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Santalales in the Núcleo Curucutu, Parque Estadual Serra do Mar, São Paulo State, Brazil[1]

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ABSTRACT – (Santalales in the Núcleo Curucutu, Parque Estadual Serra do Mar, São Paulo State, Brazil). This paper consists in the taxonomic survey of the Santalales order in the Núcleo Curucutu, Parque Estadual Serra do Mar, São Paulo State, Brazil. The taxonomic treatment includes identification key, morphological descriptions, taxonomic notes, photographs, geographical distribution, and phenological data. The order is represented by four species: *Langsdorffia hypogaea* Mart., *Phoradendron crassifolium* (Pohl *ex* DC.) Eichler, *Phoradendron fragile* Urb., and *Struthanthus acuminatus* (Ruiz & Pav.) Kuijt.
Keywords: Balanophoraceae, Loranthaceae, parasitism, Santalaceae

RESUMO – (Santalales no Núcleo Curucutu, Parque Estadual Serra do Mar, Estado de São Paulo, Brasil). Este trabalho consiste no levantamento taxonômico da ordem Santalales no Núcleo Curucutu, Parque Estadual Serra do Mar, Estado de São Paulo, Brasil. O tratamento taxonômico inclui chave de identificação, descrições morfológicas, notas taxonômicas, fotos, distribuição geográfica e dados fenológicos. A ordem está representada por quatro espécies: *Langsdorffia hypogaea* Mart., *Phoradendron crassifolium* (Pohl *ex* DC.) Eichler, *Phoradendron fragile* Urb. e *Struthanthus acuminatus* (Ruiz & Pav.) Kuijt.
Palavras-chave: Balanophoraceae, Loranthaceae, parasitismo, Santalaceae

Introduction

The order Santalales Berchtold & J. Presl comprises 14 families, 151 genera, and 1,992 species, its distribution spans all continents except Antarctica, with the highest diversity concentrated in tropical regions (Stevens 2001 onwards). In Brazil, 11 families are present, and in the São Paulo State, eight families occur (Flora e Funga do Brasil 2024).

Santalales contains the largest number of species among the parasitic plant lineages, these species depend nutritionally on other plants, developing a structure of connection and absorption called haustorium (analogous to the root). The haustorium extends beyond the organs and tissues of the parasite, reaching the hosts, and the contact region is termed the "haustorial system". The representatives of the order still include simple leaves, valvate perianth, free-central pendulous placentation, and fruits with one seed (Kuijt 1969, Su *et al.* 2015, Nickrent 2020).

The representatives of these plants are generally recognized as agricultural pests, but they also play a fundamental role in natural ecosystems, primarily serving as a food source for various animal species (Watson 2001, Nickrent 2020). These parasites establish positive interactions with other species within the community, influencing competition, nutrient cycling, and overall community biodiversity (Nickrent 2020). The most well-known species in the order is *Santalum album* L. (sandalwood), its wood of is extensively used in craftsmanship, cosmetic products, and religious rituals (Barreto 2017).

Other families of Asterids has been previously investigated in the study area, such as Gentianaceae (Pscheidt & Affonso 2008) and Ericaceae (Takeuchi & Affonso 2009). This study is a part of the Flora of Núcleo Curucutu project, conducted through a collaboration between Universidade Santo Amaro (UNISA) and the PMSP Herbarium.

In order to progress in the taxonomic investigation of Santalales in the Núcleo Curucutu, we carried out collections, identifications, descriptions, taxonomic notes, photographs, an identification key, analysis of geographic distribution, and data of flowering and fructification of the species.

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Material and methods

The Núcleo Curucutu, located in the Parque Estadual Serra do Mar, encompasses a total area of 332,000 hectares, spanning the municipalities of Itanhaém, Juquitiba, Mongaguá, and São Paulo. It has an altitude ranging from 750 to 850 meters. The annual precipitation ranges between 2000-3000 mm/year, showcasing a temperate climate with hot and rainy summers and milder winter temperatures. The predominant vegetation comprises cloud forests and grasslands (Bellato & Mendes 2002, Secretaria de Meio Ambiente, Infraestrutura e Logística 2024).

This study utilized specimens from the Núcleo Curucutu, which had been previously collected, along with specimens collected in August 2022. Collection, preservation, and herborization of the botanical material followed the methodology of Fidalgo & Bononi (1989). After collection, the material was identified and deposited in the herbaria collections of PMSP, UNISA, and SP.

