAPAI, AND S. CHANDRA. 1968. Contributions to the morphology of the fern genus *Oleandra*. Botanical Journal of the Linnean Society. 60:265–282.

OGURA, Y. 1938. Anatomy and morphology of *Oleandra Wallichii* (Hk.) Pr., with some notes on the affinities of the genus *Oleandra*. Japanese Journal of Botany 9:193–211.

PICHI-SERMOLLI, R. E. G. 1965. Adumbratio Florae Aethiopicae. 11. Oleandraceae. Webbia 20:745–769.

PPG I. 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution. Evol. 54:563–603.

PRESL, C. B. 1836. *Tentamen Pteridographiae: seu genera filicacearum praesertim juxta venarum decursum et distributionem exposita*, vol. 3. Typis Filiorum Theophili Haase, Prague, 290 pp.

ROUX, J. P. 2009. Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar, and neighbouring islands. Strelitzia 23:1–296.

SCHUETTPELZ, E. AND K. PRYER. 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon 56(4):1037–1050.

SCHWARTSBURD, P. B., C. V. MIRANDA, AND J. PRADO. 2016. *Oleandra* (Oleandraceae) in the Brazilian Atlantic Forest. American Fern Journal 106:191–205.

SMITH, J. 1841. Enumeration Filicum Philippinarum. Journal of Botany III: 393–422.

SMITH, J. 1842. An arrangement and definition of the genera of Ferns, with observations on the affinities of each genus. Journal of Botany. 4:38–70.

SMITH, J. 1866. Ferns, British and Foreign. P. 73. London.

SMITH, A. R., K. M. PRYER, E. SCHUETTPELZ, P. KORALL, H. SCHNEIDER, AND P. G. WOLF. 2008. Fern classification. Pp. 417–467. *In:* T. A. Ranker & C. H. Haufler (eds.), Biology and evolution of ferns and lycophytes. Cambridge University Press, Cambridge.

SPLITGERBER, F. L. 1840. Enumeratio Filicum et Lycopodiacearum quas in Surinamo legit F. L. Splitgerber. Tijdschrift voor Natuurlijke Geschiedenis en Physiologie Amsterdam 7:411.

SWARTZ, O. 1801. Genera et species filicum ordine systematico redactarum. Journal für die Botanik [Edited by H. A. Schrader] Göttingen 1800.

SWARTZ, O. 1806. Synopsis Filicum. Bibliopolii novi academici, Kiel, 44 pp.

TARDIEU-BLOT, M. L. 1958. Polypodiacees (sensu lato). Dennstaedtiacees. Aspidiacees. In: H. Humbert (ed), Flore de Madagascar et des Comores (Plantes Vasculaires). Fam. 5. 1:1–391. Typographie Firmin-Didot, Paris.

TARDIEU-BLOT, M. L. 1964. Pteridophytes. In: Aubréville, A. (ed), Flore du Cameroun, 3. – Paris.

THIERS, B. 2020. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Disponível em http://sweetgum.nybg.org/science/ih/. Acesso em: Oct 2021.

TINDALE, M. D. 1961. Pteridophyta of South Eastern Australia. Davalliaceae. Contributions from New South Wales National Herbarium Flora Series. 208–211:1–4.

TRYON, R. M. 1997. Systematic notes on *Oleandra*. Rhodora 99(900):335–343.

TSUTSUMI, C. AND M. KATO. 2006. Evolution of epiphytes in Davalliaceae and related ferns. Botanical Journal of the Linnean Society. 151:495–510.

WETTER, C. 1951. Über die Luftwurzeln von *Oleandra*. Planta (Berlin) 39:471–475.

FIGURE LEGENDS

Fig. 1A–E. *Oleandra amazonica*: A – Habit, B – Detail of the attachment between phyllopodia and stipe, C – Stem scale, D – Midrib scale, E – Lamina, abaxially, showing midrib scales, glabrous veins, laminar tissue, and laminar margins, sori, and indusia.

Fig. 2A–C. *Oleandra hovenkampii*: A – Habit, B – Detail of stem, phyllopodia and stipe, C – Stem scale. **D–G.** *Oleandra steyermarkii*: D – Habit, E – Detail of stem, phyllopodia and stipe, F – Stem scale; G – Lamina, abaxially, showing lanose midrib, veins, laminar tissue, and laminar margins.

Fig. 3A–D. *Oleandra baetae:* A. Habit. B. Stem scale. C. Detail of lamina abaxially and laminar margin. D. Indusia. **E–J.** *O. brasiliana*. E. Habit. F. Habit. G. Stem scale. H. Articulation between phyllopodia and stipe. I. Indusia. J. Detail of lamina abaxially and laminar margin (from a mature glabrescent specimen). **K, L.** *O. hirta.* K. Habit. L. Detail of partly anastomosing veins, abaxially.

Fig. 4A–B. *Oleandra baetae* × *O. brasiliana*: A. Habit. B. Detail of lamina abaxially and laminar margin (see in section *Putative Hybrids*). **C–F.** *O. australis:* C. Habit. D. Stem scale. E. Detail of midribs, abaxially. F. Detail of lamina abaxially and laminar margin. **G–J.** *O. quartziticola*: G. Habit. H. Stem scale. I. Indusia. J. Detail of lamina abaxially and laminar margin.

Fig. 5A–D. *Oleandra aequatorialis:* A. Habit. B. Detail of stem and phyllopodia. C. Lamina, abaxially, showing midrib scales, veins, laminar tissue, laminar margins and sori. D. Detail of pilose veins, laminar tissue between the veins glabrous and indusia. **E–H.** *O. arbuscula:* E. Habit. F. Detail of stem and phyllopodia. G. Lamina, abaxially, showing midrib scales, veins, laminar tissue, laminar margins and sori. H. Detail of pilose veins, laminar tissue between the veins pilose and pilose indusia.

Fig. 6A–D. *Oleandra areniticola:* A. Habit. B. Detail of stem and phyllopodia. C. Lamina, abaxially, showing midrib scales, veins, laminar tissue, pilose laminar margins and sori. D. Detail of veins, laminar tissue and pilose indusia. **E–H.** *O. articulata*: E. Habit. F. Detail of stem and phyllopodia. G. Lamina, abaxially, showing midrib scales, veins, laminar tissue, laminar margins and sori. H. Detail of veins, laminar tissue and indusia.

Fig. 7A–D. *Oleandra costaricensis:* A. Habit. B. Detail of stem and phyllopodia. C. Lamina, abaxially, showing midrib scales, veins, laminar tissue, laminar margins and sori. H. Indusia. **E–H.** *O. nigropaleacea:* E. Habit. F. Detail of stem and phyllopodia. G. Lamina, abaxially, showing midrib scales, veins, laminar tissue, laminar margins and sori. H. Pilose indusia.

Fig. 8A–C. *Oleandra nigrovenia*: A. Habit. B. Detail of stem and phyllopodia. C. Lamina, abaxially, showing midribs, black veins, laminar tissue and laminar margins. **D–G.** *O. pilosa:* D. Habit. E. Detail of stem and the mixed of stipe-like and stem-like phyllopodia. F. Lamina, abaxially, showing midrib scales, veins, laminar tissue, laminar margins and sori. G. Detail of pilose veins, laminar tissue glabrous and pilose indusia.

Fig. 9A. *Oleandra bradei:* Detail of stem scales, squarrose and more laxly spreading. **B–C.** *O. decurrens*: B. Detail of stem, phyllopodia, stipe, laminae base and midribs scales, C. Pilose indusia. **D–E.** *O. duidae:* D. Habit. E. Detail of stem and phyllopodia. **F–H.** *O. lehmannii*: F. Habit. G. Detail of stem and phyllopodia. H. Detail of midribs scales.

Fig. 10A–B. *Oleandra trinitensis:* A. Detail of stem and phyllopodia. B. Detail of midribs scales. **C–D.** *O. trujillensis:* C. Habit. D. Detail of stem and phyllopodia. **E–H.** *O. zapatana:* E. Habit. F. Detail of stem and phyllopodia. G. Detail of midribs, veins and laminar tissue. H. Detail of pilose indusia.

FIGURES

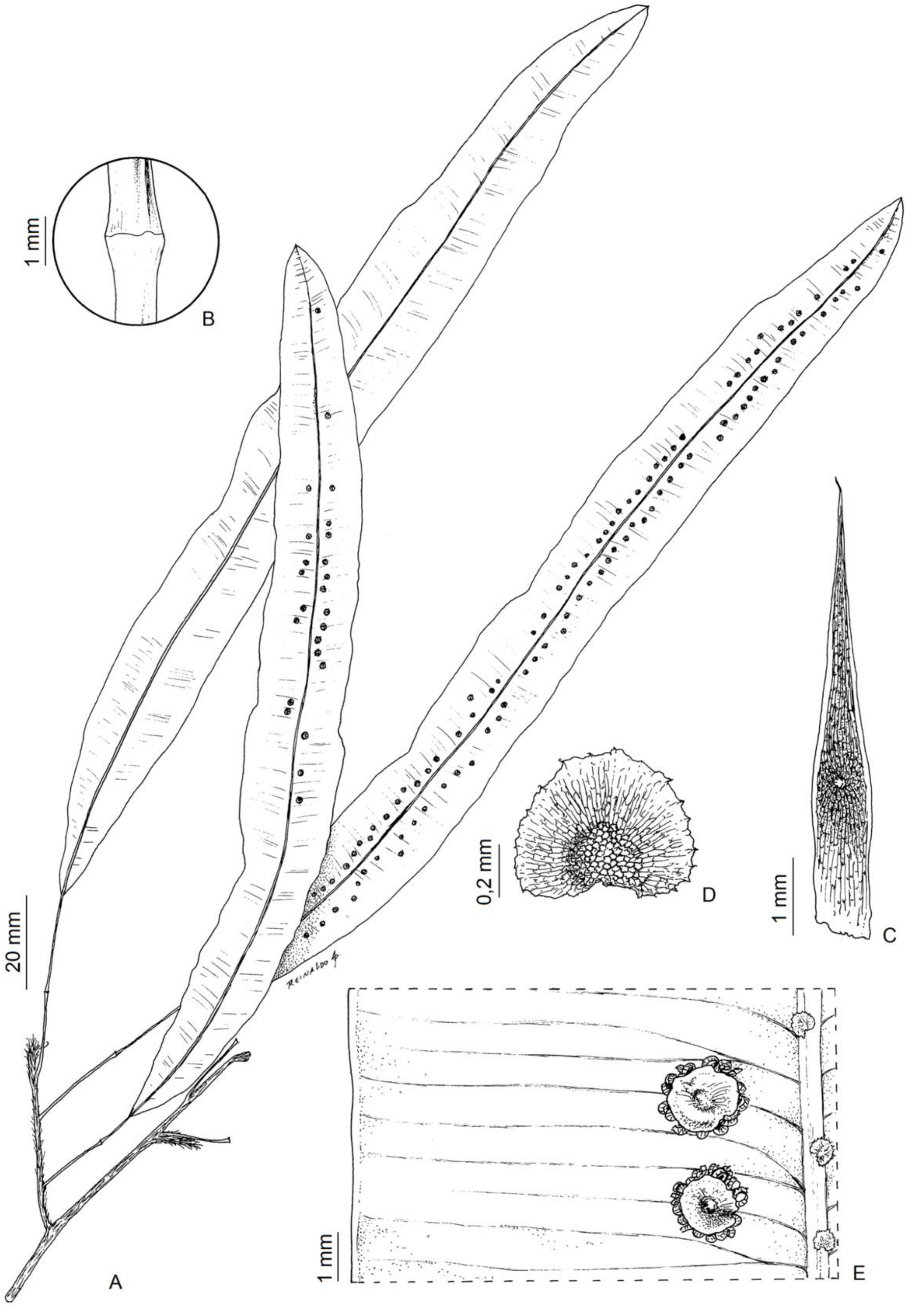


FIG.1

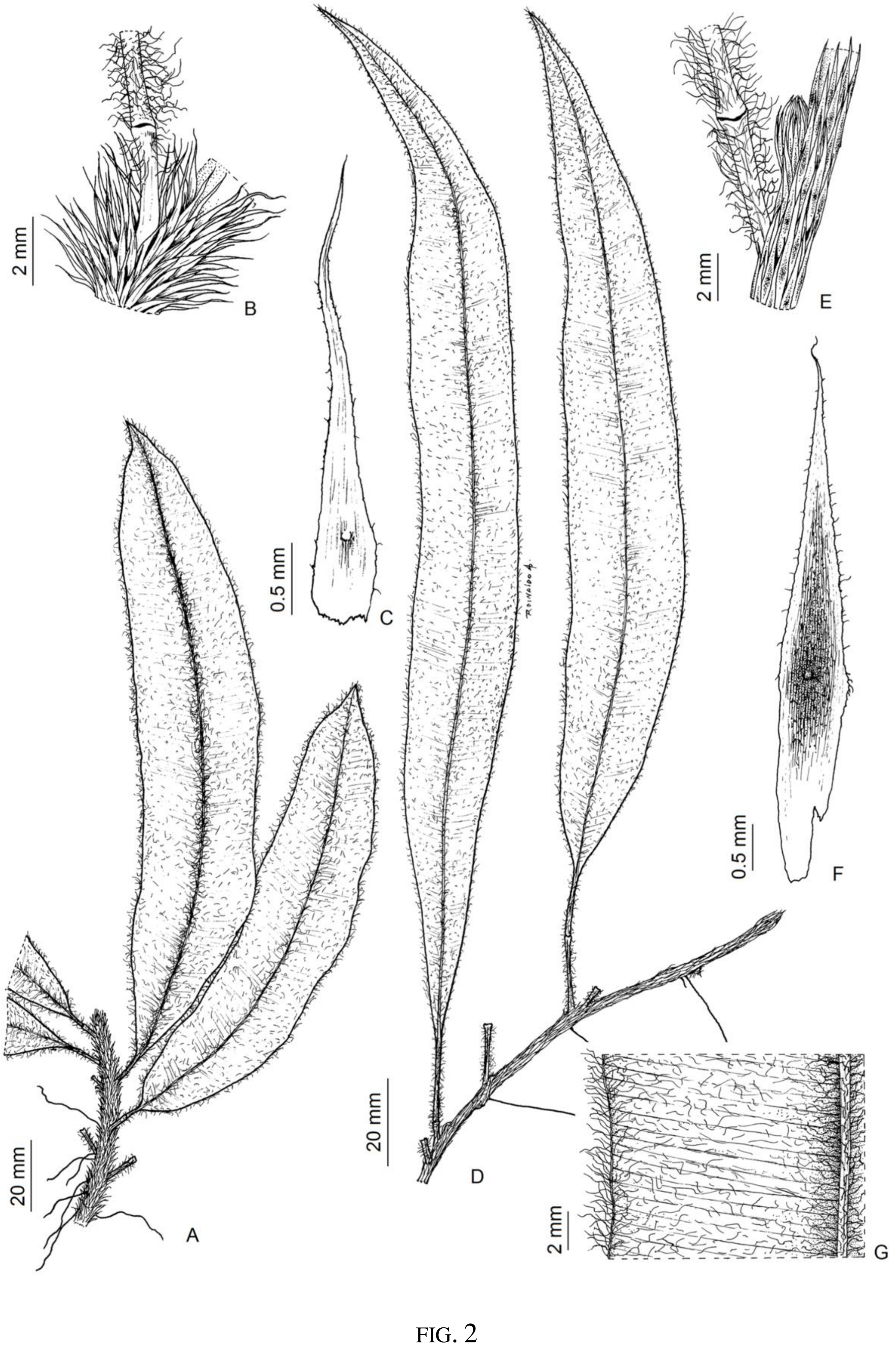
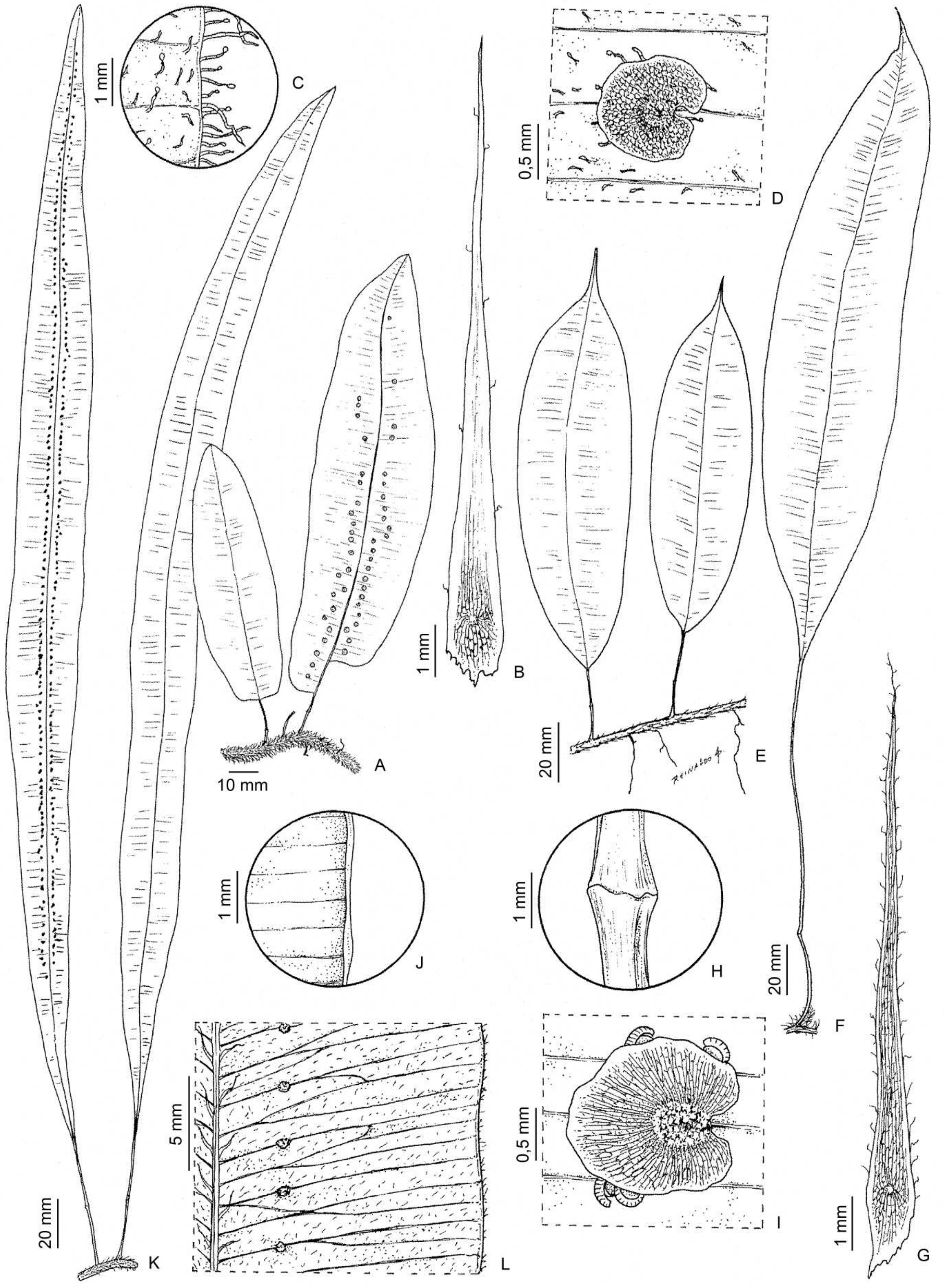


