



Review

Floral structure of *Philodendron propinquum* (Araceae) and a comparative study of the *Philodendron* subgenera

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ABSTRACT

Philodendron flowers are numerous, small, unisexual or sterile, without perianth and exclusively pollinated by beetles, representing an Angiosperm-ancient pollination syndrome. Species of the genus are traditionally classified under three subgenera, *P. subgenus Philodendron*, *P. subgenus Meconostigma*, and *P. subgenus Pteromischum*. In recent phylogenetic analyses, two main lineages of *Philodendron* were recovered, *Meconostigma* and a *Pteromischum* + *Philodendron* lineage. Although a modest advance in the knowledge of the evolutionary history of the genus has been made, little attention has been paid to floral morphology in this group, in particular to structural studies on flowers of *P. subgenus Pteromischum* in light of pollination biology. Our aims were (i) to investigate the flower structure of *P. propinquum* (*P. subgenus Pteromischum*) through light and scanning electron microscopy and histochemistry; and (ii) to compare relevant floral characters among the three subgenera. Flowers of *P. propinquum*, which is endemic to the Atlantic Forest, are described for the first time. The pistillate flower presents a shallow, broad compitum, and a large number of ovules per locule; pistillate and staminate flowers present subepidermal druses; sterile units present raphids and starch grains; the papillose epidermal cells from sterile units and staminate flowers present terpene contents and stomata, probably representing diffuse osmophores. Our analysis suggests that the balance between pollen uptake (stylar lobes) and accessibility to the locules (stylar canals and compitum) were decisive to drive gynoeceum evolution of the *Philodendron* genus. The presence and location of druses and raphids in stamen and gynoeceum indicate a protective function against florivores.

1. Introduction

Among the several lineages of angiosperms, monocots exhibit a great diversity of floral shapes. Araceae is a typical example, and its basal position in the monocot lineage may offer important clues about how floral characters have evolved since the rise of the angiosperms. *Philodendron* Schott flowers are usually numerous, small (less than 0.5 cm diameter), sessile, unisexual or sterile, without a perianth (Mayo et al., 1997). The attraction unit is composed of staminate and pistillate flowers, and the sterile units are arranged in an inflorescence subtended by a spathe (Mayo et al., 1997). *Philodendron* species are pollinated exclusively by beetles (Gottsberger and Amaral, 1984; Gibernau and Barabé, 2000; Maia et al., 2010). This pollination syndrome is recurrent in basal clades, including Amborellales, Nymphaeales, Magnoliales,

Arecales, Alismatales, and Ranunculales (Paulino-Neto, 2014). Despite this essential and evolutionarily conserved relationship, there are no floral structure studies in light of pollination biology on *Philodendron*.

The genus *Philodendron* (8.6 Mya – Pliocene) emerged during the separation of the Atlantic Forest from the Amazon Forest (8.6 Mya – Pliocene, Loss-Oliveira et al., 2016a, 2016b). Species of *Philodendron* are traditionally classified under three subgenera, *P. subgenus Philodendron* (Schott), *P. subgenus Meconostigma* (Schott) Engler, and *P. subgenus Pteromischum* (Schott) Mayo (Mayo, 1989). The evolutionary relationships among the three subgenera, as well as the monophyly of the genus *Philodendron*, have been widely discussed in recent years (Calazans et al., 2014; Cusimano et al., 2011; Gauthier et al., 2008; Loss-Oliveira et al., 2016a, 2016b; Yeng et al., 2013). The most recent phylogenetic hypothesis suggests that *P. subgenus Meconostigma* is

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Table 1
Species list, acronyms and subgenus.