For identifications and descriptions, specialized literature was consulted (Kuijt 1969, Hansen 1980, Reif & Andreata 2011, Caires 2013, Dettke & Waechter 2014, Cardoso 2014, Kuijt & Hansen 2015, Dettke & Caires 2021). Santalales collections from SP and PMSP were consulted, in addition to the virtual herbaria: ESA, HRCB, SPF, and UEC (acronyms according to Thiers, continuously updated). Morphological terms from Harris & Harris (1994), Beentje (2010), and Gonçalves & Lorenzi (2011) were utilized. Flowering and fruiting data were extracted from the labels in the exsiccates.

Results and Discussion

For the Núcleo Curucutu, four species distributed among three families of Santalales have been recorded: *Langsdorffia hypogaea* Mart. (Balanophoraceae), *Phoradendron crassifolium* (Pohl *ex* DC.) Eichler, *Phoradendron fragile* Urb. (Santalaceae), and *Struthanthus acuminatus* (Ruiz & Pav.) Kuijt (Loranthaceae).

Identification key for Santalales of Núcleo Curucutu

1. Holoparasite of roots; shoot system reddish ..... *Langsdorffia hypogaea*
1. Hemiparasite of branches; shoot system green, brownish, or yellowish
   2. Epicortical roots present; branches with exfoliating rhytidome, lenticellate; cataphylls absent ..... *Struthanthus acuminatus*
   2. Epicortical roots absent; branches without exfoliating rhytidome, lenticels absent, cataphylls present
      3. Plants monoecious-dioecious, green; leaves expanded; spike biseriate ..... *Phoradendron crassifolium*
      3. Plants dioecious, brownish to yellowish; leaves squamiform; spike triseriate ..... *Phoradendron fragile*

Langsdorffia hypogaea Mart., J. Brasil. 2: 179. 1818. Figure 1 a-f

Holoparasite of roots, dioecious; shoot system reddish. Rhizome thick, cylindrical. Scales 0.5-2 × 0.3-0.6 cm, deltoid, margin ciliate. Staminate inflorescence 3-7× 0.5-2 cm, cylindrical to oblong. Staminate flowers 0.6-1 cm long, bracteate; pedicel 0.3-0.7 mm long; tepals 3, homomorphic; stamens 3, united, anthers ca. 0.1 cm long, connective inconspicuous. Pistillate inflorescence 2-4.5 × 2-4 cm, globose, pistillate flowers ca. 0.15 cm long, without bracts, sessile; tepals 3, homomorphic; style 1, ca. 0.5 mm long, exserted. Fruits not observed.

Examined material: Brazil. São Paulo: Itanhaém, Parque Estadual Serra do Mar, Núcleo Curucutu, Trilha do Rio Branco, 28-IV-2000, fl., *R.J.F. Garcia 1993* (PMSP).

Additional examined material: Brazil. São Paulo: Embu Guaçu, Sítio no Bairro Penteado, 9-IX-2006, fl., *S. Watanabe s.n.* (PMSP 9534); São Paulo, Parque do Estado, fl., 8-V-1931, *F.C. Hoehne s.n.* (SP 27517); Parque Jabaquara, 7-V-1939, fl., *G. Hashimoto 150* (SP).

Langsdorffia hypogaea is widely distributed, occurring from Mexico through Central America to South America, in Colombia, Guyana, Ecuador, and Bolivia (Hansen 1980). In Brazil, it can be found in the Amazon Rainforest, Caatinga, Cerrado, Atlantic Forest, and Pantanal. It has distribution in the Distrito Federal and in the States of Bahia, Ceará, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rondônia, Santa Catarina, São Paulo, Sergipe, and Tocantins (Cardoso 2024).

According to Melo & Alves (2013), its flowering occurs between June and December. In the Núcleo Curucutu, it was recorded only once, with flowers in April. The collected material showed only staminate inflorescences.

Caires *et al.* (2023) indicate the species occurring in leaf litter. The material from the Núcleo Curucutu was also found under the same conditions.

Langsdorffia hypogaea is similar to *Langsdorffia heterotepala* L.J.T. Cardoso, R.J.V. Alves & J.M.A. Braga, being the only species of the genus occurring in Brazil. They can be differentiated since *L. hypogaea* has homomorphic tepals and inconspicuous connectives, whereas *L. heterotepala* has heteromorphic tepals and conspicuous connectives.

The species is easily distinguished from other parasites in the study area as it is the only one that the shoot system is entirely reddish and is consistently found in the soil, as it parasitizes hosts through the roots.