FIG. 2


C
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G
20 mm
K
L

FIG. 3

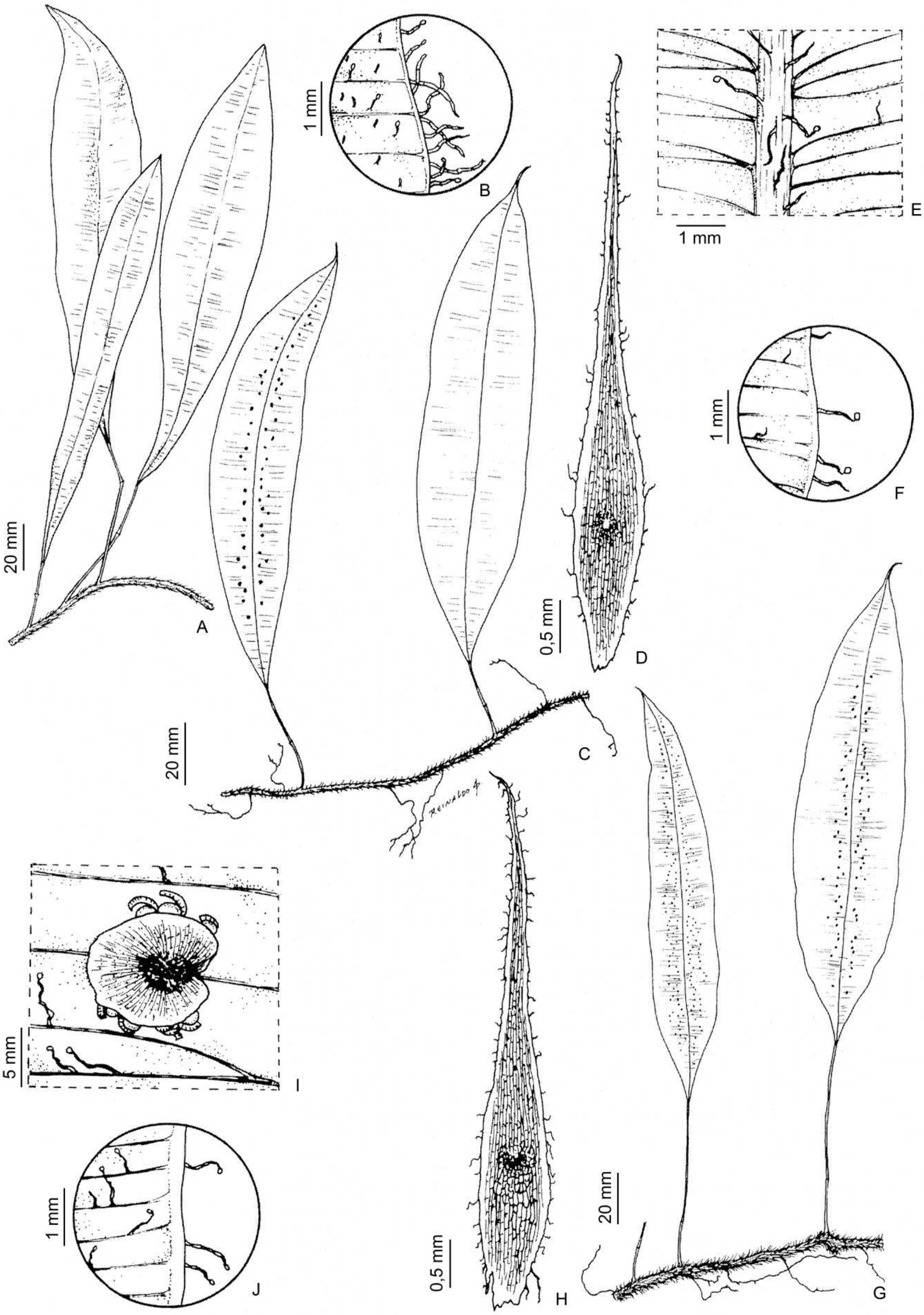
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FIG.4

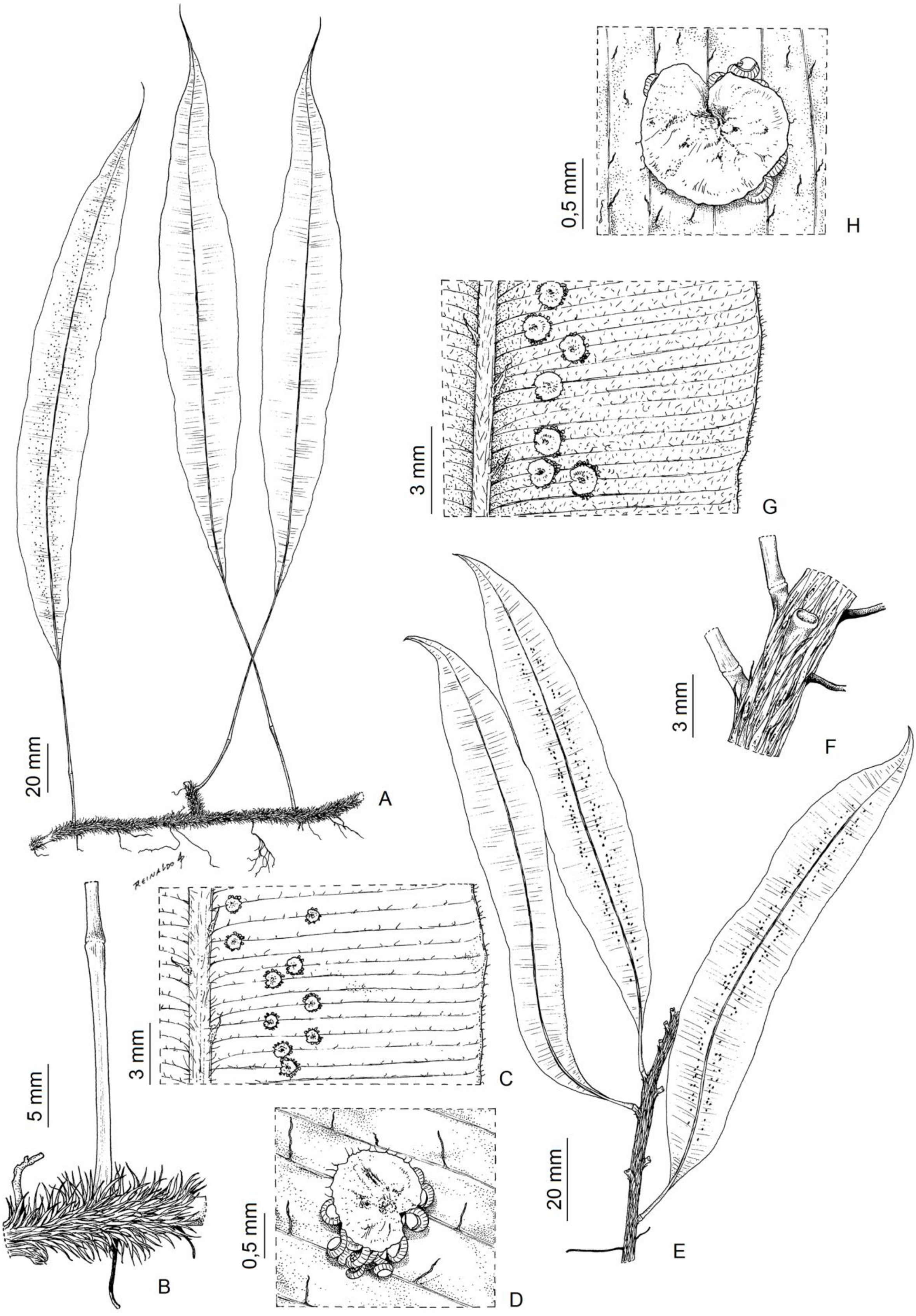

FIG. 5

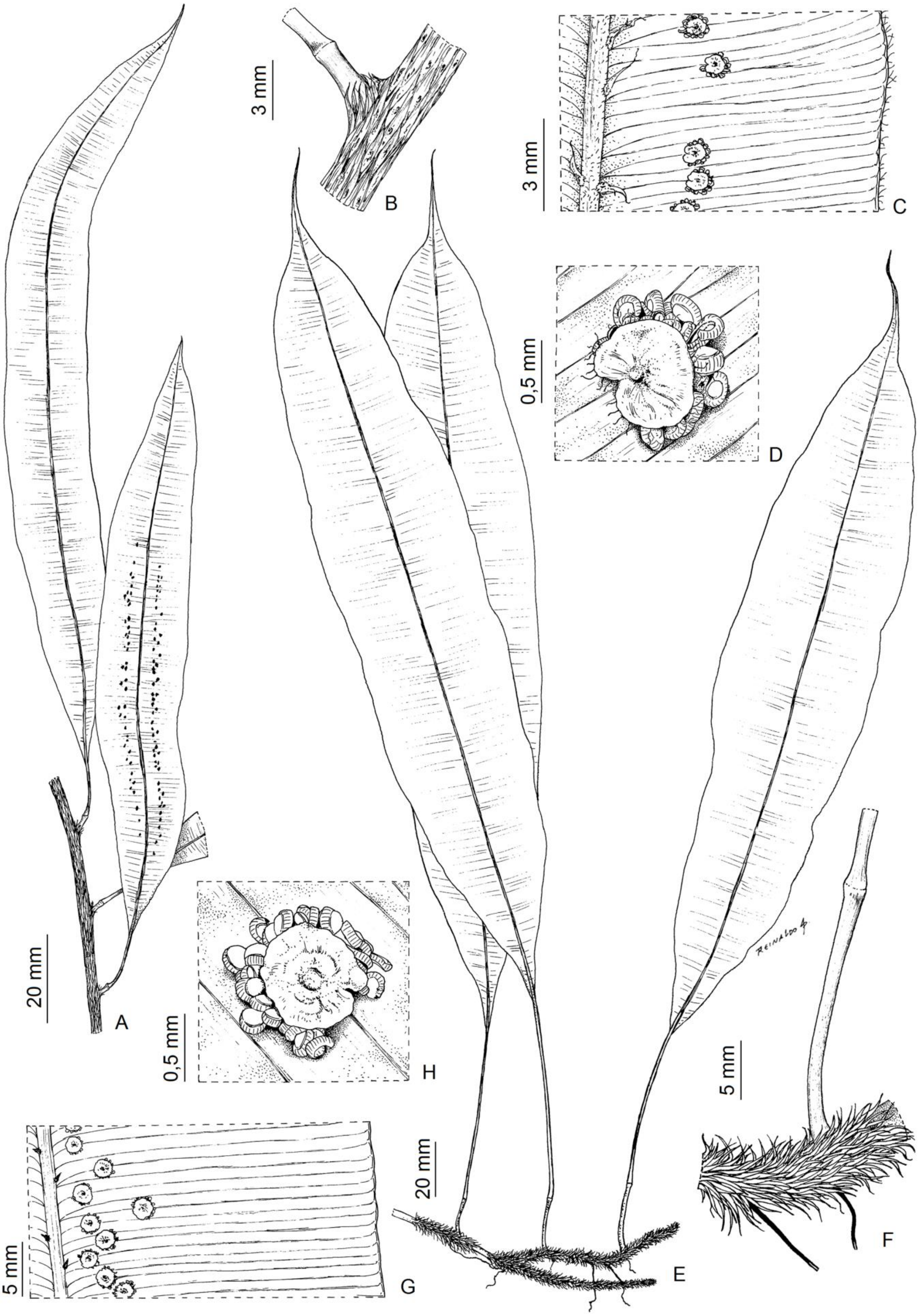

FIG. 6

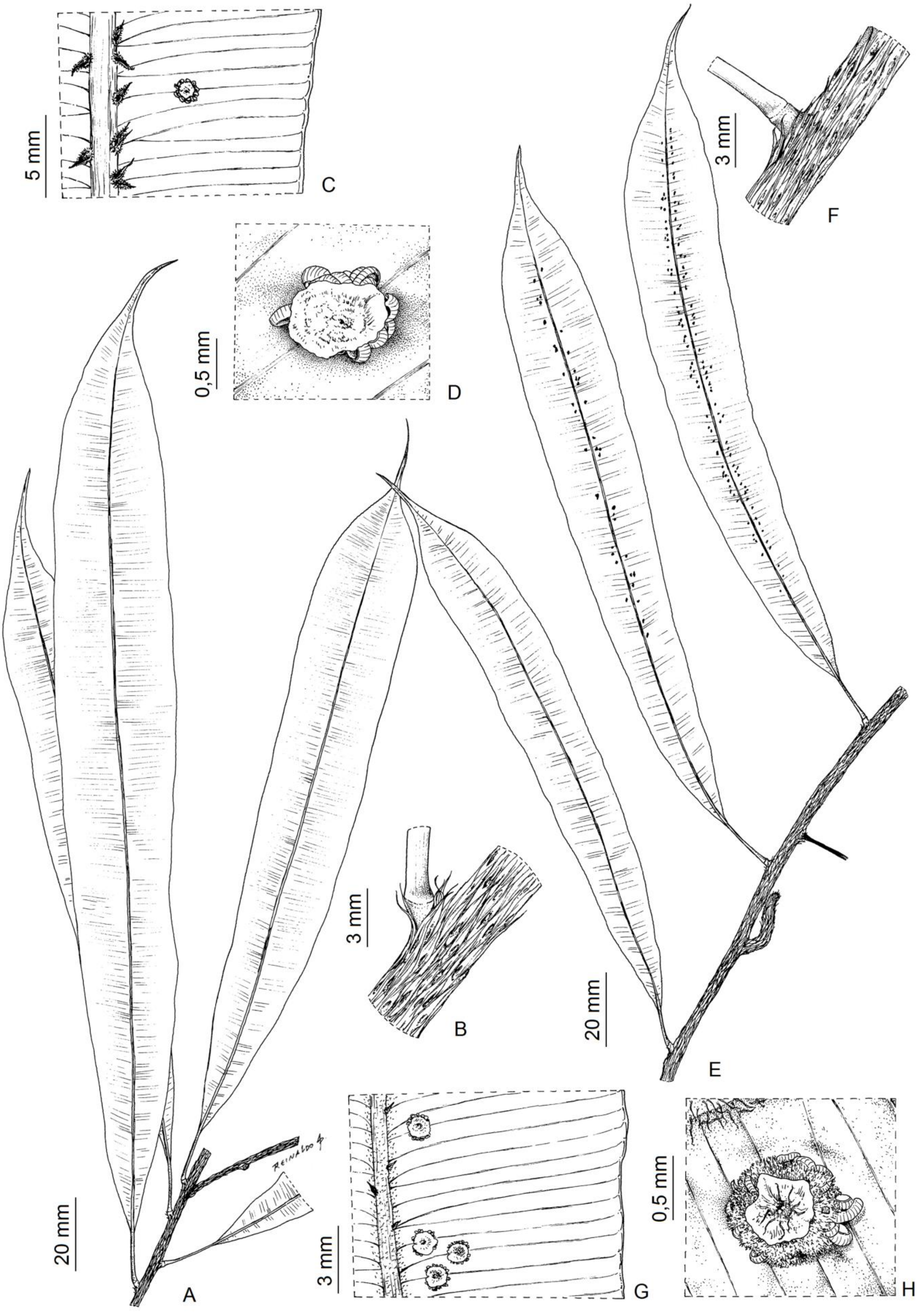

FIG. 7

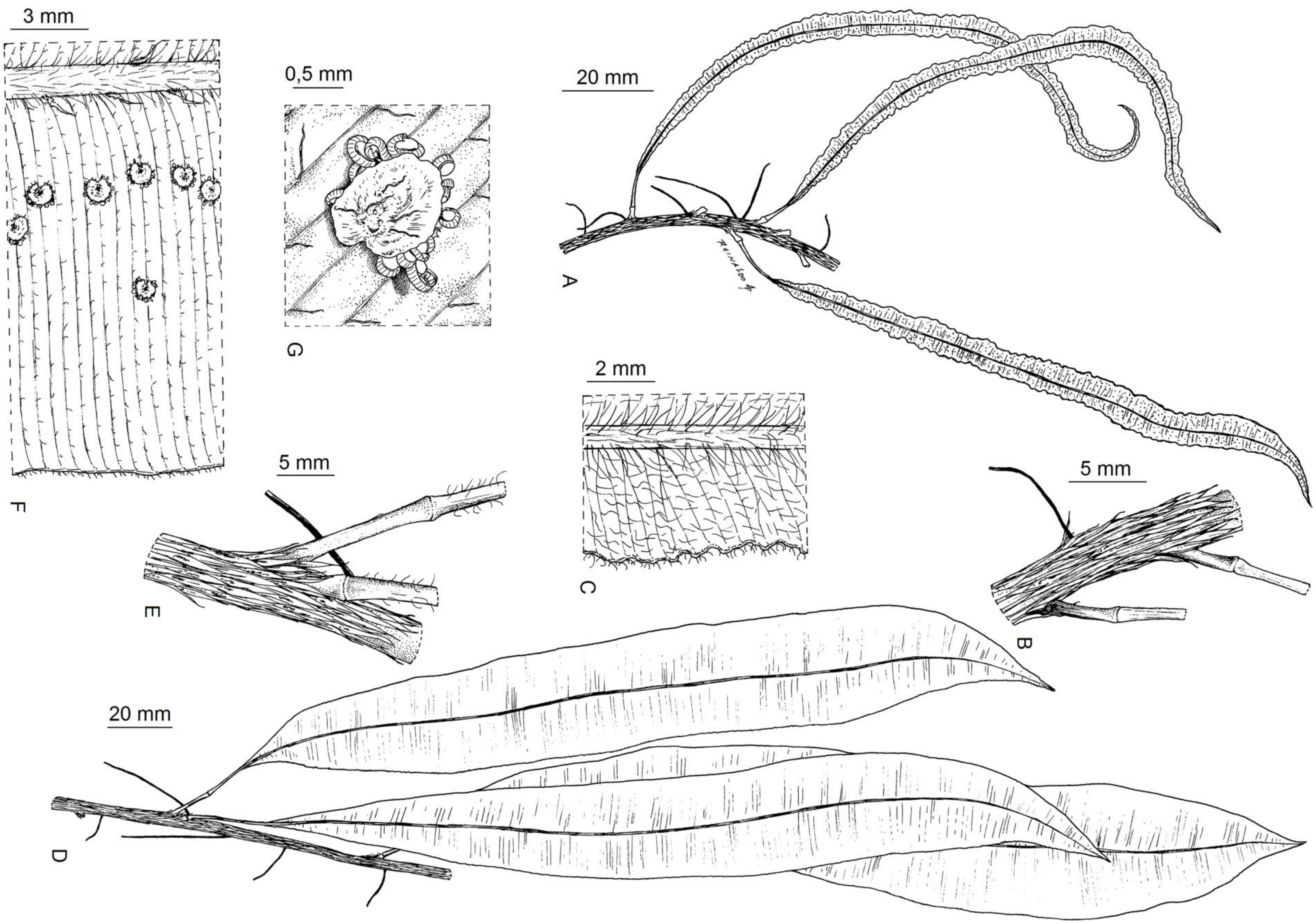

FIG. 8

FIG.9

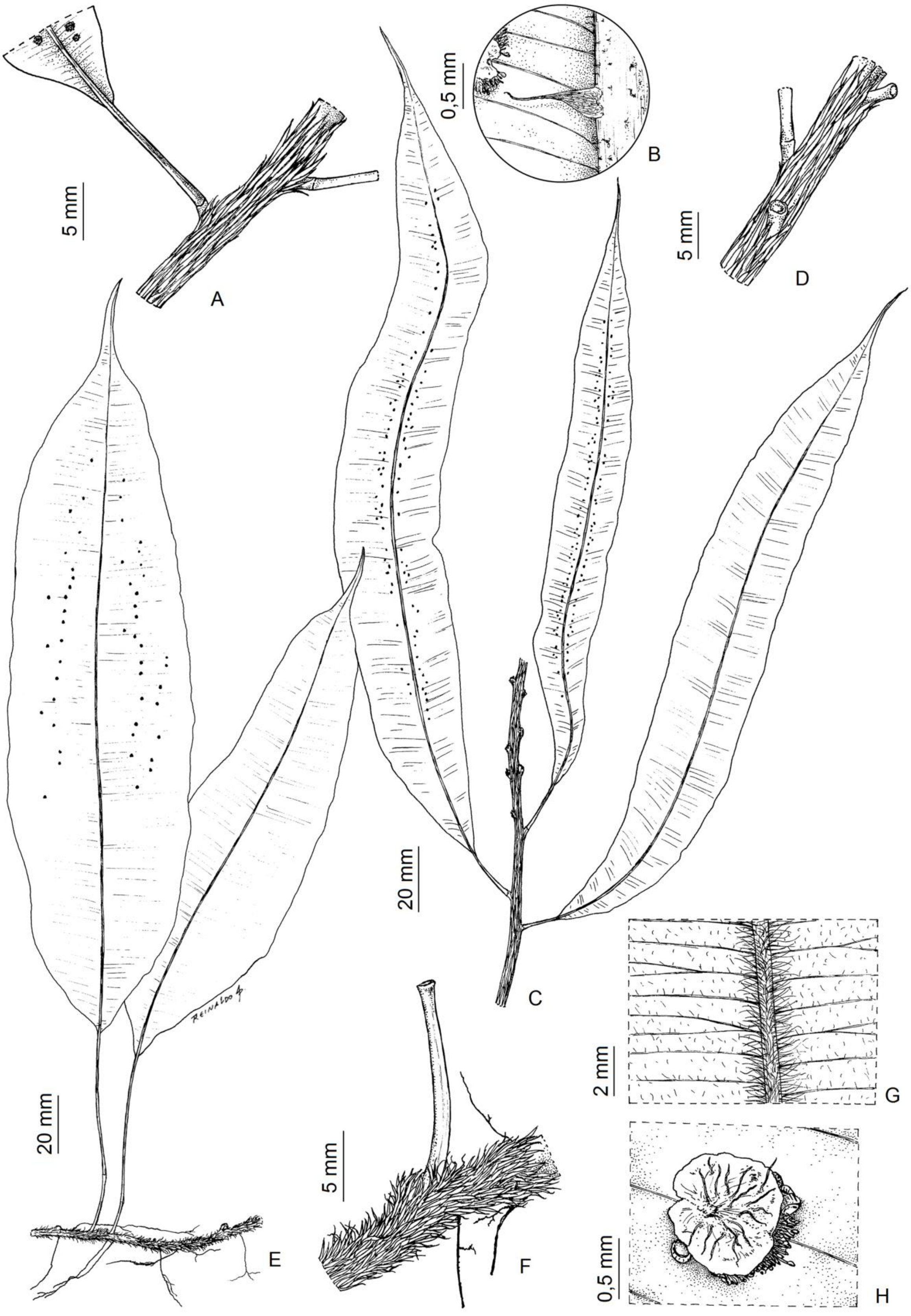

FIG. 10

Capítulo III. Miranda, C. V. & P. B. Schwartsburd. Uma filogenia preliminar de *Oleandra* (Oleandraceae, Polypodiopsida) – Periódico ainda a ser definido.