	Initials	<i>Philodendron</i> subgenus
<i>Philodendron bipinnatifidum</i> Schott ex Endl.	BI	<i>Meconostigma</i>
<i>Philodendron burle-marxii</i> G.M.Barroso	BM	<i>Philodendron</i>
<i>Philodendron goeldii</i> G.M.Barroso	GO	<i>Meconostigma</i>
<i>Philodendron insigne</i> Schott	IN	<i>Philodendron</i>
<i>Philodendron mellinoni</i> Brongn. ex Regel	ME	<i>Philodendron</i>
<i>Philodendron obliquifolium</i> Schott	OQ	<i>Pteromischum</i>
<i>Philodendron oblongum</i> (Vell.) Kunth	OB	<i>Pteromischum</i>
<i>Philodendron pedatum</i> (Hook.) Kunth	PE	<i>Philodendron</i>
<i>Philodendron propinquum</i> Schott	PR	<i>Pteromischum</i>
<i>Philodendron smithii</i> Engl.	SM	<i>Philodendron</i>
<i>Philodendron saxicola</i> A.C.Sm	SA	<i>Meconostigma</i>
<i>Philodendron tripartitum</i> (Jacq.) Schott	TR	<i>Philodendron</i>
<i>Homalomena wendlandii</i> Schott	HW	-
<i>Philodendron williamsii</i> Hook. f.	WI	<i>Meconostigma</i>
<i>Philodendron solimoense</i> A. C. Sm.	SO	<i>Meconostigma</i>

monophyletic, as well as the subgenera [*Philodendron* + *Pteromischum*] (Loss-Oliveira et al., 2016a, 2016b).

Despite the studies mentioned above, the species of the subgenus *Pteromischum* remain poorly studied and have been little represented in works using multiple approaches, including floral morphology. Species of *P.* subgenus *Pteromischum* occurs exclusively in Neotropical rainforests and are frequently endemic (Barbosa and Sakuragui, 2014). The 11 number of *P.* subgenus *Pteromischum* species are endemic in the Amazon Forest, nine species are endemic in the Atlantic Forest, and two occur both biomes (Barbosa and Sakuragui, 2014). Comparative floral morphological studies on different species of the genus *Philodendron*, and particularly of the *P.* subgenus *Pteromischum* species, are still lacking. Therefore, we aimed to analyze for the first time the flowers of *Philodendron propinquum* (*P.* subgenus *Pteromischum* and endemic of Atlantic Forest) and to compare them to the flowers of *Philodendron* subgenus *Meconostigma* and subgenus *Philodendron*.

2. Materials and methods

Plant material

Inflorescences (n = 7) at different development stages were collected from seven mature individuals of *P. propinquum* (*P.* subgenus *Pteromischum*) at the Tinguá Biological Reserve (Reserva Biológica do Tinguá), in the municipality of Nova Iguaçu, Rio de Janeiro State, Brazil (22°33'14"S; 43°27'13"W). Plants were monitored in the field during the flowering season (September through December 2014 through 2016) for collecting the inflorescences. Voucher specimens were deposited in the herbarium of the Museu Nacional, Universidade Federal do Rio de Janeiro (acronym R), and are labeled with their locality information and collector number, as follows: *P. propinquum* Schott, Tinguá, Rio de Janeiro, J.F. Barbosa 56; and *P. propinquum* Schott, Tinguá, Rio de Janeiro, J.F. Barbosa 57.

The terminology used to describe inflorescence and flowers followed Mayo (1989). The pollen terminology followed Hesse et al. (2009). The term “sterile unit” was used to indicate the units present in the inflorescence sterile zone since, a priori, they have no reproductive

Table 2

Select characters of the pistillate flowers, sterile units and staminate flowers from selected *Philodendron* species. Presence = + and Absence = -. Abbreviations has exposed in Frame 1.