Phoradendron Nutt.

Hemiparasites of branches, perennial; dioecious or monoecious-dioecious; occurring in clusters or scattered on the host; glabrous; branches of variable color; branches emerging from the haustorial connection 1-many. Branches

cylindrical to angular. Cataphylls present in all internodes or only in the proximal internodes of lateral branches; 1-7 pairs at the base or arranged along the internode; free or forming a sheath; fertile or sterile. Leaves opposite, entire, margins smooth, petiolate or sessile. Inflorescence in axillary spikes; segmented. Flowers with insertion, leaving foveas after dehiscence, monoclamydeous, actinomorphic, 3-merous, petals triangular, apex acute, erect; ovary inferior; nectariferous disc at the base of the style. Staminate flowers with epipetalous stamens, sessile to subsessile, poorly developed pistillode. Pistillate flowers with straight style, short, stigma concave, without staminodes. Fruits pomaceous-viscid with persistent petals, globose. Seeds ellipsoidal, flattened.

In Brazil, *Phoradendron* comprises 41 species, with 11 being endemic, distributed across all States and phytogeographical domains, with the highest diversity observed in the Amazon region. In the São Paulo State, 19 species are recorded (Dettke & Caires 2024).

Phoradendron crassifolium (Pohl *ex* DC.) Eichler, Fl. bras. 5(2): 125, Fig. 40. 1868.
Figure 2 a-f

Monoecious-dioecious; occurring in clusters on the host. Branches erect to pendant, cylindrical to angular, green; internodes 0.5-1 × 0.2 cm, the basal ones reaching up to 0.9 cm wide, nodes not thickened. Cataphylls present on all internodes, 5-7 pairs, 1 pair located 0.3-0.5 cm



Figure 1. a-f. *Langsdorffia hipogeae* Mart. a. Staminate inflorescences. b. Details of the inflorescence. c. Staminate flower. d. Pistillate inflorescences. e. Rhizome. f. Details of the inflorescence. g-l. *Struthanthus acuminatus* (Ruiz & Pav.) Kuijt. g. Branches. h. Lenticels. i. Inflorescences with pistillate buds. j. Inflorescences with staminate flowers. k. Staminate flowers. l. Fruits. Photos: Kelvin Mori: a-b, d-f; Juliana Bianchi: g, i, l; Leandro Vaz: c, h, j-k.

from the base, free. Leaves expanded; petiole 0.3-0.8 cm long; blades 5.5-11.5 × 1.5-7 cm, chartaceous, elliptic to obovate, base obtuse, apex acute to acuminate, venation palmate, 5 primary veins conspicuous on the adaxial and abaxial faces, 3 on the younger leaves. Inflorescences 1.5-2 cm long, biseriate, 1-2(-3) per axil; 1-4 pairs of sterile bracts at the base; 4-6 fertile segments; 3-6 flowers per fertile bract, fovea deep. Staminate flower ca. 1 cm diam., 1 apical, petals smooth. Pistillate flowers ca. 1 cm diam., below the apical, petals smooth. Fruit ca. 0.3 cm diam., smooth, yellow-orange to yellow, perianth slightly open. Seed 0.1-0.2 × 0.1 cm.

Examined material: BRAZIL. São Paulo: São Paulo, Parque Estadual Serra do Mar, Núcleo Curucutu, Trilha do Mirante, 13-XII-1997, fr., *R.J.F. Garcia et al. 1436* (PMSP, UNISA); Ao lado da casa do visitante, 29-VIII-2022, fl., *L.C. Vaz et al. 30* (SP).

Additional examined material: BRAZIL. São Paulo: Ubatuba, Núcleo Picinguaba, Trilha do Corisco, 10-XI-1993, fl., *F. Barros et al. 29833* (SP, SPF); Itupeva, 19-IV-1995, fl., *R. Simão-Bianchini et al. 683* (SP).

The species has a broad geographic distribution, ranging from Central America to the southern territory of Brazil (Kuijt 2003). In Brazil, it occurs in all States and phytogeographical domains (Dettke & Caires 2024).