Uma filogenia preliminar de *Oleandra* (Oleandraceae, Polypodiopsida)*

(A preliminary phylogeny of *Oleandra* (Oleandraceae, Polypodiopsida)

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* Manuscrito a ser traduzido para o inglês e submetido à publicação em revista científica a ser definida

Resumo

Oleandra possui entre 35-40 espécies reconhecidas atualmente no mundo. Neste trabalho, realizou-se uma filogenia preliminar do gênero, abrangendo espécies neotropicais e paleotropicais. Foram utilizadas 25 sequências de *Oleandra* de 14 espécies diferentes (5 espécies asiáticas, 1 espécie africana e 8 espécies neotropicais). A árvore filogenética apresentada definiu dois clados geográficos muito bem sustentados (um clado neotropical + africano e um clado asiático), porém não apresentou uma boa resolução entre as espécies dentro de cada um dos clados. Das 8 espécies neotropicais apresentadas, sequências de 6 delas foram geradas neste trabalho. Os grupos morfológicos dentro do gênero propostos em trabalhos baseados apenas em morfologia não foram corroborados por esta filogenia, sendo considerados grupos artificais, apesar de serem muito utéis para o reconhecimento e diferenciação das espécies.

Abstract

Oleandra has between 35-40 species currently recognized in the world. In this work, a preliminary phylogeny of the genus was performed, covering Neotropical and Paleotropical species. 25 *Oleandra* sequences from 14 different species were used (5 Asian species, 1 African species and 8 Neotropical species). The phylogenetic tree presented defined two very well supported geographic clades (a Neotropical + African clade and an Asian clade), but it did not show a good resolution between the species within each of the clades. Of the 8 neotropical species presented, sequences of 6 of them were generated in this work. The morphological groups within the genus proposed in works based only on morphology were not corroborated by this phylogeny, being considered artificial groups, despite being very useful for the recognition and differentiation of species.

Introdução

Oleandra Cav. é um gênero de samambaias de distribuição pantropical, pertencente à família Oleandraceae. O gênero já variou muito em posição hierárquica taxonômica e já foi inserido em diferentes famílias (*i.e.*, Davalliaceae, Dennstaedtiaceae, Polypodiaceae), até que estudos moleculares demonstraram sua monofilia e posição em sua própria família monogenérica (Schuettpelz & Pryer, 2007; Kuo et al., 2011; Zhang & Zhang, 2015). Segundo o PPG I (2016), Oleandraceae é grupo-irmão de um clado formado por Polypodiaceae + Davalliaceae. O clado contendo estas três famílias é bem sustentado e tem principal apomorfia a formação de filopódios no caule. Atualmente são reconhecidas entre 35 e 40 espécies de *Oleandra* para o mundo, levando-se em conta os principais trabalhos taxonômicos para as diferentes regiões do globo (Hovenkamp & Ho, 2012; Roux, 2009; Miranda et al,. 2021; Miranda & Schwartsburd, *in prep.*). Para a região Neotropical, Miranda et al. 2021 reconheceram a presença de 19 espécies válidas, e Miranda & Schwartsburd (*in prep.*) estão ampliando este número para 23 spp.

Estudos moleculares com o gênero *Oleandra* propriamente dito ainda são escassos, onde apenas algumas poucas espécies (na grande maioria paleotropicais) foram incluídas em trabalhos mais abrangentes ou com enfoque em outras famílias (*i.e.,* como *outgroups*). Portanto, há uma grande lacuna nas relações infragenéricas do gênero. Os principais trabalhos que sequenciaram espécies de *Oleandra* foram os de (Tsutsumi & Kato, 2006; Schuettpelz & Pryer, 2007; Kuo et al., 2011; Ding et al., 2014; Moran et al., 2014; Nitta et al., 2020).

Desde o trabalho de Maxon (1914), existe uma tendência dos pesquisadores a se considerar grupos morfológicos dentro de *Oleandra*. Maxon (1914) propôs dois grupos morfológicos: 1) espécies com escamas do rizoma adpressas e filopódios similares a extensões do próprio caule (*stem-like*); e 2) espécies com escamas do rizoma patentes e filopódios similares a extensões do pecíolo (*stipe-like*).

Já Miranda et al. (2021) propuseram a divisão das espécies em três grupos morfológicos distintos, considerando um grupo morfológico intermediário entre os dois grupos de Maxon (1914). Nos grupos morfológicos de Miranda et. al. (2021) as espécies paleotropicais se enquadram principalmente no grupo 1 de Maxon (1914): espécies com escamas do rizoma adpressas e filopódios *stem-like*. já as espécies neotropicais se distribuem principalmente nos grupos 2 de Maxon (1914): espécies com escamas do rizoma patentes e filopódios *stipe*-like) e 3 (espécies com escamas do rizoma adpressas e filopódios *stipe*-like),com algumas poucas espécies no grupo 1.

Com o exposto acima, neste trabalho objetivou-se realizar uma filogenia molecular de *Oleandra* para testar os grupos morfológicos propostos por Maxon (1941) e Miranda et al. (2021), bem como observar como as características morfológicas evoluíram no gênero.

Material e métodos

Amostragem taxonômica, extração de DNA e amplificação das sequências

Foram utilizadas amostras de folhas preservadas em sílica-gel ou amostras retiradas de material de herbários (exsicatas). O DNA foi extraído seguindo o método de Roy et al. (1992), modificado. Foram realizadas 81 extrações no total, com a maioria dos materiais (57 amostras) retirados de exsicatas. As regiões de interesse foram amplificadas por meio de PCR (reação em cadeia de polimerase), utilizando-se primers específicos. Depois de extraídos, os fragmentos foram purificados e submetidos ao sequenciamento (automático, pelo método de Sanger) pela empresa ACTGene (Rio Grande do Sul, Brasil).

Foram amplificados dois marcardores cloroplastidiais: o gene *rbcL* e o espaçador intergênico *trnL-trnF*, regiões muito utilizadas e consideradas filogeneticamente informativas para as samambaias de um modo geral (e.g., Pryer et al. 2004, Korall et al. 2007, Schneider et al. 2004, Sundue et al. 2014, Moran & Labiak 2015, Assis et al. 2016, Cárdenas et al. 2019). Foram também utilizadas sequências disponíveis no GenBank, referentes a estes marcadores (disponível em: https://www.ncbi.nlm.nih.gov/genbank/). Como grupo externo, foram selecionaadas espécies dos grupos-irmãos Polypodiaceae [*Campyloneurum brevifolium* (Lodd. ex Link) Link e *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm.] e Davalliaceae [*Davallia mariesii* H. J. Veitch e *Davallia fejeensis* Hook.], além de *Pteridium esculentum* subsp. *campestre* (Dennstaedtiaceae) como grupo externo mais distante.

Alinhamento e Análises Filogenéticas

Todas as sequências foram alinhadas, concatenadas e editadas utilizando o software Geneious Prime 2021.0.3 (Biomatters Ltda., San Francisco, CA). A partir dos alinhamentos concatenados foram produzidas árvores filogenéticas pelo método da Máxima Verossimilhança (ferramenta RaxML-HPC2 on XSEDE), via Portal Cipres (disponível em: https://www.phylo.org/portal2/login!input.action). O FigTree versão 1.3.1 (Rambaut, 2010) foi utilizado para visualização e edição das árvores geradas. Para o filograma principal foram utilizadas sequências de cinco espécimes de grupo externo e 25 de *Oleandra.* Destas 25, 6 foram geradas neste trabalho e 19 foram utilizadas do GenBank.

Evolução de caracteres

Para os filogramas de evolução de caractéres, foram utilizadas matrizes menores contendo apenas um espécime por espécie. Nestes filogramas há avaliação de 14 espécies de *Oleandra* (além das cinco de grupo externo).

Os dados morfológicos foram obtidos através do estudo de exsicatas e através de dados disponíveis na literatura (Maxon 1914, Nayar et al. 1968, Liew 1977, Tryon 1997, Miranda et al. 2021). Os caractéres selecionados foram: hábito, caule, escamas do caule, filopódios, indumento da costa (pêlos e escamas), organização dos soros, indúsio, distribuição geográfica, formato da lâmina, e divisão da lâmina. Após as árvores filogenéticas estarem prontas, foram plotados os caracteres morfológicos e avaliados no software Mesquite (Maddison & Maddison, 2011), através do método de Parsimônia. As árvores obtidas foram analisadas e editadas no FigTree versão 1.3.1 (Rambaut, 2010) e a consistência das árvores foi avaliada pelo programa Tracer (Rambaut et al., 2013).

Resultados

Não houve sucesso na extração de DNA a partir de amostras de exsicatas; todas as sequências geradas com sucesso neste trabalho foram a partir de materiais frescos que foram secos e armazenados em sílica-gel.

O filograma principal gerado é o maior já produzido para *Oleandra;* ele contém 25 espécimes, que correspondem a 14 espécies de *Oleandra* (além de cinco espécies de grupo externo) – Fig. 1. O gênero *Oleandra* foi construído de modo monofilético com 100% de *boostrap*. Dentro do gênero houve a formação de dois clados geográficos principais: um asiático (99% de *bootstrap*) e outro neotropical + africano (98% de *bootstrap*). Dentro do clado asiático não houveram resoluções cosideráveis para se analisar a formação de sub-clados consistentes.

Já no no clado neotropical + africano houve a formação de dois sub-clados consitentes: um contendo *Oleandra baetae* (do Brasil) e *O. distenta* (da África), com 100% de *bootstrap;* e outro contendo espécies neotropicais, também com 100% de *bootstrap*. Dentro deste sub-clado não houve resolução considerável para o agrupamento das espécies, ficando elas praticamente numa grande politomia.

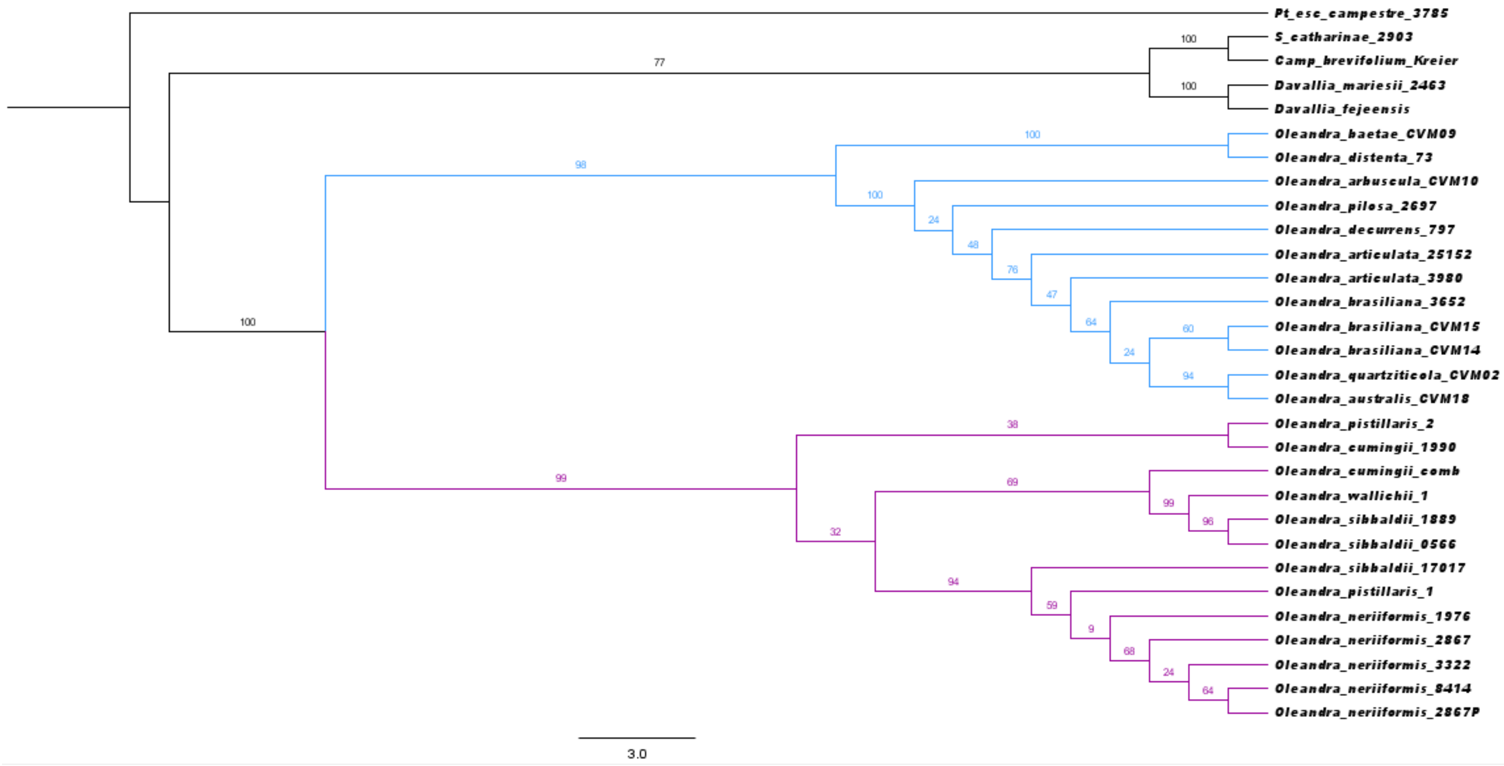

Fig.1. Árvore filogenética de consenso pelo método da Máxima Verossimilhança, resultante de dados do gene plastidial *rbcL* e do espaçador intergênico plastidial *trnL-trnF*. Os números são valores de *bootstrap.*

Discussão

Resolução das árvores e grupos morfológicos

Com os valores de *bootstrap* apresentados no filograma da Figura 1, conclui-se que os marcadores *rbcL* e *trnL-trnF* analisados em sintonia foram funcionais para o *backbone* da filogenia de *Oleandra*, demonstrando a filogenia do gênero, a divisão em dois clados geográficos (asiático *vs.* neotropical + africano), e a divisão do clado neotropical + africano em dois sub-clados surpreendentes (um contendo uma sp. brasileira e uma africana e outro neotropical). Já para as relações entre as espécies, principalmente do clado asiático e do sub-clado neotropical, as resoluções destes marcadores não foram suficientes para análises mais refinadas, apresentando politomias e até "espécies parafiléticas", como *O. articulata, O. cumingii, O. pistilaris* e *O. sibbaldii.* Sugere-se a adição de mais marcadores de evolução rápida para se atingir melhores resoluções entre as espécies.

Por exemplo, Schwartsburd et al. (2016) desmembraram o complexo *Oleandra articulata* em seu trabalho em cinco espécies e um provável híbrido, ocorrentes na Foresta Atlântica brasileira. Na Revisão Taxonômica das espécies neotropicais, realizada por Miranda & Schwartsburd (*in prep.*), os autores consideraram as cinco espécies propostas, além de *O. articulata s. str.* . No presente trabalho não se conseguiu obter um respaldo molecular para a diferenciação das supostas espécies deste complexo. Talvez, isto possa ser futuramente resolvido com a adição de mais marcadores à análise. Por outro lado, por serem "espécies" morfologicamente muito semelhantes, pode ser que tenha ocorrido uma extrapolação do conceito de espécie pelos autores que as desmembraram. Dentre as espécies brasileiras, *O. baetae* apresentou um resultado interessante em todas as árvores geradas. Tryon (1997) sinonimizou esta espécie sob *O. articulata s.l.* Morfologicamente, Schwartsburd et al. (2016) consideraram duas espécies muito distintas, devido à diferenças na pilosidade, escamas do rizoma, entre outras características. Nas árvores geradas, *O. baetae* forma um clado, com 100% de *bootstrap*, com a espécie africana *O. distenta*, não se agrupando com as espécies do complexo *O. articulata*.

Os filogramas gerados não corroboraram, também, os grupos morfológicos propostos por Maxon (1914), e nem por por Miranda et al. (2021), com a maioria dos caracteres que se acreditava separar estes grupos se mostrando caracteres homoplásicos. Tal separação em grupos morfológicos, apesar de ser funcional para a identificação taxonômica das espécies, é artificial e não deve ser usada para uma classificação formal de subgênero ou seção.

Evolução de Caracteres

Oleandra é um grupo de evolução aparentemente muito recente, portanto, quase todos os caracteres avaliados se apresentaram homoplásicos, sem a presença de apomorfias separando claramente os clados. No entanto, a evolução de caracteres mostrou resultados interessantes, principalmente nas relações evolutivas entre as espécies do neotrópico e África e espécies asiáticas, derrubando a crença de grupos morfológicos bem delimitados de acordo com a localização geográfica.

Hábito

No hábito, nota-se que o ancestral comum do gênero *Oleandra* possuía hábito epífito, que é o hábito que continua a predominar na maior parte das espécies ao longo da evolução do grupo (Fig. 2). O surgimento do hábito rupestre surge independentemente nos dois clados geográficos (neotropical + africano e asiático), constituindo, portanto, uma caracter homoplásico. Já o hábito terrestre, hábito do grupo externo mais distante (*Pteridium esculentum* subsp. *campestre*), surge uma única vez no clado das espécies asiáticas (Fig. 2).

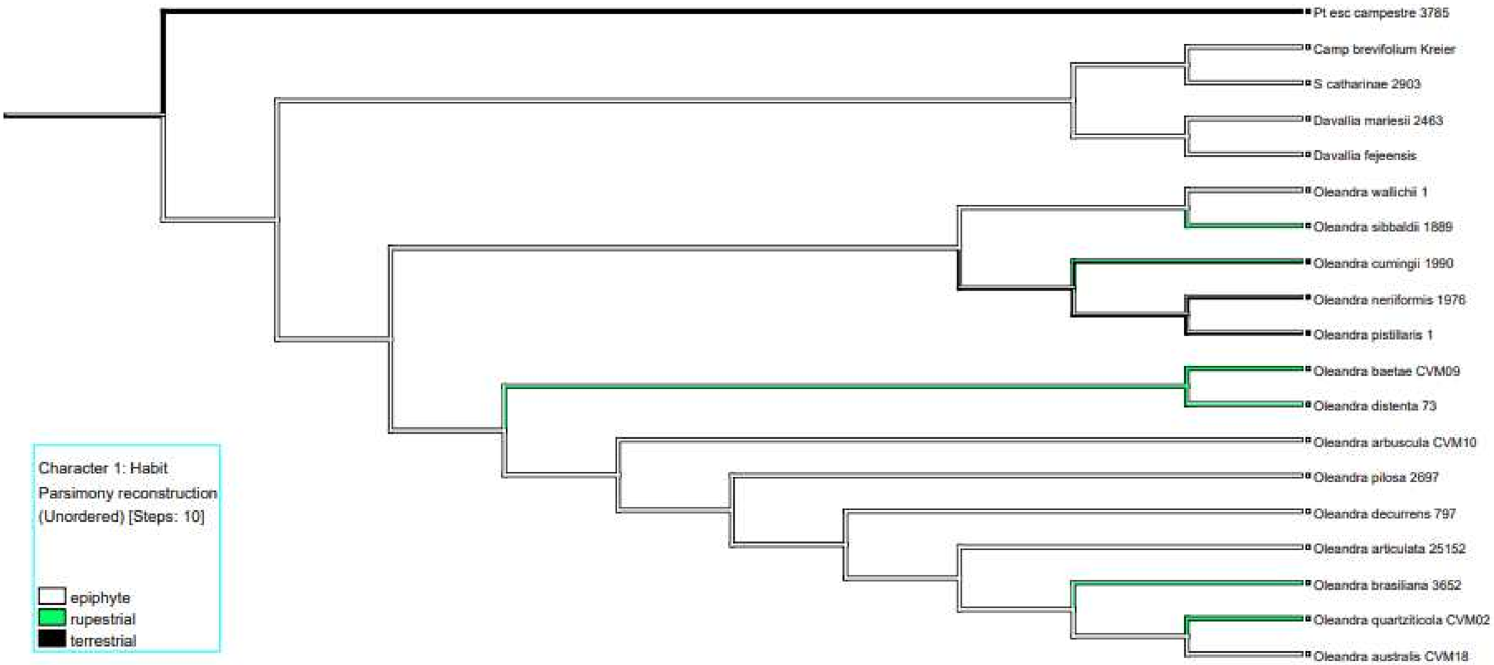

Fig.2. Evolução do hábito no gênero *Oleandra* e grupos externos.