	PR	OB	OQ	BI	SA	WI	GO	SO	PE	IN	ME	TR	SM	BM	HW
Stylar region without lobes	+	+	+	-	-	-	-	-	+	+	+	+	+	+	-
Shallow compitum	+	+	+	-	-	-	-	-	-	-	+	-	-	-	+
Many ovules per locule (more of 10 per locule)	+	+	+	-	-	-	-	-	-	-	+	-	-	-	+
Papillose epidermis – Sterile units	+	+	+	+	+	+	+	+	-	-	+	-	-	-	+
Papillose epidermis – Stamens	+	+	+	+	+	+	+	+	+	-	-	-	-	-	+
Drusiferous idioblasts in the subepidermal stratum – Stamens	+	+	+	-	-	-	-	-	+	+	+	+	+	-	+

function due to the incomplete development of gynoecium or androecium (Barabe and Lacroix, 2000; Barabé and Lacroix, 2001).

Light microscopy (LM)

The samples taken from the pistillate, sterile and staminate inflorescence zones were conserved in ethanol, dehydrated in an ethanol series, embedded in (2-hydroxyethyl)-methacrylate (Historresin® Leica, Wetzlar, Germany) (Gerrits and Horobin, 1991), and sectioned with glass knives at 3–4 µm on a RM2245 (Leica, Wetzlar, Germany) rotary microtome. The sections were stained with 0.05% toluidine blue (O'brien et al., 1964).

Histochemical tests were carried out to detect the presence of starch using Lugol (Johansen, 1940) and essential oils using the NADI reagent (David and Caerde, 1964). The NADI reagent test was conducted directly on free-hand sectioned fresh materials.

Observations, measurements, and photomicrographs were obtained using an Olympus BX-50 microscope (Olympus, Tokyo, Japan) with a digital CoolSnap Pro camera (1392 × 1040, 4.65-µm pixels).

Scanning electron microscopy (SEM)

The sterile units, pistillate, and staminate flowers were conserved in ethanol (Chamberlain, 1932), dehydrated in an ethanol series, critical point dried using a Bal Tec CPD 030 (Bal-Tec AG, Liechtenstein) critical-point dryer with CO₂, mounted on aluminum stubs with colloidal carbon, gold coated using a Bal Tec SCD 050 vacuum sputter coater, and examined using a JEOL – JSM-6490LV microscope, at 15, 20 or 30 kV. All images were processed using Adobe Photoshop CS5.

Comparative study of floral morphotypes

We collected data from 15 species of the genus *Philodendron* (5 *P.* subgenus *Meconostigma*, 6 *P.* subgenus *Philodendron* and 3 *P.* subgenus *Pteromischum*) and one *Homalomena* species from Mayo (1986), listed in Table 1. The morphological data shown in Table 2 was used to proceed with the morphological inferences in the Discussion section.

3. Results

The inflorescence of *P. propinquum* (Fig. 1. A) consists of a cylindrical spadix (n = 7; max = 8.1 cm; min = 5.0 cm long), surrounded by the spathe (n = 7; max = 8.3 cm; min = 5.2 cm long). The spadix proximal region, 24.2% (n = 7; max = 2.3 cm; min = 1.0 cm long), is occupied by pistillate flowers; the medial region, 9.3% (n = 7; max = 0.7 cm; min = 0.5 cm long), by the sterile units; the distal region, 66.5% (n = 7; max = 5.1 cm; min = 3.5 cm long), by the staminate flowers (Fig. 1B). Flowers are cylindrical or club-shaped, numerous, small (less than 1.5 mm long), sessile, without bracts, achramydeous, and unisexual or sterile.

Pistillate flowers

The syncarpous gynoecium comprises a terminal stigma, a straight, non-lobed, shallow and wide stylar region, and a wide ovary (Fig. 2A). The stigma has apical, long and unicellular trichomes, which secrete a polysaccharide exudate (Fig. 2B, C). The stylar region, in the longitudinal section, has a uniseriate epidermis and 22–26 parenchyma layers, with vascular bundles and idioblasts with druses or raphids. The compitum is shallow, with unicellular trichomes reaching the onset of the ovarian septum. The ovary, in cross-section, presents 3–4 multi-ovulate locules, with 50–60 ovules per locule (Fig. 2D). The ovary wall

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