Based on Dettke & Waechter (2014), it blooms and bears fruit throughout the year, with reproductive phenophases



Figure 2. a-d. *Phoradendron crassifolium* (Pohl *ex* DC.) Eichler. a. Reproductive branches. b. Fruits. c. Cataphyll. d. Fovea. e-i. *Phoradendron fragile* Urb. e. Arrangement of branches in the host. f. Detail of the fovea. g. Staminate flower. h. Pistillode pointed by arrow, stamens on the sides. i. Fruits. Photos: Mauricio Mercadante: a-b; Leandro Vaz: c-d, f-h; Juliana Bianchi: e, i.

pronounced between October and March. In the study area, it was collected only with fruits in October and December.

As indicated by Caires & Proença (2008), Dettke & Waechter (2014), and Dettke & Caires (2024), *P. crassifolium* is a generalist species in relation to its hosts. It was recorded parasitizing one Fabaceae species in the Núcleo Curucutu (*L.C. Vaz et al. 30*).

According to Dettke & Caires (2021), *P. crassifolium* is one of the most common mistletoes in Brazil, easily recognized by the presence of two to five pairs of fertile cataphylls, in addition to large leaves. In this study, the analyzed specimens presented up to two additional pairs of fertile cataphylls, reaching a total of seven.

Phoradendron crassifolium may be confused with *Phoradendron piperoides* (Kunth) Trel., however, while *P. crassifolium* exhibits palmate venation and fertile cataphylls at the nodes, *P. piperoides* displays pinnate venation and sterile cataphylls at the nodes.

It is the only species occurring in the study area that exhibits biseriate inflorescences and cataphylls on all internodes.

Phoradendron fragile Urb., Bot. Jahrb. Syst. 23, Beibl. 57: 13. 1897.
Figure 2 e-i

Dioecious; scattered on the host. Branches erect, cylindrical, brownish to yellowish-green; internodes 2-3 × 0.3-0.6 cm, the basal ones reaching up to 0.7 cm wide, nodes slightly thickened. Cataphylls only on the proximal internodes of lateral branches, 1-2 pairs. Leaves squamiform 0.8-0.9 cm long. Inflorescences 1-2.8 cm long, triseriate, 1 per axil; 1(-2) pairs of sterile basal bracts; 3-4 pairs of fertile bracts; 4-12 flowers per fertile bract, fovea shallow. Staminate flowers ca. 0.8-1 cm diam., petals papillose, greenish; stamens united by a tube attached to the pistillode. Pistillate flowers not observed. Fruit 0.5 cm diam., smooth to papillose, white-orange, perianth open. Seed 0.2 × 0.1 cm.

Examined material: BRAZIL. São Paulo: São Paulo, Parque Estadual Serra do Mar, Núcleo Curucutu, Trilha do Mirante, 13-VII-1997, fr., *R.J.F. Garcia et al. 1429* (PMSP, UNISA); 16-VI-2000, fr., *R.J.F. Garcia et al. 2017* (PMSP, SP, UNISA); Trilha Nova do Mirante, 29-VII-2022, fr., *L.C. Vaz et al. 31* (SP).

Additional examined material: BRAZIL. São Paulo: Tapiraí, Mata Pluvial Atlântica de Encosta, Rodovia SP 79, 11-V-1994, fl., *R. Mello-Silva et al. 2017* (HRCB, SP, UEC); Santo André, Trilha construída pela CESP, estrada da Torre, 31-I-1996, fl., *M. Sugiyama et al. 1407* (SP).

Phoradendron fragile is restricted to the Cerrado and Atlantic Forest of Brazil, occurring in the Distrito Federal and the States of Goiás, Minas Gerais, Rio de Janeiro, and São Paulo (Dettke & Caires 2024).

According to the analysis conducted by Reif & Andreata (2006), the species was collected with buds in May, flowers in November and December, and fruits in November. In the study area, it was collected only with fruits in August, October, and December.

Rizzini (1950) suggested that *P. fragile* could be a holoparasite. Dettke & Caires (2024) leave this possibility open. Due to the inconsistency of this data, we maintain the species as a hemiparasite, as with other species in the genus. However, we emphasize the absence of visibly green structures. Nevertheless, its branches exhibit some green pigmentation amidst the brown and yellowish coloration.

Rizzini (1950) also states that *P. fragile* is a species found in high-altitude locations, which explains its occurrence in the Núcleo Curucutu.

The species is considered a generalist (Dettke & Caires 2024). In the Núcleo Curucutu, it was found parasitizing a species of Melastomataceae (*R.J.F. Garcia et al. 2017*).

Phoradendron fragile can be confused with *Phoradendron tunaeforme* (DC.) Eichler, as both are leafless. However, while *P. fragile* has cylindrical branches that are brownish to yellowish-green, *P. tunaeforme* exhibits dorsiventrally flattened green branches.