Rizoma

O ancestral comum de toda a árvore e também o ancestral comum do gênero *Oleandra* apresentava rizoma do tipo reptante (curto ou longo), com o rizoma ereto ou ascendente surgindo independente em espécies dos dois clados geográficos (neotropical + africano e asiático), e com uma reversão no clado neotropical + africano (Fig. 3).

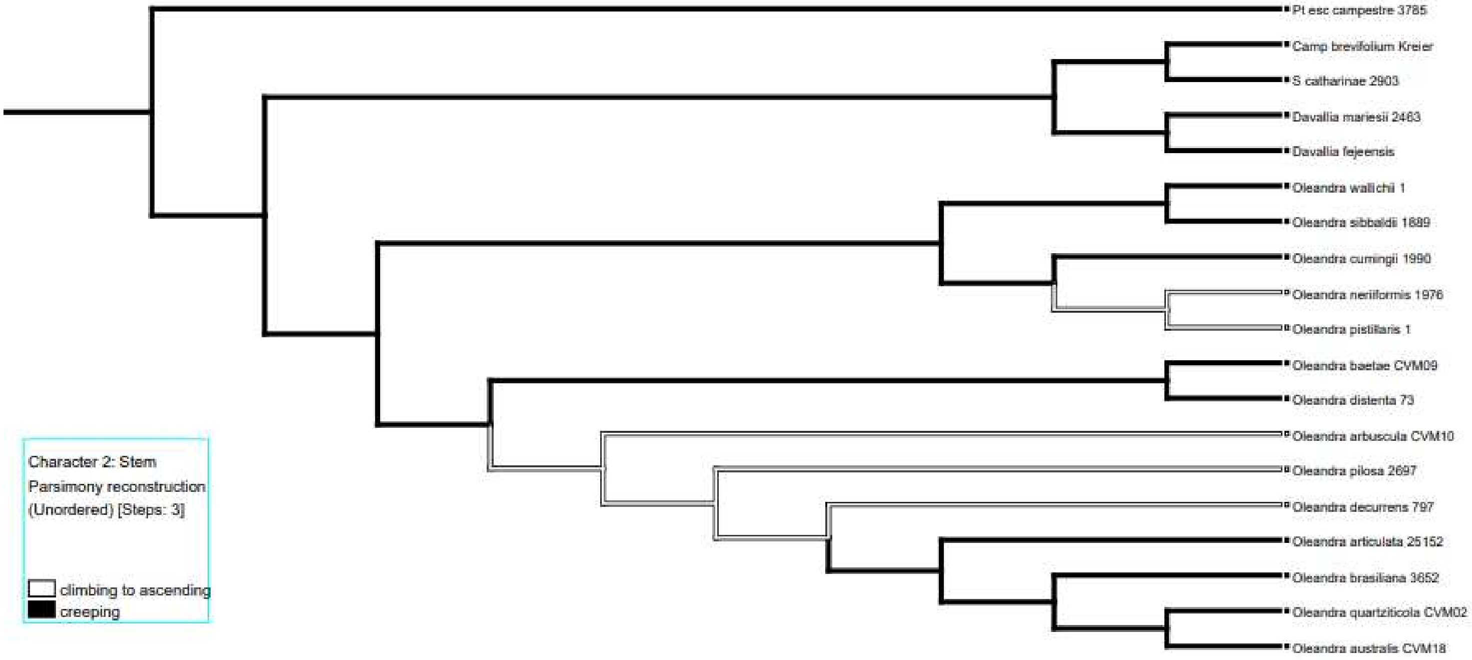

Fig.3. Evolução do rizoma no gênero *Oleandra* e grupos externos.

Escamas do rizoma

As escamas do rizoma, que podem ser patentes, adpressas ou esparsas e caducas, são muito variáveis entre patentes e adpressas nas espécies neotropicais de *Oleandra*, com predominância de escamas patentes nas espécies da Floresta Atlântica. Já as espécies asiáticas de *Oleandra* possuem predominância de escamas adpressas, com a exceção de *Oleandra sibbaldii* Grev., que possui escamas bem esparsas, que se desprendem com o tempo. Contudo, as escamas do rizoma constituem mais uma homoplasia dentro do gênero. A condição do ancestral do gênero é incerta (Fig. 4). Na reconstrução da história deste caracter, o ancestral do clado asiático provavelmente possuía escamas adpresas; ja no clado neotropical + africano, aparentemente há dois surgimentos de escamas patentes, ou então algumas sequências de reversões de caractéres (Fig. 4).

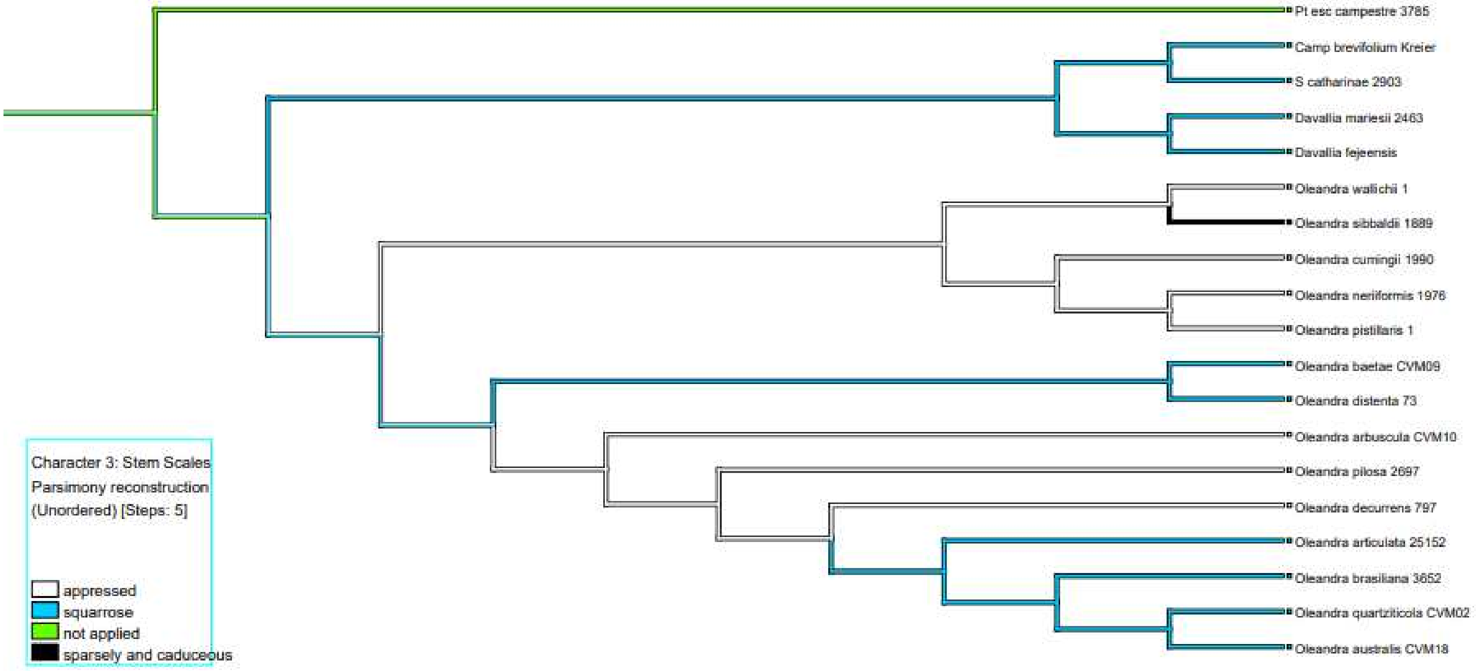

Fig.4. Evolução das escamas do rizoma no gênero *Oleandra* e grupos externos.

Filopódios

Os filopódios surgem como *stem-like* na base do ancestral do mega-clado Polypodiaceae, Davalliaceae + Oleandraceae) (Fig. 5). Em *Oleandraceae* o surgimento do filopódio *stipe-like* , mais alongado e similar a pecíolos, se deu várias vezes ao longo da evolução (Fig. 5), se mostrando tipicamente como uma característica homoplásica.

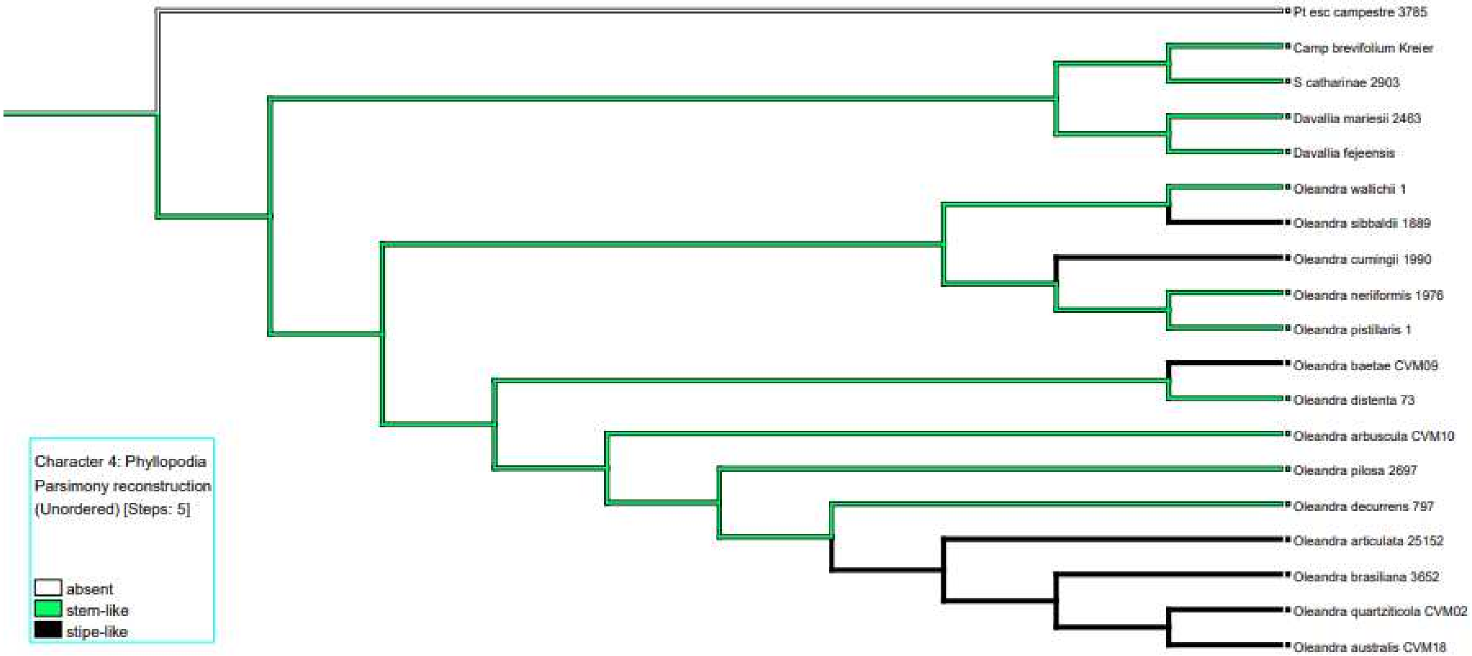

Fig.5. Evolução do filopódio no gênero *Oleandra* e grupos externos.

Formato da lâmina

Em *Oleandra* todas as espécies apresentam folhas simples, sem exceção. Dentro do gênero, as lâminas variamno formato, de linear-lanceoladas a elípticas. Pensáva-se, inicialmente, existir uma divisão morfológica clara entre as espécies paleotropicais e neotropicais em relação a esta característica. Espécies paleotropicais possuem lâminas geralmente lineares, enquanto as espécies neotropicais possuem lâminas geralmente elípticas. Porém, na reconstrução evolutiva deste caractere, percebe-se que se trata, mais uma vez, de um caracter homoplásico dentro do gênero, com o ancestral comum do gênero apresentando lâminas linear-lanceoladas, e as lâminas elípticas surgindo algumas vezes, independentemente, dentro do gênero, inclusive no clado das espécies paleotropicais (Fig. 6).

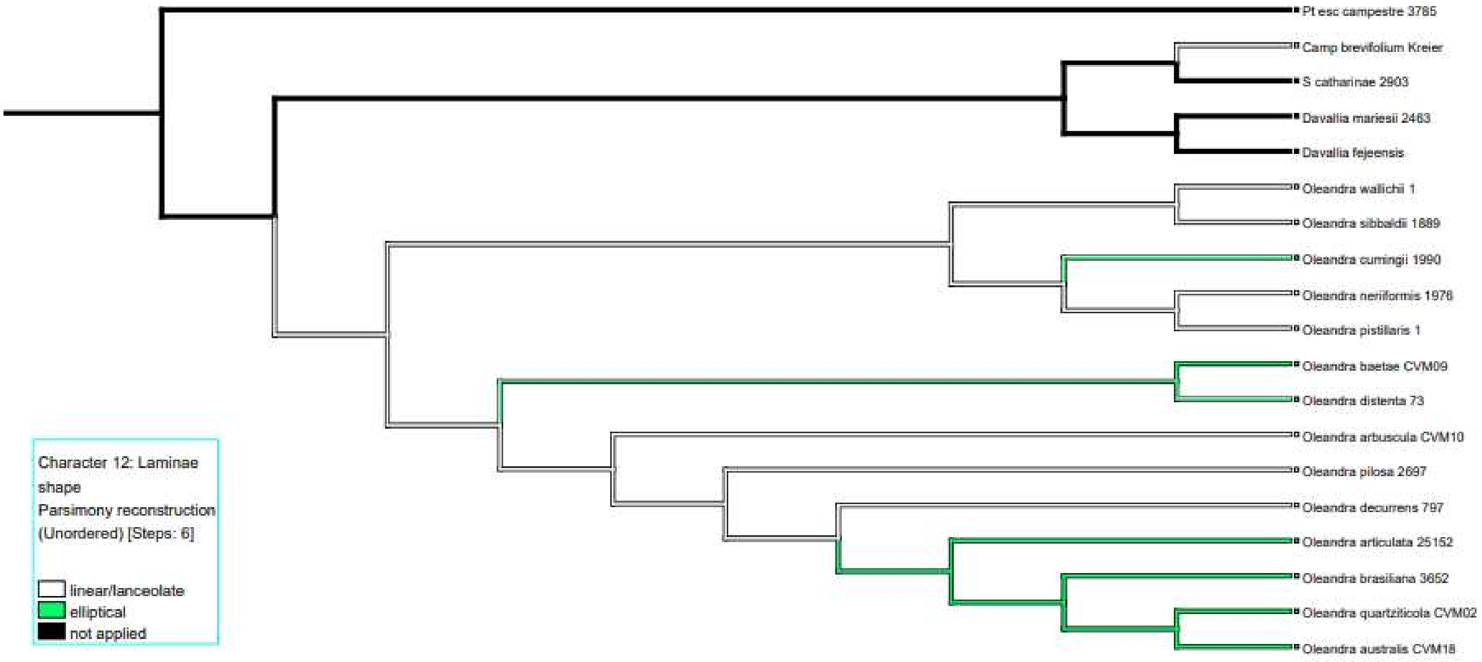

Fig.6. Evolução do formato da lâmina no gênero *Oleandra* e grupos externos.

Divisão da lâmina

Todas as espécies de *Oleandra*, sem exceção, possuem lâmina inteira. Notamos que o ancestral comum de Oleandraceae, Polypodiaceae e Davalliaceae possuía lâmina inteira ou dividida (reconstrução incerta) (Fig. 7). Dentro do clado formado por Polypodiaceae e Davalliaceae a divisão da lâmina é variável, com espécies de lâmina inteira, como *Campyloneurum brevifolium*, lâmina 1-pinada, como *Serpocaulon catharinae*, e lâmina 2-pinada ou mais dividida, como as espécies de *Davallia*. A lâmina consiste numa apomorfia de todo gênero *Oleandra,* e toda a família Oleandraceae, por consequência (Fig. 7).

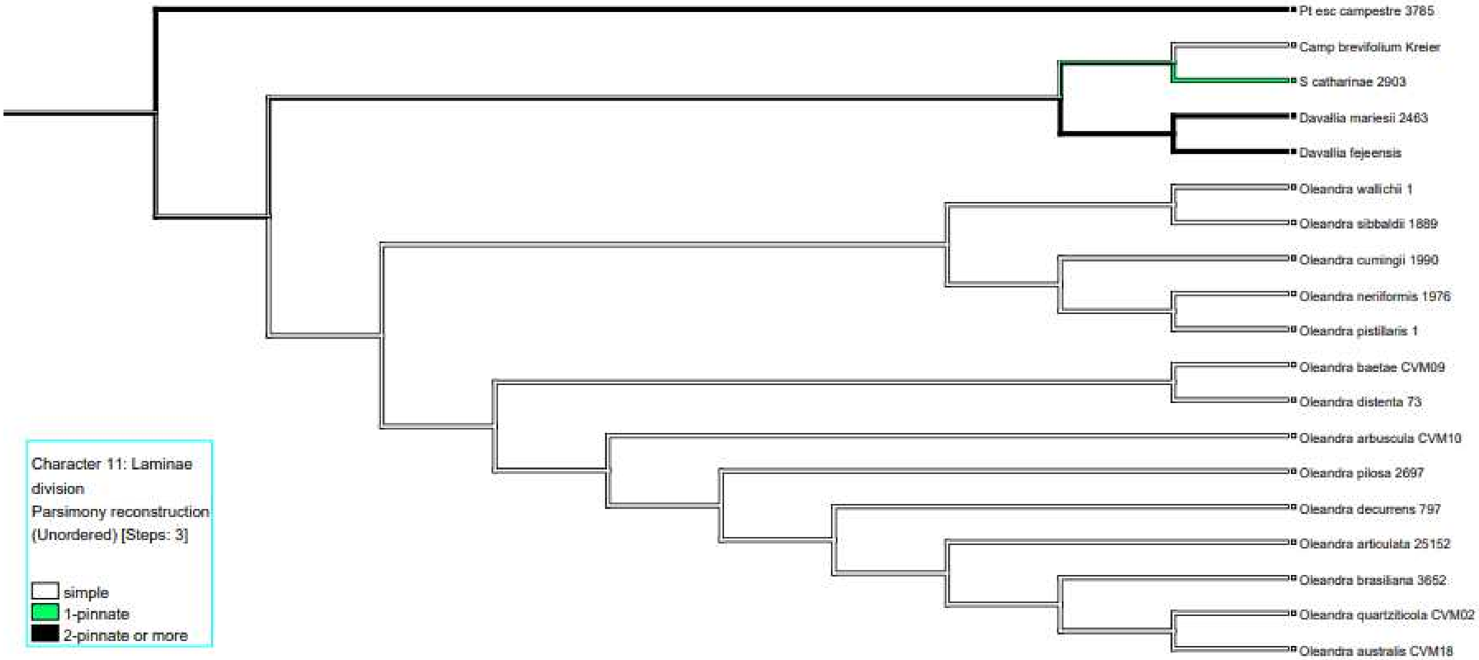

Fig.7. Evolução da divisão da lâmina no gênero *Oleandra* e grupos externos.

Aspecto geral da lâmina

A pilosidade da lâmina, ou sua ausência, é um fator que já gerou muitos debates dentro do gênero *Oleandra.* Tryon (1997), por exemplo, não considerou a pilosidade uma característica relevante como diagnóstica de espécies, sendo apenas uma característica variável influenciada pelo ambiente. Porém, nos últimos trabalhos publicados para o gênero, a característica se consolidou muito como diagnóstica das espécies, inclusive sendo determinantes na descrição de novas espécies (e.g., Schwartsburd et al., 2016; Miranda et al, 2021). Apesar de segregar de forma eficiente as espécies dentro do gênero, a pilosidade não distingue clados filogenéticos dentro do gênero, sendo mais um caractere homoplásico observado e não importante do ponto de vista de uma análise evolutiva (Fig. 8).

