ScienceDirect

Flora

Volume 240, March 2018, Pages 1-6

Review

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

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https://doi.org/10.1016/j.flora.2017.12.007

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Highlights

- Druses and raphides work as protection on both staminate and pistillate flowers.
- *P. propinqqum* presents osmophore in staminate flowers and sterile units.
- Osmophore is a common characteristic for staminate flowers in genus Philodendron..
- *P.* subgenus *Pteromischum* and *P.* subgenus *Philodendron* present shallow compitum.
- Pollen uptake and locules' accessibility were decisive in *Philodendron* evolution.

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.* subg. *Pteromischum* in light of pollination biology. Our aims were (i) to investigate the flower structure of *P. propinquum* (*P.* subg. *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 gynoecium evolution of the *Philodendron* genus. The presence and location of druses and raphides in stamen and gynoecium indicate a protective function against florivores.

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, Loss-Oliveira et al., 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, Loss-Oliveira et al., 2016b; Yeng et al., 2013). The most recent phylogenetic hypothesis suggests that *P*. subgenus *Meconostigma* is monophyletic, as well as the subgenera [*Philodendron* + *Pteromischum*] (Loss-Oliveira et al., 2016a, Loss-Oliveira et al., 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*.

Section snippets

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…

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…

Discussion

Our data shows that the pistillate flowers of *P. propinquum* (*P.* subg. *Pteromischum*) present the stigma region with unicellular trichomes that produce polysaccharide exudates. Also, the compitum and the stylar canals of *P. propinquum* are shorter compared to basal species of *P.* subg. *Meconostigma* (see Mayo, 1989). The compitum and stylar canal size of *P. propinquum* also corroborate the pattern found for other species of *P.* subg. *Pteromischum* (Mayo, 1989). The stigmatic surfaces play an essential…

Acknowledgements

We are grateful to the ReBio Tingua (RJ) staff for sharing their infrastructure, Paulo Roberto Martins, Weverson Cavalcante, Michel Ribeiro, and Rodrigo Theófilo for fieldwork support; Jardim Botânico of Rio de Janeiro staff and Dr. Reginaldo Trindade for methodological assistance; and Luana Calazans, for valuable suggestions to a late version of the manuscript. The first author gratefully acknowledges CAPES for awarding a grant of graduate studies in the period 2015–2016.…

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