The species distinguishes itself from others in the study area by featuring triseriate inflorescences and branches that are brownish to yellowish-green.

Struthanthus acuminatus (Ruiz & Pav.) Kuijt, Phytologia 98(2): 118. 2016.
Figure 1 g-l

Hemiparasites of branches. Epicortical roots along the branches. Branches pendant, cinereous, with circular lenticels, rhytidome exfoliating; internodes 2-12 × 0.2-0.3 cm, nodes not thickened. Leaves opposite to subalternate; petiole 0.3-0.9 cm; blade 5.4-7 × 1-2 cm, lanceolate to elliptic, membranaceous, base rounded to obtuse, apex acute to acuminate, mucronate, venation eucamptodromous, midrib conspicuous on the adaxial surface, prominent on the abaxial surface. Inflorescence in spike to spiciform 2-5 cm long, 1-2 per axil; main peduncle 0.3-0.6 cm; 4-6 pairs of triads; bracts ca. 1 mm, deltoid. Staminate bud 0.4-0.5 cm, claviform, greenish, sessile; flower 5-6 mm, 6-merous, green to cream; calyculus ca. 1 mm, botuliform; 3 larger stamens ca. 5 mm, and 3 smaller stamens ca. 4 mm; pistillode 0.2 cm long. Pistillate bud 4-5 × 1 mm, cylindrical, greenish, sessile; flower 3-4 mm, 6-merous, green to cream; calyculus ca. 1 mm, botuliform; staminodes present; pistil ca. 3 mm. Fruit 0.4-0.5 × 0.2-0.4 cm, pyriform, brown, orange to blackened. Seed 0.3-0.4 × 0.2-0.3 cm, ovoid.

Examined material: BRAZIL. São Paulo: São Paulo, Parque Estadual Serra do Mar, Núcleo Curucutu, Floresta ribeirinha ao longo do Rio Mambu, 13-IV-2001, fr., *F.M. Souza et al. 126* (ESA); Trilha do Embu, 22-VIII-1997, fl., *P. Affonso et al. 99* (UNISA); Trilha do Campo, fl., 1-VII-1999, *L.C.Q.M.P. Sampaio 236* (PMSP, UNISA); Trilha da Mata, 26-VI-2001, fr., *M.A.S. Mayworm & R.J.F. Garcia 223* (UNISA); Trilha do Mirante, 13-XII-1997, fl., *R.J.F. Garcia et al. 1409* (PMSP, UNISA); Trilha Nova do Mirante, 28-IV-2000, fr., *M.A.S. Mayworm et al. 163* (UNISA); 29-X-2022, fl., fr., *L.C. Vaz et al. 29* (SP).

Distributed in Argentina (Abbiatti 1946) and in Brazil in the States of Alagoas (Costa 2021), Minas Gerais,

Paraíba (Vasconcellos & Melo 2015), Rio de Janeiro (Reif & Andreata 2011), Rondônia, and São Paulo (Caires & Dettke 2024).

Struthanthus acuminatus blooms year-round and bears fruit between March and August (Vaz *et al.* in press). In the Núcleo Curucutu, flowers were collected in August, October, and December, while fruit collections occurred in April, June, July, and October.

The material *R.J.F. Garcia et al. 1409* is the only one throughout the São Paulo State to exhibit a spiciform inflorescence (Vaz *et al.* in press).

In the Núcleo Curucutu, the only host record was from a Fabaceae species (*L.C. Vaz et al. 29*).

Struthanthus acuminatus is morphologically similar to *Struthanthus salicifolius* (Mart.) Mart., but they can be distinguished due to *S. acuminatus* exhibits epicortical roots along the branches, without the formation of a woodrose and hexamerous staminate flowers, whereas *S. salicifolius* has branches with reduced woodrose formation and the absence of epicortical roots, with staminate flowers being tetramerous.

The species distinguishes itself from others in the study area by featuring pendulous branches with exfoliating bark, mucronate leaf blades, and flowers with a calyculus.

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Conflict of interests

There is no conflict of interest.

Author contributions

Andreia de Abrantes Pereira: Contribution in identification of the studied species; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Jaislla Mariane Mendes Ramos: Contribution in identification of the studied species; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Marco Aurélio Sívero Mayworm: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Leandro Matheus de Carvalho Vaz: Contribution in the concept and design of the study; Contribution to data collection and identification of the studied species; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

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