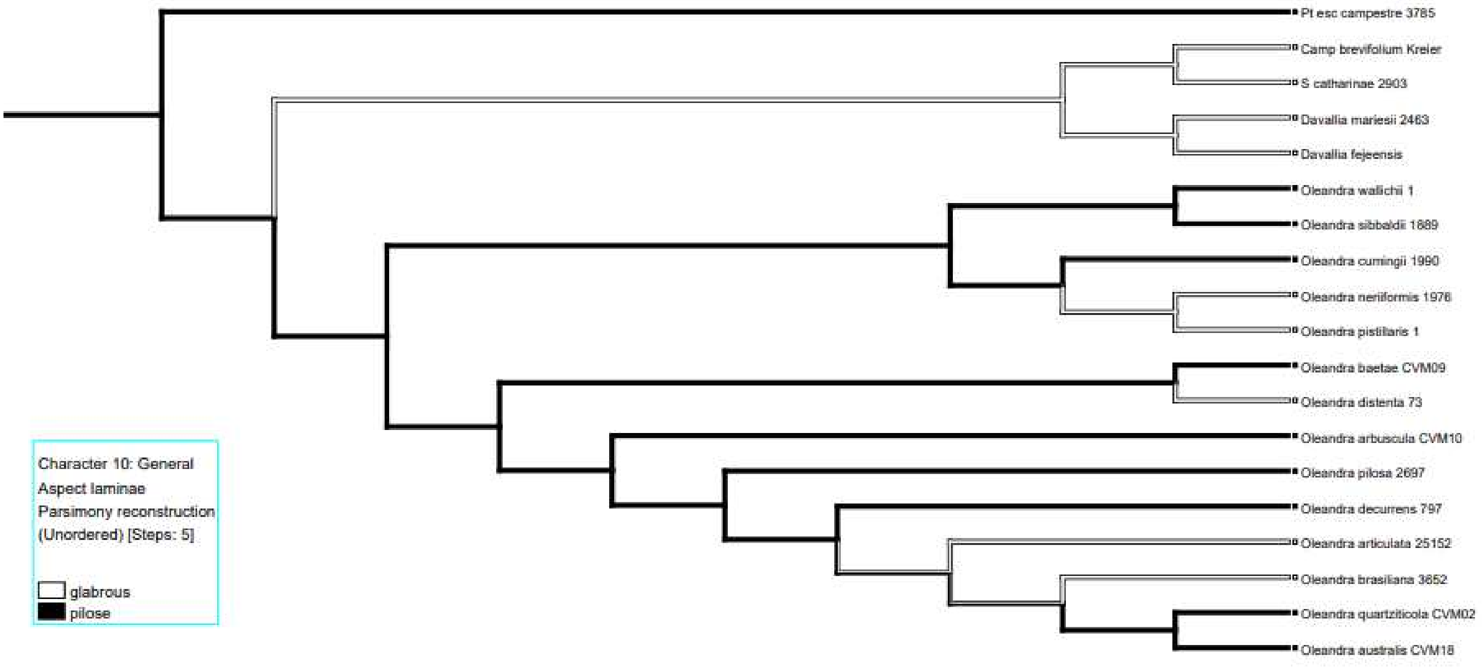

Fig.8. Evolução do aspecto geral da lâmina no gênero *Oleandra* e grupos externos.

Indumento da costa – pelos

A pilosidade na costa é um fator muito variável dentro do gênero *Oleandra* como um todo, seja em espécies paleotropicais quanto em espécies neotropicais. O ancestral comum das espécies do gênero aparece como piloso ou não piloso na árvore (incerto), e assim, na evolução, algumas espécies apresentam a pilosidade e outras não apresentam (Fig. 9). A característica, portanto, não gera clados.

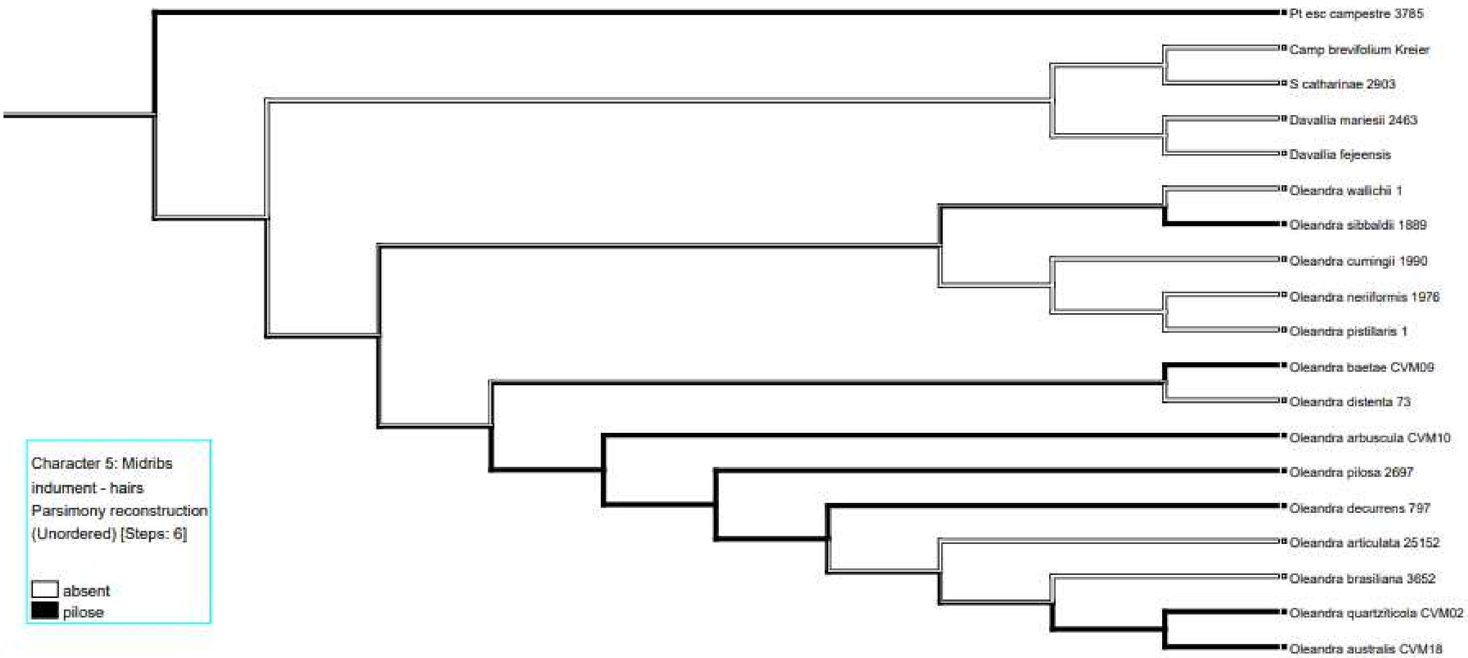

Fig.9. Evolução do indumento da costa (pelos) no gênero *Oleandra* e grupos externos.

Indumento da costa – escamas

A presença de escamas na costa das espécies de *Oleandra* sempre se configurou como uma caracter diagnóstico muito importante na diferenciação das espécies dentro do gênero. Todas as espécies analisadas, com exceção de *Oleandra australis* (que não apresenta nenhum tipo de escama na costa), apresenta algum tipo de escama na costa, sejam essas escamas numerosas e persistentes ou poucas e caducas. Porém, esta característica não diferencia clados dentro do gênero, apenas diferencia espécies. As escamas persistentes predominam tanto nas espécies paleotropicais quanto nas espécies neotropicais, e espécies com escamas caducas aparecem independentemente durante a evolução do gênero (Fig. 10).

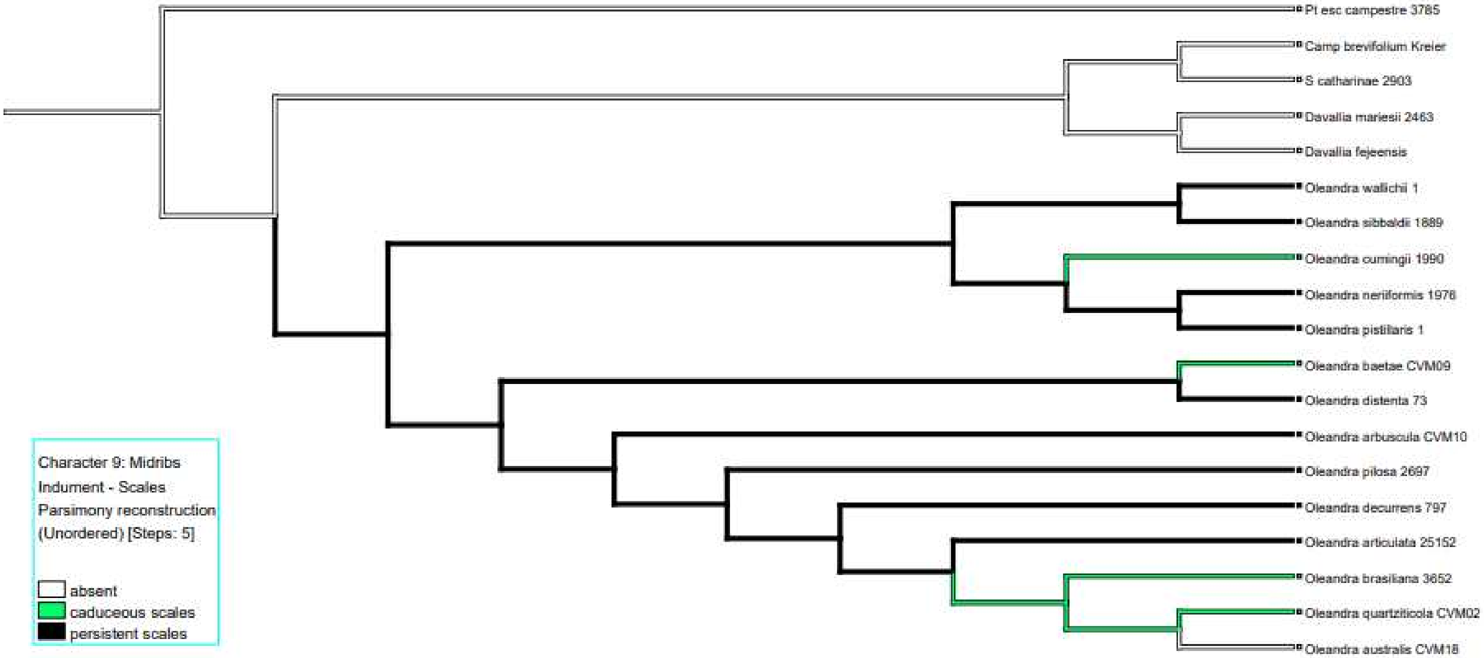

Fig. 10.Evolução do indumento da costa (escamas) no gênero *Oleandra* e grupos externos.

Organização dos soros

A organização dos soros era outra característica que acreditava-se distinguir as espécies paleotropicais das espécies neotropicais. As espécies paleotropicais teriam uma tendência aos soros mais organizados, ou como aqui chamamos, homogêneos, por apresentar apenas uma fileira única de soros mais próximos e paralelos à costa. Portanto, apenas duas espécies em todo este estudo apresentam este tipo de organização: *Oleandra neriiformis, O. pistillaris* e *Oleandra wallichii*. Ambas são espécies paleotropicais, porém as demais apresentam soros heterogêneos, como é predominante em todo o gênero no geral, assim como no ancestral comum. Os soros homogêneos surgiram, portanto, de forma independente em duas linhagens diferentes, se apresentando, então, como caractere homoplásico (Fig. 11).

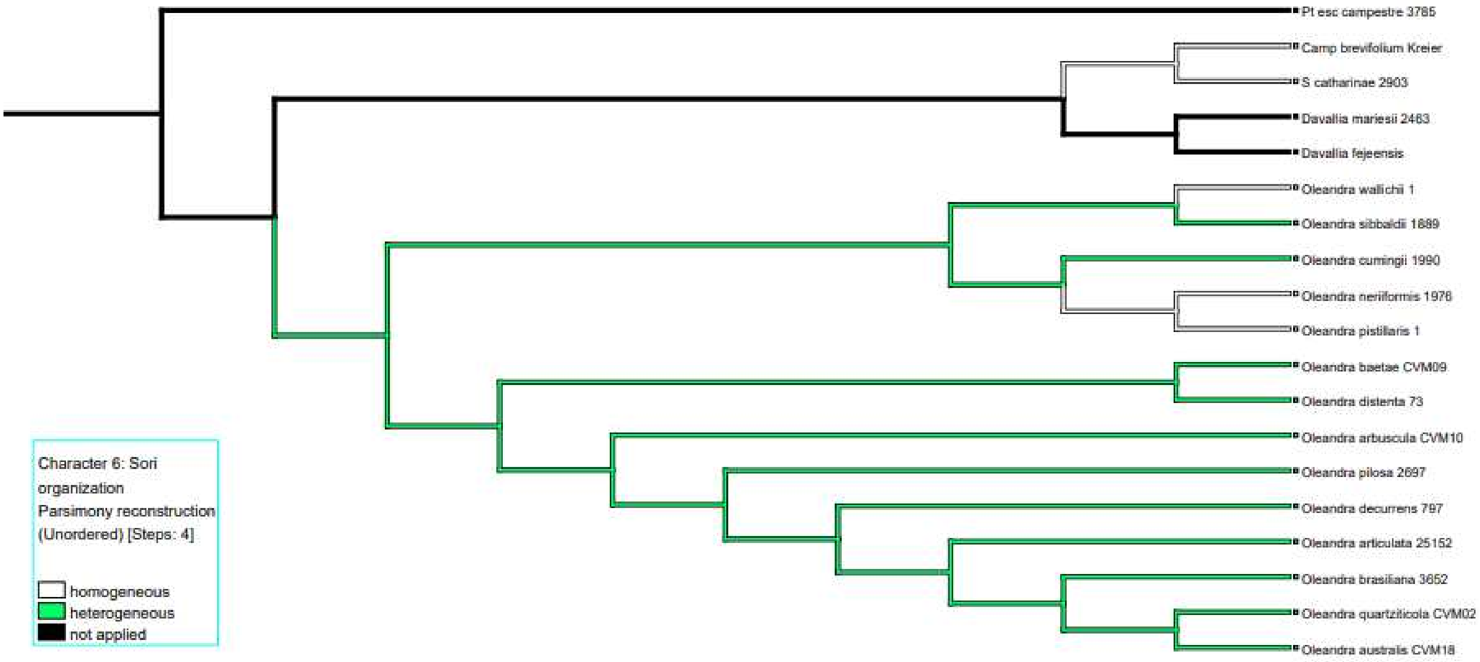

Fig.11.Evolução da organização dos soros no gênero *Oleandra* e grupos externos.

Indúsio

O indúsio reniforme se mostrou uma apomorfia das espécies *Oleandra neriiformis* e *O. pistillaris* (Fig. 12). Sendo a condição ancestral do gênero e a plesiomorfia da maior parte dele o indúsio orbicular-reniforme (Fig. 12).

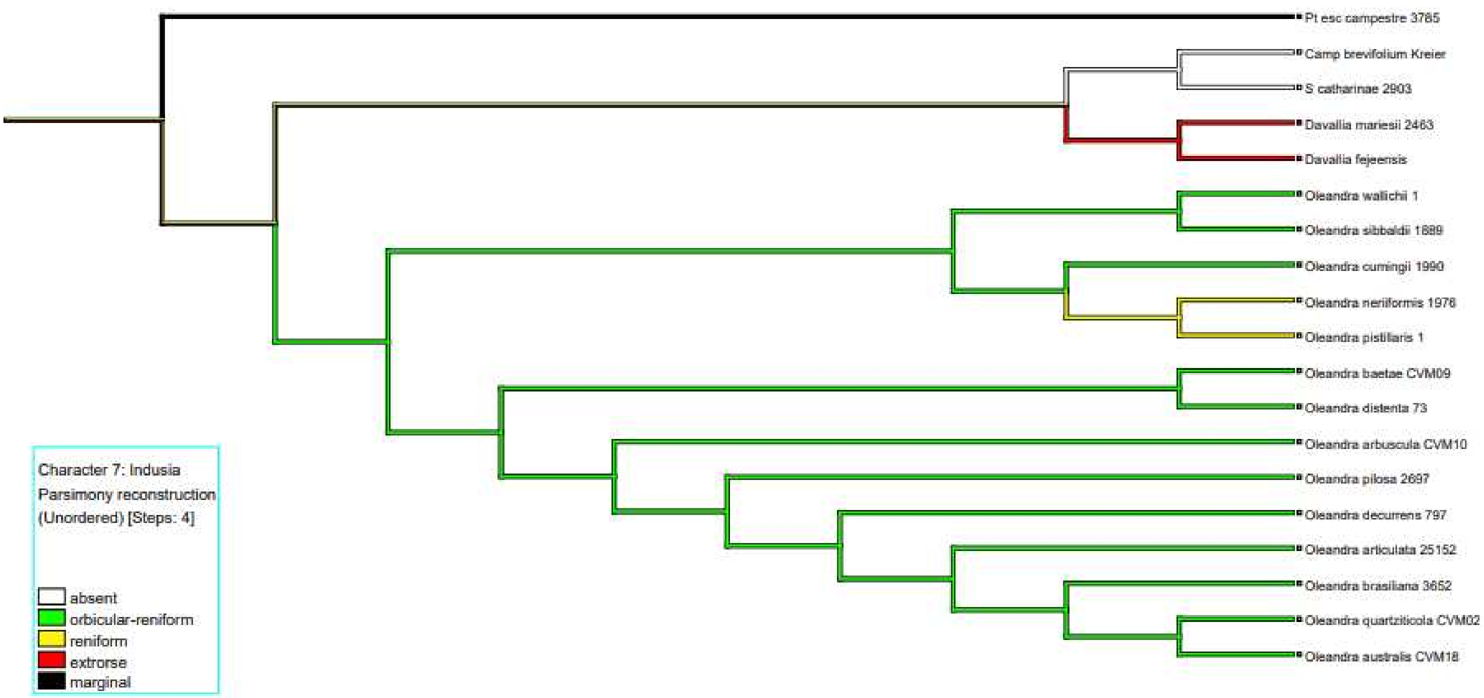

Fig.12.Evolução do indúsio no gênero *Oleandra* e grupos externos.

Distribuição geográfica

Como este trabalho se trata de um estudo molecular preliminar, com poucas espécies para uma análise mais complexa, não foi possível fazer inferências robustas sobre a biogeografia de *Oleandra*. Porém é possível fazer algumas considerações preliminares. A presença de um clado totalmente asiático e um clado neotropical contendo uma espécie africana (*O. distenta*), foi um dos principais resultados desta filogenia (Fig. 13). O resultado não possibilita inferir sobre a origem do gênero, se asiática ou neotropical – na árvore abaixo a condição neotropical prevalece, porém sabe-se que isto é um artefato devido aos grupos externos escolhidos e ao maior número de espécies neotropicais analisadas na árvore. Porém, pode-se afirmar que cedo na evolução do grupo houve a divisão entre estes dois caldos principais: asiático e neotropical + africano. Apenas uma espécies africana foi incluídas nas análises, porém, nota-se que ela surge no dentro de espécies neotropicas. Aparentente o ancestral deste clado era neotropical, e do neotrópico o gênero migrou para a África (Fig. 13). Estudos incluindo mais espécies africanas são necessários para se corroborar esta hipótese.

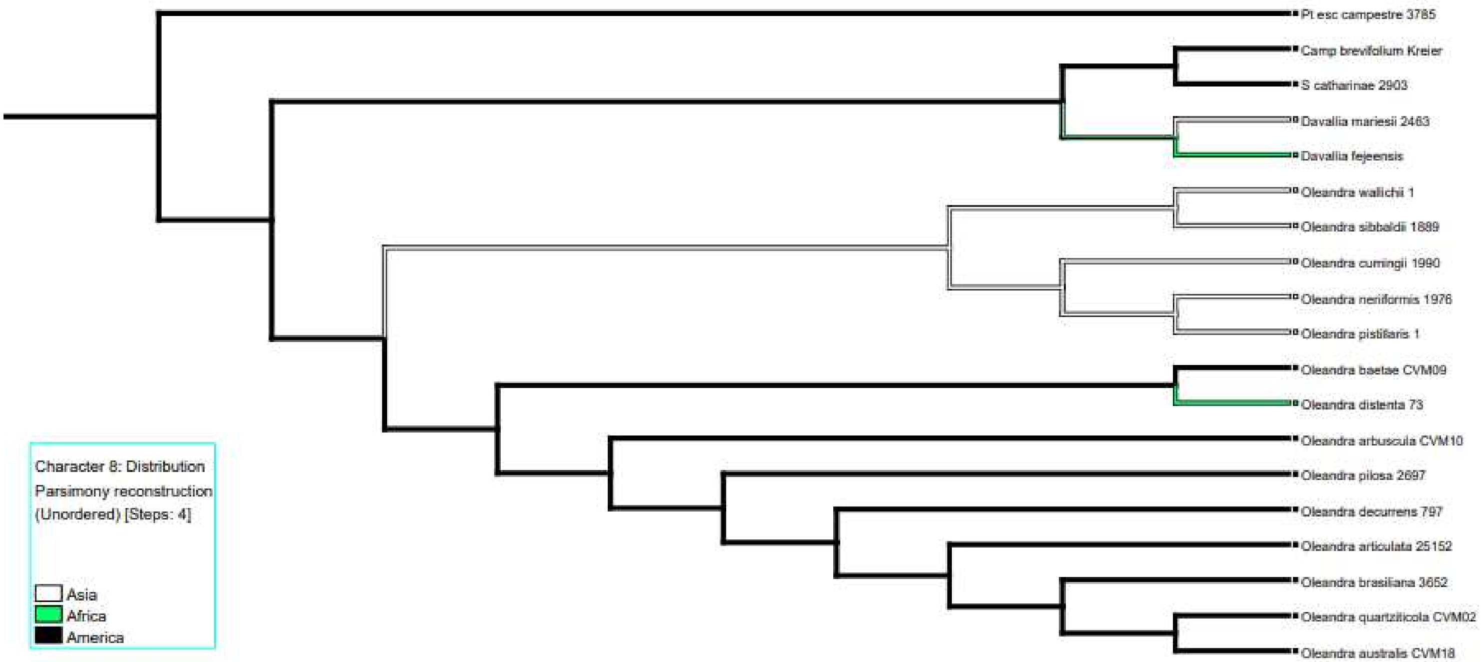

Fig.13. Distribuição geográfica do gênero *Oleandra* e grupos externos.

Conclusão e perspectivas

Oleandra é um gênero de evolução aparentemente ainda muito recente, portanto não apresentando grandes apomorfias entre os clados, com grande presença de homoplasias. Porém, o trabalho foi interessante para observar os clados geográficos. Um clado asiático muito bem sustentado, e outro neotropical + africano. Neste clado, ainda, dois sub-clados foram fortemente sustentados: um estritamente neotropical e outro contendo uma espécies brasileira (endêmica do estado de Minas Gerais) e uma espécie africana, mostrando que houve uma migração entre estas duas regiões – a princípio do neotrópico para a África.

Dentro dos clados, a relação entre as espécies (tanto asiáticas quanto neotropicais) ficou mal resolvida com a utilização de apenas os marcadores *rbcL* e *trnL-trnF,* necessitando mais marcadores para se chegar a melhores resoluções.

Como estudo molecular preliminar do gênero, este estudo ainda necessita de muito mais robustez, seja com a inclusão de mais marcadores na análise, bem como mais materiais coletados e frescos para gerar mais sequências. Com os interessantes resultados na união entre *Oleandra* *baetae* e *O. distenta*, as perspectivas de futuros estudos biogeográficos se tornaram ainda maiores pelos autores deste trabalho, além de deixar este filogenia molecular mais completa, robusta e responsiva.

Referências Bibliográficas

Assis FC, Almeida TE, Russell SJ, Schneider H, Salino A (2016) Molecular phylogeny and recircumscription of the fern genus *Pecluma* (Polypodiaceae – Polypodiopsida). Phytotaxa 247: 235.

Cárdenas GG, Lehtonen S, Tuomisto H (2019) Taxonomy and evolutionary history of the neotropical fern genus *Salpichlaena* (Blechnaceae). Blumea 64: 1–22.

Ding H-H, Chao Y-S, Callado JR, Dong S-Y (2014) Phylogeny and character evolution of the fern genus *Tectaria* (Tectariaceae) in the Old World inferred from chloroplast DNA sequences. Molecular Phylogenetics and Evolution 80: 66–78.

Hovenkamp P, Ho B-C (2012) A revision of the fern genus *Oleandra* (Oleandraceae) in Asia. Phytokeys 11:1–37.

Korall P, Conant DS, Metzgar JS, Schneider H, Pryer KM (2007) A molecular phylogeny of scaly tree ferns (Cyatheaceae). American Journal of Botany 94: 873–886.

Kuo L-Y, Li F-W, Chiou W-L, Wang C-N (2011) First insights into fern matK phylogeny. Molecular Phylogenetics and Evolution 59: 556–566.

Liew FS (1977) Scanning electron microscopical studies of the spores of Pteridophytes. The family Oleandreaceae. - Gard. Bull. Singapore 30: 101–110.

Maddison WP, Maddison DR (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75. Disponível em: http://mesquiteproject.org

Maxon WR (1914) The American species of *Oleandra*. Contributions from the United States National Herbarium 17:392–398.

Miranda CV, Schwartsburd PB, Labiak PH, Prado J (2021) Three new species of *Oleandra* (Oleandraceae, Polypodiopsida) from the Neotropics, and notes on the morphological groups among the Neotropical species. Brittonia 73(2): 1–9.

Miranda CV & Schwartsburd PB (*in prep*) A Taxonomic revision of the Neotropical species of *Oleandra* (Oleandraceae, Polypodiopsida). American Fern Journal: *artigo submetido*.

Moran RC, Labiak PH, Hanks JG, Prado J (2014) The Phylogenetic Relationship of *Tectaria brauniana* and *Tectaria nicotianifolia*, and the Recognition of Hypoderris (Tectariaceae). Systematic Botany 39(2): 384–395.

Moran RC, Labiak PH (2015) Phylogeny of the polybotryoid fern clade (Dryopteridaceae). International Journal of Plant Sciences 176: 880–891.

Nayar BK (1968) Contributions to the morphology of the fern genus *Oleandra*. Journal of the Linnean Society of London 60: 265–282.

Nitta JH, Ebihara A, Smith AR (2020) A taxonomic and molecular survey of the pteridophytes of the Nectandra Cloud Forest Reserve, Costa Rica. PLoS One 15(11): 1–14.

PPG I (2016) A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 54: 563–603.

Pryer KM, Schuettpelz E, Wolf PG, Schneider H, Smith AR, Cranfill RB (2004) Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. American Journal of Botany 91(10): 1582–1598.

Rambaut A (2010) FigTree v 1.3.1, A Graphical Viewer of Phylogenetic Trees. Disponível em: http://tree.bio.ed.ac.uk/software/figtree/

Rambaut A, Suchard MA, Xie D, Drummond AJ (2013) Tracer v 1.5. Disponível em: http://beast.bio.ed.ac.uk/Tracer

Roux JP (2009) Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar, and neighbouring islands. Strelitzia 23:1–296.

Roy A, Frascaria N, Mackay J, Bousquet J (1992) Segregating random amplified polymorphic DNAs (RAPDs) in *Betula alleghaniensis*. Theoretical and Applied Genetics 85: 173–180.

Schneider H, Russell SJ, Cox CJ, Bakker F, Henderson S, Rumsey F, Barrett J, Gibby M, Vogel JC (2004) Chloroplast phylogeny of Asplenioid Ferns based on *rbcL* and *trnL-F* spacer sequences (Polypodiidae, Aspleniaceae) and its implications for Biogeography. Systematic Botany 29: 260–274.

Schuettpelz E, Pryer KM (2007) Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon; Official News Bulletin of the International Society for Plant Taxonomy Utrecht 56: 1037–1050.

Sundue MA, Parris BS, Ranker TA, Smith AR, Fujimoto EL, Zamora-Crosby D, Morden CW, Chiou W-L, Chen C-W, Rouhan G, Hirai RY, Prado J (2014) Global phylogeny and biogeography of grammitid ferns (Polypodiaceae). Molecular Phylogenetics and Evolution 81: 195–206.

Tryon RM (1997) Systematic notes on *Oleandra*. Rhodora 99 (900): 335–343.
Zhang L-B, Zhang L (2015) Didymochlaenaceae: A new fern family of eupolypods I (Polypodiales). Taxon 64(1): 27–38.

Tsutsumi C & Kato M (2006) Evolution of epiphytes in Davalliaceae and related ferns. Botanical Journal of the Linnean Society 151: 495-510.

Appendix. Taxon, voucher information (when available), and GenBank accession numbers of *rbcL* and *trnL-trnF*, respectively. The m-dash means “not available”; asterix means “in process of submition to GenBank”.

Campyloneurum brevifolium, Kreier s.n.; EF551063; –;
Davallia mariesii, Wu 2463; JX103717; JX103801;
Davallia fejeensis, –; DQ646006; –;
Oleandra arbuscula, P. M. Campos, s.n. (VIC); *; *;
Oleandra articulata, Mori 25152; KF667645; KF667614;
Oleandra articulata, Christenhusz 3980; EF463242; –
Oleandra australis, F. B. Matos et al. 2635; *; *;
Oleandra brasiliana, Labiak 3652; KF667644; KF667613
Oleandra brasiliana, W. S. Costa 14; *; *;
Oleandra brasiliana, W. S. Costa 15; *; *;
Oleandra baetae, J. N. Fregonezi & A. R. Fregonezi s.n. (VIC); *; *;
Oleandra cumingii, Y.S. Chao 1990; KJ196816; KJ196690;
Oleandra cumingii, –; AY093597; AY093596; –
Oleandra decurrens, J.H. Nitta 797; MW138210; –
Oleandra distenta, S. Hennequin R73; KF992505; –
Oleandra neriiformis, Y.S. Chao 1976; KJ196815; KJ196689;
Oleandra neriiformis, T. Flynn 8414; MT657643; –
Oleandra neriiformis, G.M. Plunkett 2867; MT657644; –
Oleandra neriiformis, M.P. Gregory 3322; MZ957128; –
Oleandra neriiformis, M.P. Gregory 2867; MZ957129; –
Oleandra pilosa, Palacios 2697; KF667646; KF667615
Oleandra pistillaris, –; UO5639; –
Oleandra pistillaris, –; AB232405; –
Oleandra quartziticola, C.V. Miranda 91; *; *;
Oleandra sibbaldii, JNG 0566; KY099837; –
Oleandra sibbaldii, Schuettpelz 1889; MT216070; –
Oleandra sibbaldii, K.R. Wood 17017; MT657645; –

Oleandra wallichii, –; MF786603; –

***Pteridium esculentum* subsp. *campestre*,** Schwartsburd 3785; MT426294; –

Serpocaulon catahrinae, Smith 2903; EF551067; EF551122

Anexo I. Pena, N.T.L & Miranda, C.V. (2020) Ferns and lycophytes from a forest associated with quartzitic rocky outcrops in southern Espírito Santo, Brazil. Heringeriana 14(1): 33−48.

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Ferns and lycophytes from a forest associated with quartzitic rocky outcrops in southern Espírito Santo, Brazil

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ABSTRACT: This study presents a checklist of ferns and lycophytes from a forest associated with quartzitic rocky outcrops in southern Espírito Santo state, Brazil. We recorded 52 species and one hybrid (six lycophytes and 47 ferns) belonging to 15 families and 30 genera. Polypodiaceae, Blechnaceae, Cyatheaceae, and Selaginellaceae are the main representative families. *Selaginella, Cyathea*, *Serpocaulon*, and *Trichomanes* are the main representative genera. Most species are terrestrial (34.6%) and lithophytes (32.6%); epiphytes (14.4%) and species with more than one habit (19%) are scarce. We did not record any hemiepiphytic or scandent species. The region is subject to an intense quartzite mining activity, which poses serious threats to the local biodiversity. Morro Branco (Morro de Sal) was recently the site of new taxonomic discoveries in ferns (*Oleandra quartziticola*) and angiosperms (*Paepalanthus capixaba*), demonstrating the biological relevance of forest fragments associated with quartzitic rocky outcrops in Espírito Santo, and reinforcing the need for the effective protection of these areas.

Key words: floristic inventories, Morro Branco, Morro de Sal, Neotropics, pteridophytes.

RESUMO (Samambaias e licófitas de uma floresta associada a afloramentos rochosos quartzíticos no sul do Espírito Santo, Brasil): Este estudo apresenta uma lista de samambaias e licófitas de uma floresta associada a afloramentos rochosos de quartzito no sul do Espírito Santo, Brasil. Foram registradas 52 espécies e um híbrido (seis licófitas e 47 samambaias) pertencentes a 15 famílias e 30 gêneros. Polypodiaceae, Blechnaceae, Cyatheaceae e Selaginellaceae são as principais famílias, enquanto que *Selaginella, Cyathea* e *Trichomanes* são os principais gêneros. A maioria das espécies são terrestres (34.6%) e litófitas (32.6%). As epífitas (14.4%) e as espécies com mais de um hábito (19%) são escassas. Não foram registradas nenhuma espécie hemiepífita ou escandente. A região está sujeita à uma intensa atividade mineradora de quartzito, a qual apresenta sérios riscos para a biodiversidade local. Morro Branco (Morro de Sal) foi recentemente o local de novas descobertas taxonômicas para samambaias (*Oleandra quartziticola*) e angiospermas (*Paepalanthus capixaba*), demonstrando a relevância biológica dos fragmentos florestais associados aos afloramentos rochosos de quartzito no Espírito Santo e reforçando a necessidade de uma proteção efetiva dessas áreas.

Palavras-chave: inventários florísticos, Morro Branco, Morro de Sal, Neotrópicos, pteridófitas.

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INTRODUCTION

Espírito Santo is a southeastern Brazilian state that harbors a great diversity of plants, including ca. 513 species of pteridophytes (ferns and lycophytes) and more than 5780 species of angiosperms (BFG 2015, Dutra *et al.* 2015, Prado *et al.* 2015). The state is also a center of endemism for certain groups of plants (Prance 1982, Werneck *et al.* 2011), comprising 13 endemic species of pteridophytes and 564 endemic species of angiosperms (BFG 2015, Prado *et al*, 2015).

In the last 10 years, several studies have focused on the cryptogamic flora (e.g., Silva & Piasi 2010, Silva & Bastos 2012, Andrade *et al.* 2016, Sylvestre *et al.* 2016, Schwartsburd *et al.* 2017, Pena *et al.* 2019) and on the phanerogamic flora (e.g., Luber *et al.* 2016, Souza *et al.* 2016, Pena & Alves-Araújo 2017) of Espírito Santo. Although most of these studies were conducted in protected areas (Natural Reserves), there are also unprotected areas that have yielded valuable information about the floristic diversity of the state (Ribeiro *et al.* 2009, Pena *et al.* 2017). According to the Brazilian Ministry of Environment (MMA 2020), the study of unprotected areas is extremely important in the process of recognizing new priority areas for biodiversity conservation.

The landscape of Espírito Santo is often characterized by the presence of large granitic or gneissic rock outcrops (also known as *inselbergs*) that support a peculiar flora (e.g., Esgario *et al.* 2008, 2009, Pena & Alves-Araújo 2017). From the Municipality of Vargem Alta, Brade (1956) described some unique landscapes of quartzitic soil and xeric vegetation that have recently become the site of taxonomic novelties in ferns (*Oleandra quartziticola* Schwartsb. & J.Prado) and angiosperms (*Paepalanthus capixaba* Trovó, Fraga & Sano). In a recent paper describing a new species of Eriocaulaceae, Trovó *et al*. (2016) pointed out that the quartizitic patches in Vargem Alta are now under intense mining activity, with the surrounding forests being quickly replaced by pastures or managed forests. They also highlighted the lack of a conservation unit in this region.

From 2010 to 2020, the number of known ferns and lycophytes ocurring in Espírito Santo has increased from 331 to 513 species (Prado & Sylvestre 2010, Prado *et al.*, 2015). However, there still is a significant gap of knowledge regarding the ferns and lycophytes of quartzitic formations in the state. With the goal of filling this gap, we present a checklist of the ferns and lycophytes occurring in Morro Branco (a.k.a. Morro de Sal), Vargem Alta, Espírito Santo, Brazil.

MATERIAL AND METHODS

The study area is located on the outskirts of Sítio Morro Branco (20°39'31”S and 41°00'34"W), Vargem Alta city, Espírito Santo, Brazil (Figure 1, 2), to which features quartzite rocky outcrops and a mosaic of sandy soils associated by weathering. It is locally known as Morro Branco or Morro de Sal (i.e., White Hill or Salt Hill), due to its white sandy soil that resembles salt. It has about 14 ha, at 600–800 m above sea level. According to the Climate-Data (2020), the climate is humid and mesothermic with average annual rainfall of 1,237 mm and average annual temperature of 20.7°C. Following Köppen & Geiger (1936), the region is classified as Cfa-Cfb, a humid temperate climate with cold and dry winter and hot and wet summer.

Field trips were carried out between 2018–2019, and the collected specimens were deposited at VIC and VIES, which are Brazilian herbaria of Universidade Federal de Viçosa and Universidade

Federal do Espírito Santo, respectively (Thiers 2020). All collected samples were prepared according to the methods proposed by Windisch (1992). For the determination of specimens, we consulted taxonomic monographs (e.g., Tryon 1942, Brade 1964, Tryon & Tryon 1982, Lellinger 1988, Moran 1995a, 1995b, 2000, Sylvestre 2001, Salino & Semir 2002, 2004a, 2004b, Mickel & Smith 2004, Labiak & Prado 2008, Moran *et al.* 2010, Windisch 2014, Dittrich *et al.* 2015, 2018, Viveros & Salino 2015, Heringer *et al.* 2016, Mickel 2016, Schwartsburd *et al.* 2018), and used the herbarium collections of VIC and MBML. The classification system adopted was PPG I (2016), and the names of authors and species were confirmed through IPNI (2020). Species not found in our field trips, but with confirmed occurrence in the area were also included in our checklist (CRIA 2020, Reflora 2020). For verification of the threat status of each species, we followed Sylvestre *et al.* (2019) and IUCN (2020). The final checklist contains information about the habit of each species (epiphytes, lithophytes, terrestrial), and their respective vouchers.

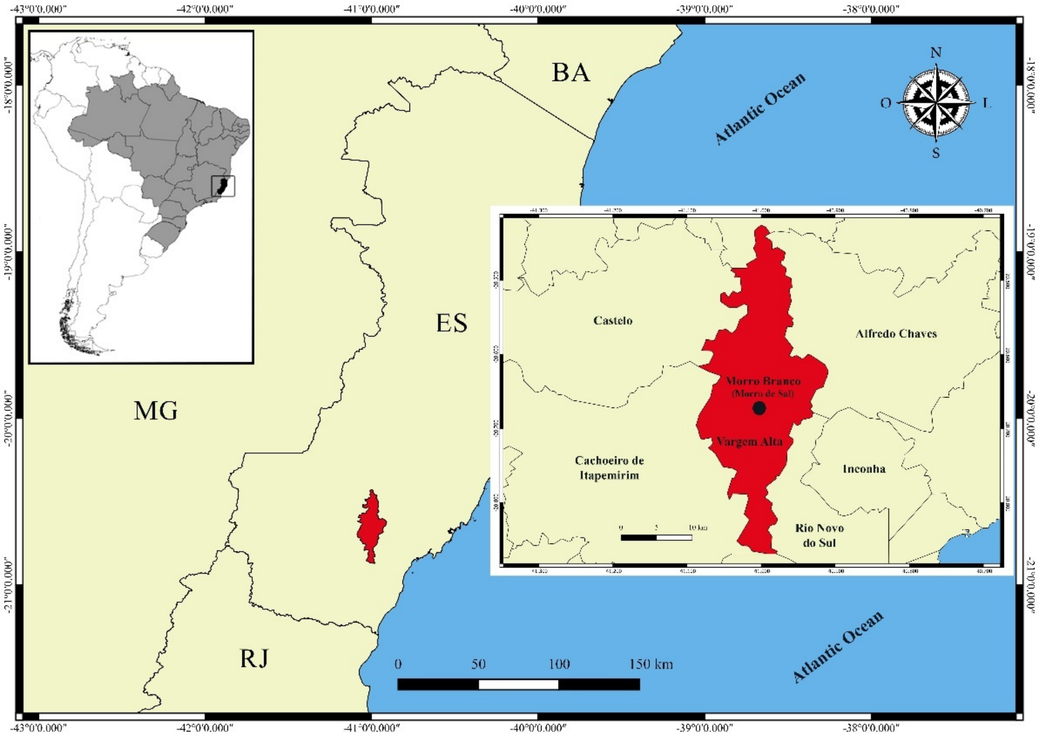

Figure 1. Location map of Morro Branco (Morro de Sal) in Vargem Alta, southern Espírito Santo state, Brazil.

RESULTS AND DISCUSSION

In Morro Branco, we found 52 species and one hybrid, distributed in 30 genera and 15 families of ferns (47 species) and lycophytes (six species) (Table 1; Figures 3, 4). The most representative families are Polypodiaceae J.Presl & C.Presl (12 species), Blechnaceae Newman. (5 spp. and 1 hybrid), Cyatheaceae Kaulf. (5 spp.), and Selaginellaceae Willk (5 spp.). The most representative genera are *Selaginella* P.Beauv. (5 spp.), *Cyathea* Sm., *Serpocaulon* A.R. Sm., and *Trichomanes* L. (4 spp. each).

Among the 53 taxa, 18 spp. (34.6%) are terrestrial, and 17 spp. (32.6%) are litophytic – being these the most representative life forms. Only 8 spp. (14.4%) are epiphyte. Other taxa showed two or more life forms, being terrestrial/lithophytic (17% - 9 spp.) and terrestrial/lithophytic/epiphytic (2% - *Serpocaulon triseriale* (Sw.) A.R.Sm. [Polypodiaceae]).

Figure 2. Images from Morro Branco (Morro de Sal). A. Forest fragment associated with rocks. B. Forest fragment associated with temporary river. C. Forest fragment interior. D. Quartzite soil fragment.

According to Prado *et al.* (2015), *Serpocaulon hirsutulum* (T. Moore) Schwartsb. & A.R. Sm. (Polypodiaceae) had no confirmed occurrence for Espírito Santo. Therefore, we present here the first record of this specie in the state. *Oleandra quartziticola* Schwartsb. & J.Prado is a recently described species (Schwartsburd *et al.* 2016) known only from the type locality. It is therefore a narrow endemic. According to the Flora Ameaçada do Espírito Santo (Sylvestre *et al.* 2019), *Oleandra quartziticola* is critically endangered (CR). Seventeen species are endemic to the Atlantic Forest, and *Macrothelypteris torresiana* (Gaudich.) Ching is the only invasive species recorded there (Table 1; Figure 5).

Asplenium auritum Wall. [*Fontana 7311*, MBML], *Cyathea corcovadensis* Domin [*Assis 4593*, VIES], *Selaginella decomposita* Spring [*Brade 19360*, RB], *Serpocaulon menisciifolium* (Langsd. & Fisch.) A.R.Sm. [*Fiaschi 3557*, MBML] and *Pteris decurrens* C.Presl [*Fontana 7332*, MBML] were incorporated into the checklist based on herbarium specimens that were previously collected at Morro Branco (Morro de Sal).

The landscapes that feature rocky outcrops are very interesting areas. According to Porembski *et al.* (1997a), two or more types of floristic environments can be observed in this kind of formation. Particularly at Morro Branco (Morro de Sal), two types of floristic environments were observed: I. the area of forest surrounding the

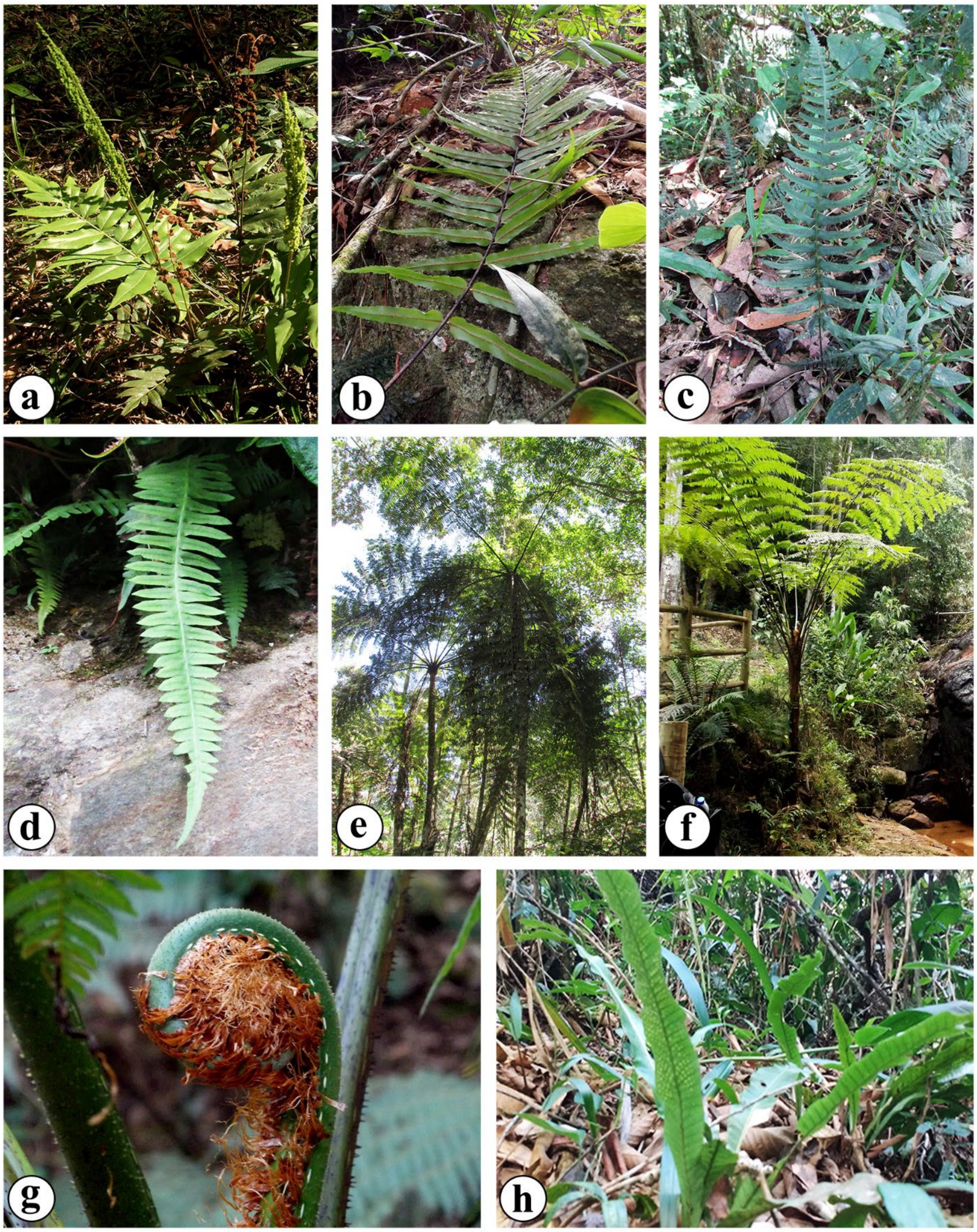

Figure 3. Some fern species collected at Morro Branco (Morro de Sal) in Vargem Alta, southern Espírito Santo, Brazil. A. *Anemia phyllitidis* (Anemiaceae). B. *Asplenium serra* (Aspleniaceae). C. *Blechnum occidentale* (Blechnaceae). D. *Blechnum polypodioides* (Blechnaceae). E. *Cyathea delgadii* (Cyatheaceae). F. *Cyathea phalerata* (Cyatheaceae). G. Crozier of *Cyathea phalerata* (Cyatheaceae). H. *Campyloneurum nitidum* (Polypodiaceae).

quartzitic outcrops is wetter, shaded, and with deep soils that favor the growth of tree ferns and assosiated epiphytes; II. the quartzitic outcrops have islands of vegetation that are formed from crevices in the rock and have lithophytes as the more abundant life form. This last pattern was also found in other studies that investigated the flora of rocky outcrops (e.g., França *et al.* 1997, Caiafa &

Silva 2005, Santos & Sylvestre 2006, Araújo *et al.* 2008, Porembski 2007). Those species that are exclusively terrestrial, along those exclusively lithophytic, represent more than 50% of the ferns and lycophytes in the area. Curiously, some epiphytic

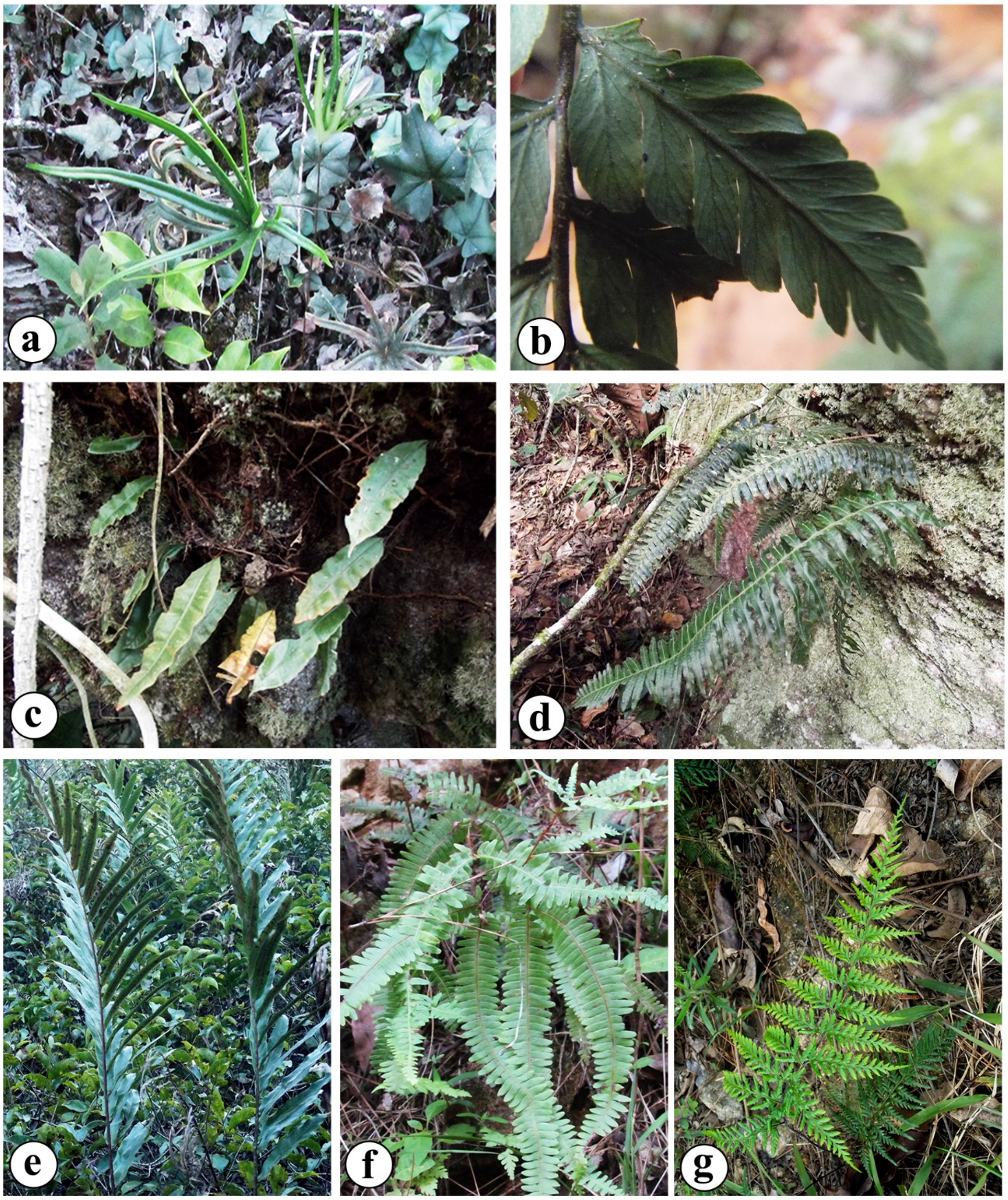

Figure 4. Some fern species collected in Morro Branco (Morro de Sal) in Vargem Alta, southern Espírito Santo, Brazil. A. *Lytoneuron ornithopus* (Pteridaceae). B. *Polybotrya osmundacea* (Dryopteridaceae). C. *Oleandra quartziticola* (Oleandraceae). D. *Pecluma chnoophora* (Polypodiaceae). E. *Serpocaulon triseriale* (Polypodicaeae). F. *Sticherus bifidus* (Gleicheniaceae). G. *Pityrogramma calomelanos* var. *calomelanos* (Pteridaceae).

ferns were found on the trunks of tree ferns (Cyatheaecae Kaulf.), in the vegetation surrounding the quartzitic outcrops. The tree ferns are: *Alsophila sternbergii* (Sternb.) D.S.Conant, *Cyathea corcovadensis* Domin, *C. dichromatolepis* Domin, *C. delgadii* Sternb., *C. phalerata* Mart., and their trunks are substrate to *Asplenium mucronatum* C.Presl (Aspleniaceae), *Trichomanes pilosum* Raddi and *T. polypodioides* L. (Hymenophyllaceae), and *Pecluma filicula* (Kaulf.) M.G.Price (Polypodiaceae). The studies performed by Moran *et al.* (2003) also showed this interesting relationship between epiphytic ferns living on tree fern trunks and two important points are highlighted for this occurrence: I. the root mantle on tree ferns that has the characteristic of being coarse with many interstices provides favorable microhabitats (higher humidity) for the establishment of fern. II. chemistry of the root mantle substance, such as pH and presence of tannins, favors the fern spores germination by inhibiting development of algae and fungi-organisms that compete with fern gametophytes for light, nutrients, and space.

According to Benzing (1987), even though epiphytic species are typically found growing on terrestrial plants, some of these species may have adaptive strategies that make them able to colonize rocks. This is likely the case of *Serpocaulon triseriale* (Sw.) A.R.Sm. (Polypodiaceae), a species with more than one life form. This may also explain the low number of epiphyte species, after all, in the field expeditions, some of these species may have been found only as lithophytes. However, the scarcity of epiphyte species in our checklist may represent negative effect of disturbances on the local diversity of plants, mainly due to habitat loss due to the extraction of quartzite rocks, resulting in secondary forest fragments still in the process of regeneration, and low humidity due to quartzite soils fragments with white sand presenting in the studied area.

The biology of plants growing on quatzitic rock outcrops is still poorly understood. According to Silva (2016), even with the increase of studies in Brazil in the 90's, most studies are focused on granitic-gneissic outcrops, and the botanical groups studied were mainly angiosperms and bryophytes. Regarding ferns and lycophytes, there are few floristic studies focusing on rocky outcrops within the Atlantic Rainforest, and the existing ones were also conducted on granitic-gneissic outcrops (e.g., Santos & Silvestre 2006, Nettesheim *et al*. 2014, Pena *et al.* 2019). Other works like as Schwartsburd & Labiak (2007) and Michelon & Labiak (2013), present occurrence of ferns and lycophytes in sandstone rock formations in their study areas in southern Brazil. Comparing the species of the present study in relation to the studies presented above, the following species have common occurrence:

I. Santos & Silvestre (2006): *Anemia villosa, Macrothelypteris torresiana*, *Microgramma vacciniifolia*, *Palhinhaea cernua, Pityrogramma calomelanos* var. *calomelanos, Pteridium esculentum* subsp. *arachnoideum, Selaginella muscosa,* and *Serpocaulon triseriale*.

II. Nettesheim *et al*. (2014): *Anemia phyllitidis*, *Cyathea corcovadensis, Macrothelypteris torresiana, Neoblechnum brasiliense,* and *Selaginella muscosa*.

III. Pena *et al*. (2019): *Blechnum occidentale*, *Campyloneurum nitidum*, *Macrothelypteris torresiana, Microgramma crispata, Microgramma vacciniifolia, Pityrogramma calomelanos* var. *calomelanos, Selaginella flexuosa* and *Serpocaulon triseriale*.

IV. Schwartsburd & Labiak (2007): *Amauropelta rivularioides*, *Anemia phyllitidis, Blechnum polypodioides, Campyloneurum nitidum, Christella conspersa, Cyathea corcovadensis, C. delgadii, C. phalerata, Macrothelypteris torresiana, Microgramma vacciniifolia, Neoblechnum brasiliense, Palhinhaea cernua, Parablechnum cordatum, Pteridium esculentum* subsp. *arachnoideum, Pteris decurrens, Selaginella decomposita, S. flexuosa, S. muscosa, Sticherus lanuginosus* and *Trichomanes pilosum*.

V. Michelon & Labiak (2013): *Anemia phyllitidis, Amauropelta rivularioides, Asplenium auritum, A. mucronatum, Blechnum occidentale, Blechnum polypodioides, Campyloneurum nitidum, Christella conspersa, Cyathea corcovadensis, C. delgadii, C. phalerata, Lytoneuron ornithopus, Microgramma vacciniifolia, Neoblechnum brasiliense, Palhinhaea cernua, Parablechnum cordatum, Pecluma filicula, Pityrogramma calomelanos* var *calomelanos, Pteridium esculentum* subsp. *arachnoideum, Pteris decurrens, Selaginella flexuosa, Sticherus lanuginosus, Trichomanes pilosum* and *Trichomanes polypodioides.*

Unfortunatelly, there are no studies of ferns and lycophytes from quartzitic formations in the state of Espírito Santo. For this reason, the floristic comparisons made above, contemplate areas with granitic-gneissic and sandstone outcrops, formations that are distinct from the studied area. For areas with granitic-gneissic the floristic similarity was lower and may be related to the characteristics of the rocks. In granitic-gneiss rocks outcrops, boulders associated with deep weathering mantles are observed and most tree species are found among large rocky outcrops. Quartzitic outcrops, on the other hand, are often found with cracks and full soil depressions, those are important features that control soil and vegetation development. In addition, soils developed on granitic rocks are more acidic due to the large amounts of aluminum and iron, and have a slightly higher silt and clay content than soils developed on quartzite (e.g., Porembski *et al.* 1997b, Benites *et al.* 2007).

In relation to studies focused on sandstone formations, there was greater floristic similarity. According to Auler & Piló (2019), quartzites and sandstones are rocks similar in composition (mainly silica), is that quartzites are basically sandstones that have undergone metamorphism, that is, have been subjected to high temperature and pressure. The greater number of similar species among the studied areas with quartzite and sandstone rock formations, may be strongly related to the existing geological similarities, since the soil characteristics influence the floristic composition.

Another important point is that the flora surrounding the rocky outcrops receives the nutrients and water from the outcrop flow, creating a specific feature that houses species different from those at the top of the rock formation (e.g., Sarthou *et al*. 2003, Silva 2016). In this way, floristic studies focused on forest areas covered by rocky outcrops are important for better knowledge of biodiversity, which suffer strong anthropic pressure, and which may reveal new species for science (e.g., Leme *et al.* 2010, Viveros & Salino 2015, Mickel 2016, Schwartsburd *et al.* 2016, Trovó *et al.* 2016).

Table 1. Lycophytes and ferns recorded in Morro Branco (Morro de Sal), Vargem Alta, southern Espírito Santo, Brazil. Life forms: LT = lithophytes; TR = terrestrial; EP = epiphytes. Species endemic to the Atlantic Forest (*).

Taxa	Life form	Voucher	Herbarium
Lycopodiaceae P.Beauv. ex Mirb.			
Palhinhaea cernua (L.) Franco & Vasc.	LT	N.T.L.Pena 699	VIC
Selaginellaceae Willk			
Selaginella contigua Baker*	LT	N.T.L.Pena 695	VIC
Selaginella decomposita Spring*	LT	A.C.Brade 19360	RB
Selaginella flexuosa Spring	LT	N.T.L.Pena 725	VIC
Selaginella muscosa Spring*	LT	N.T.L.Pena 706	VIC
Selaginella producta Baker	LT	N.T.L.Pena 690	VIC
Anemiaceae Link.			
Anemia phyllitidis (L.) Sw.	TR	N.T.L.Pena 714	VIC
Anemia villosa Humb. & Bonpl. ex Willd.	TR	C.V.Miranda 68	VIC
Aspleniaceae Newman.			
Asplenium auritum Wall.	LT	A.P.Fontana 7311	MBML
Asplenium mucronatum C.Presl*	EP	N.T.L.Pena 727	VIC
Asplenium serra Langsd. & Fisch.	LT	C.V.Miranda 72	VIC
Athyriaceae Alston			
Diplazium asplenioides (Kunze) C.Presl*	TR	C.V.Miranda 49	VIC
Blechnaceae Newman.			
Blechnum × confluens Schltdl. & Cham.	TR/LT	N.T.L.Pena 700	VIC
Blechnum occidentale L.	TR/LT	C.V.Miranda 53	VIC
Blechnum polypodioides Raddi	TR/LT	N.T.L.Pena 721	VIC
Lomaridium plumieri (Desv.) C.Presl*	TR	C.V.Miranda 95	VIC
Neoblechnum brasiliense (Desv.) Gasper & V.A.O.Dittrich*	TR	N.T.L.Pena 702	VIC
Parablechnum cordatum (Desv.) Gasper & Salino	TR	N.T.L.Pena 704	VIC
Cyatheaceae kaulf.			
Alsophila sternbergii (Sternb.) D.S.Conant	TR	C.V.Miranda 71	VIC
Cyathea corcovadensis Domin	TR	A.M.Assis 4593	VIES
Cyathea dichromatolepis Domin	TR	C.V.Miranda 71	VIC
Cyathea delgadii Sternb.	TR	N.T.L.Pena 723	VIC
Cyathea phalerata Mart.	TR	C.V.Miranda 76	VIC
Dennstaedtiaceae Lotsy			
Pteridium esculentum subsp. *arachnoideum* (Kaulf.) Thomson	TR	N.T.L.Pena 717	VIC
Dryopteridaceae Herter			
Elaphoglossum hymenodiastrum (Fée) Brade*	LT	N.T.L.Pena 741	VIC
Megalastrum grande (C.Presl) A.R.Sm. & R.C.Moran*	TR	CVMirada 77	VIC

Taxa	**Life form**	**Voucher**	**Herbarium**
Polybotrya osmundacea Humb. & Bonpl. ex Willd.	TR	N.T.L.Pena 731	VIC
Gleicheniaceae C.Presl			
Sticherus lanuginosus (Moric. ex Fée) Nakai	TR/LT	C.V.Miranda 48	VIC
Sticherus bifidus (Willd.) Ching	TR/LT	C.V.Miranda 52	VIC
Sticherus nigropaleaceus (J.W.Sturm) J.Prado & Lellinger*	TR/LT	P.B.Schwartsburd	VIC
Hymenophyllaceae Mart.			
Trichomanes cristatum Kaulf	LT	P.B.Schwartsburd 3523	VIC
Trichomanes elegans Rich.	LT	C.V.Miranda 44	VIC
Trichomanes pilosum Raddi	EP	N.T.L.Pena 708	VIC
Trichomanes polypodioides L.	EP	N.T.L.Pena 693	VIC
Oleandraceae Ching ex Pic.Serm.			
Oleandra quartziticola Schwartsb. & J.Prado*	LT	C.V.Miranda 59	VIC
Polypodiaceae J.Presl & C.Presl			
Campyloneurum atlanticum R.C.Moran & Labiak	LT	N.T.L.Pena 735	VIC
Campyloneurum nitidum C.Presl*	LT	N.T.L.Pena 732	VIC
Microgramma crispata (Fée) R.M.Tryon & A.F.Tryon*	EP	P.B.Schwartsburd 3519	VIC
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	EP	C.V.Miranda 86	VIC
Pecluma filicula (Kaulf.) M.G.Price*	EP	C.V.Miranda 75	VIC
Pecluma chnoophora (Kunze) Salino & Costa Assis*	LT	N.T.L.Pena 730	VIC
Pleopeltis astrolepis (Liebm.) E.Fourn.	EP	C.V.Miranda 42	VIC
Phlebodium pseudoaureum (Cav.) Lellinger	TR/LT	P.B.Schwartsburd 3520	VIC
Serpocaulon hirsutulum (T.Moore) Schwartsb. & A.R.Sm.*	TR/LT	P.B.Schwartsburd 3527	VIC
Serpocaulon fraxinifolium (Jacq.) A.R.Sm.	EP	N.T.L.Pena 737	VIC
Serpocaulon menisciifolium (Langsd. & Fisch.) A.R.Sm.*	TR/LT	P.Fiaschi 3557	MBML
Serpocaulon triseriale (Sw.) A.R.Sm.	TR/LT/EP	N.T.L.Pena 716	VIC
Pteridaceae Ching			
Lytoneuron ornithopus (Mett. ex Hook. & Baker) Yesilyurt	LT	N.T.L.Pena 711	VIC
Pityrogramma calomelanos (L.) Link var. *calomelanos*	LT	C.V.Miranda 64	VIC
Pteris decurrens C.Presl	TR	A.P.Fontana 7332	MBML
Thelypteridaceae Pic.Serm.			
Amauropelta rivularioides (Fée) Salino & T.E.Almeida	TR	C.V.Miranda 69	VIC
Christella conspersa (Schrad.) Á.Löve & D.Löve	TR	N.T.L.Pena 712	VIC
Macrothelypteris torresiana (Gaudich.) Ching	TR	N.T.L.Pena 697	VIC

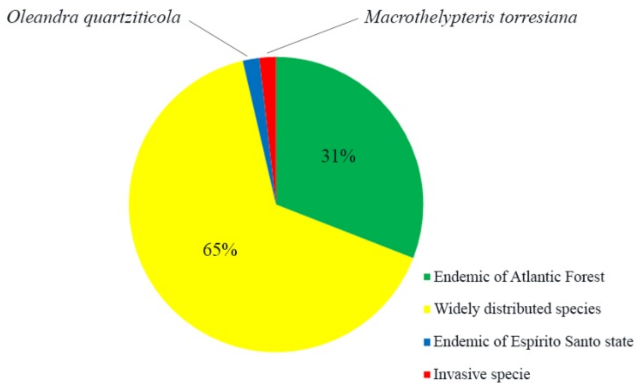

Figure 5. Graph of species occurring in Morro Branco (Morro de Sal) in Vargem Alta, southern Espírito Santo, Brazil.

CONCLUSION

The pteridophytic flora of Morro Branco is considerably different from the flora of the granitic-gneissic inselbergs that have been studied in Espírito Santo. The ongoing mining activities taking place in the area may result in the destruction of the local vegetation, causing the extinction of narrow endemic species, such as *Oleandra quartziticola.* This highlights the relevance of floristic studies, specially outside conservation units, as the one presented here. Such studies may increase the knowledge on the distribution of certain species of ferns and lycophytes, providing subsidies for the creation of priority conservation areas.

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REFERENCES

Andrade, R.C., Sylvestre, L.S. & Menezes, L.F.T. (2016) Ferns and lycophytes in three fragments of Tabuleiro lowland forest in northern Espírito Santo state, Brazil: composition and floristic relationships in Atlantic forest. *Brazilian Journal of Botany* 39: 1–11. https://doi.org/10.1007/s40415-016-0311-x

Araújo, F.S., Oliveira, R.F. & Lima-Verde, L.W. (2008) Composição, espectro biológico e síndromes de dispersão da vegetação de um inselbergue no domínio da caatinga, Ceará. *Rodriguésia* 59: 659–671.

Auler, A.S. & Piló, L.B. (2019) Geologia de cavernas e sua interpretação a luz da legislação ambiental espeleológica. In: Cruz, J.B. & Piló, L.B. (Eds.) Espeleologia e Licenciamento Ambiental. CECAV/ICMBIO, pp. 41–76.

Benites, V.M., Machado, P.P.O.A., Fidalgo, E.C.C., Coelho, M.R. & Madari, B.E. (2007) Pedotransfer functions for estimating soil bulk density from existing soil survey reports in Brazil. *Geoderma* 139: 90–97.

Benzing, D.H. (1987) Vascular epiphytism: taxonomy participation and adaptative diversity. *Annals of the Missouri Botanical Garden* 74: 183–204.

BFG - The Brazil Flora Group. (2015) Growing knowledge: an overview of seed plant diversity in Brazil. *Rodriguésia* 66: 1085–1113. https://doi.org/10.1590/2175-7860201566411

Brade, A.C. (1956) Melastomataceae novae IV. *Arquivos do Jardim Botânico do Rio de Janeiro* 14: 211–240.

Brade, A.C. (1964) Contribuição para o conhecimento das espécies brasileiras do gênero

Doryopteris (Polypodiaceae). *Arquivos do Jardim Botânico do Rio de Janeiro* 18: 39–72.

Caiafa, A.N. & Silva, A.F. (2005) Composição florística e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais - Brasil. *Rodriguésia* 56: 163–173.

Climate-data. (2020) Dados climáticos para cidades mundiais. Available from: https://pt.climate-data.org/ (accessed 6 March 2020).

CRIA - Centro de Referência e Informação Ambiental. (2020) SpeciesLink - simple search. Available from: http://www.splink.org.br/ (accessed 6 July 2020).

Dittrich, V.A.O., Salino, A. & Monteiro, R. (2015) The *Blechnum occidentale* (Blechnaceae – Polypodiopsida) species group in southern and southeastern Brazil. *Phytotaxa* 231: 201–229. https://doi.org/10.11646/phytotaxa.231.3.1

Dittrich, V.A.O., Salino, A., Monteiro, R. & Gasper, A.L. (2018) The fern genera *Lomaria*, Lomariocycas, and *Parablechnum* (Blechnaceae, Polypodiopsida) in southern and southeastern Brazil. *Phytotaxa* 362: 245–262. https://doi.org/10.11646/phytotaxa.362.3.1

Dutra, V.F., Alves-Araújo, A. & Carrijo, T.T. (2015) Angiosperm checklist of Espírito Santo: using electronic tools to improve the knowledge of na Atlantic Forest biodiversity hotspot. *Rodriguésia* 66: 1145–1152. https://doi.org/10.1590/2175-7860201566414

Esgario, C.P., Ribeiro, L.R. & Silva, A.G. (2008) O Alto Misterioso e a vegetação sobre rochas em meio à Mata Atlântica, no Sudeste do Brasil. *Natureza on line* 6: 55–62.

Esgario, C.P., Fontana, A.P. & Silva, A.G. (2009) A flora vascular sobre rocha no Alto Misterioso, uma área prioritária para conservação da Mata Atlântica no Espírito Santo, Sudeste do Brasil. *Natureza on line* 7: 80–91.

França, F., Melo, E. & Santos, C.C. (1997) Flora de inselbergs da região de Milagres, Bahia, Brasil: I. Caracterização da vegetação e lista de espécies de dois inselbergs. *Sitientibus* 17: 163–184.

Heringer, G., Valdespino, I.A. & Salino, A. (2016) *Selaginella* P. Beauv. from Minas Gerais, Brazil. *Acta Botanica Brasilica* 30: 60–77. https://doi.org/10.1590/0102-33062015abb0247

IPNI - The International Plant Names Index. (2020) Available from: http://www.ipni.org/ipni/ (accessed 6 March 2020).

IUCN. (2020) The IUCN Red List of Threatened Species. Version 2020-1. Available from: https://www.iucnredlist.org (accessed 6 March 2020).

Köppen, W. (1936) Das geographische System der Klimate. In: Köppen, W. & Geiger, R. (Eds.) *Handbuch der Klimatologie*. Gebrüder Bornträger, Berlin, pp. 1–44.

Labiak, P.H. & Prado, J. (2008) New combinations in *Serpocaulon* and a provisional key for the Atlantic Rain Forest species. *American Fern Journal* 98: 139–159. https://doi.org/10.1640/0002-8444(2008)98[139:NCISAA]2.0.CO;2

Lellinger, D.B. (1988) Some new species of *Campyloneurum* and a provisional key to the genus. *American Fern Journal* 78: 14–35.

Leme, M.C., Fraga, C.N., Kollmann, L.J.C., Brown, G.K., Till, W., Ribeiro, O.B.C., Machado, M.C., Monteiro, F.J.S. & Fontana, A.P. (2010) Miscellaneous new species in the Brazilian Bromeliaceae. *Rodriguésia* 61(1): 21–67.

Luber, J., Amélia, C.T., Torres, F., Christ, J.A., Guidoni-Martins, K.G., Zanetti, M., Hollunder, R.K., Manhães, V.C., Zorzanelli, J.P.F., Mendonça, E.S., Garbin, M.L. & Carrijo, T.T. (2016) List of angiosperm species in an Atlantic Forest fragment reveals collection gaps in Espírito Santo state, Brazil. *Check List* 12(1): 1–10. https://doi.org/10.15560/12.1.1835

Michelon, C. & Labiak, P.H. (2013) Samambaias e Licófitas do Parque Estadual do Guartelá, PR, Brasil. *Hoehnea* 40(2): 191–204.

Mickel, J.T. (2016) *Anemia* (Anemiaceae). *Flora Neotropica Monograph.* The New York Botanical Garden, New York, 181 pp.

Mickel, J.T. & Smith, A.R. (2004) The pteridophytes of Mexico**.** *Memoirs of the New York Botanical Garden* 88: 1–1054.

MMA - Ministério do Meio Ambiente. (2020) *Criação UC's.* Ministério do Meio Ambiente, Brasília. Available from: http://www.mma.gov.br/areas-protegidas/unidades-de-conservacao/criacao-ucs.html (accessed 6 March 2020).

Moran, R.C. (1995a) *Blechnum***.** In: Davidse, G., Sousa, M. & Knapp, S. (Eds.) *Flora Mesoamericana.* Universidad Nacional Autónoma de México, Mexico, pp 325–332.

Moran, R.C. (1995b) *Pityrogramma***.** In: Davidse, G., Sousa, M. & Knapp, S. (Eds) *Flora Mesoamericana*. Universidad Nacional Autónoma de México, Mexico, pp. 137–140.

Moran, R.C. (2000) Monograph of the Neotropical species of *Lomariopsis* (Lomariopsidaceae). *Brittonia* 52: 55–111.

Moran, R.C., Klimas, S. & Carlsen, M. (2003) Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. *Biotropica* 35: 48–56.

Moran, R.C., Labiak, P.H. & Sundue, M. (2010) Synopsis of *Mickelia*, a newly recognized genus of bolbitidoid ferns (Dryopteridaceae). *Brittonia* 62: 337–356.

Nettesheim, F.C., Damasceno, E.R. & Sylvestre, L.S. (2014) Different slopes of a mountain can determine the structure of ferns and lycophytes communities in a tropical forest of Brazil. *Anais da Academia Brasileira de Ciências* 86: 199–210.

Pena, N.T.L. & Alves-Araújo, A. (2017) Angiosperms from rocky outcrops of Pedra do Elefante, Nova Venécia, Espírito Santo, Brazil. *Rodriguésia* 68: 1895–1905. https://doi.org/10.1590/2175-7860201768522

Pena, N.T.L., Saiter, F.Z. & Viégas-Aquije, G.M.F. (2017) Ferns and Lycophytes from fragments of semideciduous forest in central Espírito Santo, Brazil. *Rodriguésia* 68: 1977–1986. https://doi.org/10.1590/2175-7860201768528

Pena, N.T.L., Labiak, P.H., Schwartsburd, P.B. & Alves-Araújo, A. (2019) Samambaias e Licófitas da Pedra do Elefante, Espírito Santo, Brasil. *Rodriguésia* 70: e02482017. https://doi.org/10.1590/2175-7860201970023

Porembski, S. (2007) Tropical inselbergs: habitat types, adaptive strategies and diversity patterns. *Revista Brasileira de Botânica* 30: 579–586.

Porembski, S., Seine, R. & Barthlott, W. (1997a) Inselberg vegetation and the biodiversity of granite outcrops*. Journal of the Royal Society of Western Australia* 80: 193–199.

Porembski, S., Fischer, E. & Biedinger, N. (1997b) Vegetation of inselbergs, quarzitic outcrops and ferricretes in Rwanda and eastern Zaire (Kivu). *Bulletin du Jardin Botanique National de Belgique* 66: 81–99.

PPG I - Pteridophyte Phylogeny Group. (2016) A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and*

Evolution 54: 563–603. https://doi.org/10.1111/jse.12229

Prado, J. & Sylvestre, L.S. (2010) As samambaias e licófitas do Brasil. *In:* Forzza, R.C., Baumgratz, J.F.A., Bicudo, C.E.M., Canhos, D., Carvalho, J.R., A.A., Costa, A., Costa, D.P., Hopkins, M., Leitman, P.M., Lohmann, L.G., Lughadha, E.N., Maia, L.C., Martinelli, G., Menezes, M., Moriom, M.P., Nadruz, M., Peixoto, A.L., Pirani, J.R., Prado, J., Queiroz, L.P., Souza, V.C., Stehmann, J.R., Sylvestre, L.S., Walter, B.M.T. & Zappi, D.C. (Eds.) *Catálogo de plantas e fungos do Brasil. Vol. 1.* Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, pp. 69–74.

Prado, J., Sylvestre, L., Labiak, P.H., Windisch, P.G., Salino, A., Barros, I.C.L., Hirai, R.Y., Almeida, T.E., Santiago, A.C.P., Kieling-Rubio, M.A., Pereira, A.F.N., Øllgaard, B., Ramos, C.G.V., Mickel, J.T., Dittrich, V.A.O., Myssen, C.M., Schwartsburd, P.B., Condack, J.P.S., Pereira, J.B.S. & Matos, F.B. (2015) Diversity of ferns and lycophytes in Brazil. *Rodriguésia* 66: 1073–1083. https://doi.org/10.1590/2175-7860201566410

Prance, G.T. (1982) A review of the phytogeographic evidences for Pleistocene climate changes in the Neotropics. *Annals of the Missouri Botanical Garden* 69: 594–624.

Reflora (2020) Herbário Virtual. Available from: http://reflora.jbrj.gov.br/reflora/herbarioVirtual (accessed 6 July 2020).

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142: 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Santos, M.G. & Sylvestre, L.S. (2006) Aspectos florísticos e econômicos das pteridófitas de um afloramento rochoso do Estado do Rio de Janeiro, Brasil. *Acta Botanica Brasilica* 20: 115–124.

Salino, A. & Semir, J. (2002) Thelypteridaceae (Polypodiophyta) do estado de São Paulo: *Macrothelypteris* e *Thelypteris* subgêneros *Cyclosorus* e *Steiropteris*. *Lundiana* 3: 9–27.

Salino, A & Semir, J. (2004a) *Thelypteris* subg. *Amauropelta* (Kunze) A.R. Sm. (Thelypteridaceae–Pterophyta) no Estado de São Paulo, Brasil. *Lundiana* 5: 83–112.

Salino, A. & Semir, J. (2004b) *Thelypteris* subg. *Meniscium* (Thelypteridaceae–Pteridophyta) no estado de São Paulo, Brasil. *Revista Brasileira de Botânica* 27: 103–114.

Sarthou, C., Villiers, J.F. & Ponge, J.F. (2003) Shrub vegetation on tropical granitic inselbergs in French Guiana. *Journal of Vegetation Science* 14: 645–652.

Schwartsburd, P.B. & Labiak, P.H. (2007) Pteridófitas do Parque Estadual de Vila Velha, Ponta Grossa, Paraná, Brasil. *Hoehnea* 34(2): 159–209.

Schwartsburd, P.B., Miranda, C.V. & Prado, J. (2016) *Oleandra* (Oleandraceae) in the Brazilian Atlantic Forest. *American Fern Journal* 106:191–205. https://doi.org/10.1640/AFJ-D-16-00004.1

Schwartsburd, P.B., Miranda, C.V., Pena, N.T.L., Oliveira, M.H., Silva, R.V. & Marcolino, F. (2017) Checklist of ferns and lycophytes from Parque Estadual Mata das Flores, Castelo, Espírito Santo, Brazil. *Check List* 13: 621–633. https://doi.org/10.15560/13.5.621

Schwartsburd, P.B., Yañez, A. & Prado, J. (2018) Formal recognition of six subordinate taxa within the South American bracken fern, *Pteridium esculentum* (*P. esculentum* subsp. *arachnoideum s.l.*—Dennstaedtiaceae), based on morphology and geography. *Phytotaxa* 333: 022–040. https://doi.org/10.11646/phytotaxa.333.1.2

Silva, L.T.P. & Piassi, M. (2010) Briófitas da formação herbácea inundada do Parque Estadual Paulo César Vinha, Setiba, Guarapari, Espírito Santo, sudeste do Brasil. *Natureza on line* 8: 32–39.

Silva, L.T.P. & Bastos, C.J.P. (2012) Hepáticas Talosas (Marchantiophyta) de um fragmento de Mata Atlântica no Parque Estadual Pedra Azul (PEPAZ), Domingos Martins, Espírito Santo, Brasil. *Natureza on line* 10: 160–164.

Silva, J.B. (2016) Panorama sobre a vegetação em afloramentos rochosos do Brasil. *Oecologia Australis* 20: 451–463. https://doi.org/10.4257/oeco.2016.2004.05

Souza, W.O., Machado, J.O., Tognella, M.M.P. & Alves-Araújo, A. (2016) Checklist de angiospermas do Parque Estadual de Itaúnas, Espírito Santo, Brasil. *Rodriguésia* 67: 571–581. https://doi.org/10.1590/2175-7860201667303

Sylvestre, L.S. (2001) Revisão taxonômica das espécies da família Aspleniaceae A. B. Frank ocorrentes no Brasil. Doctoral dissertation, Universidade de São Paulo, São Paulo, 376 pp.

Sylvestre, L.S., Almeida, T.E., Mynssen, C.M. & Salino, A. (2016) Samambaias e licófitas da Reserva Natural Vale, Linhares, ES. In: Rolim, S.G., Menezes, L.F.T. & Srbek-Araújo, A.C. (Eds.) *Floresta Atlântica de Tabuleiro: diversidade e endemismos na Reserva Natural Vale.* Rupestre, Belo Horizonte, pp. 157–166.

Sylvestre, L.S., Schwartsburd, P.B., Prado, J., Salino, A., Hirai, R.Y., Matos, F.B., Gonzatti, F., Dittrich, V.A.O., Weigand, A., Mynssen, C.M., Pena, N.T.L., Contaifer, L.S. & Caitano, H.A. (2019) Samambaias e Licófitas Ameaçadas no Espírito Santo. In: Fraga, C.N., Formigoni, M.H. & Chaves, F.G. (Eds.) Fauna e Flora ameaçadas de extinção no estado do Espírito Santo. Instituto Nacional da Mata Atlântica, Santa Teresa, pp. 124–135.

Thiers, B. (2020). *Index Herbariorum: a global directory of public herbaria and associated staff.* New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/science/ih/ (accessed 6 March 2020).

Trovó, M., Fraga, C.N. & Sano, P.T. (2016) *Paepalanthus capixaba* (Eriocaulaceae), a new microendemic species from Espírito Santo, Brazil. *Phytotaxa* 258: 83–88. https://doi.org/10.11646/phytotaxa.258.1.6

Tryon, R.M. (1942) A revision of the genus *Doryopteris. Contributions from the Gray*

Tryon, R.M. & Tryon, A.F. (1982) *Ferns and allied plants, with special reference to tropical America.* Springer-Verlag, New York, 857 pp.

Viveros, R.S. & Salino, A. (2015) Two new species of *Ctenitis* (Dryopteridaceae) from South America and taxonomic notes on similar species. *Phytotaxa* 239: 1–16. https://doi.org/10.11646/phytotaxa.239.1.1

Werneck, M.S., Sobral, M.E.G., Rocha, C.T.V., Landau, E.C. & Stehmann, J.R. (2011) Distribution and endemism of angiosperms in the Atlantic Forest. *Natureza & Conservação* 9: 188–193.

Windisch, P.G. (1992) *Pteridófitas da região Norte-ocidental do estado de São Paulo: guia para estudo e excursões.* 2ª ed. Universidade Estadual Paulista, São José do Rio Preto, 110 pp.

Windisch, P.G. (2014) Hymenophyllaceae no estado do Rio Grande do Sul. *Pesquisas. Botânica* 65: 15–48.