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Estudos morfológicos e ontogenéticos com  
inflorescências e flores de *Lepidagathis* Willd.  
(Acanthaceae)

Morphological and ontogenetic studies with  
inflorescences and flowers of  
*Lepidagathis* Willd. (Acanthaceae)

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## RESUMO

A filogenia de Acanthaceae, sobretudo baseada em dados moleculares, confirma a monofilia da família, no entanto, ainda não se conhece uma sinapomorfia morfológica que a caracterize. Apesar de estar bem representada em nossa flora, a identificação de suas espécies é dificultada por problemas taxonômicos e pela falta de estudos morfológicos. A família apresenta muitas inconstâncias morfológicas dentro dos gêneros, por exemplo no padrão de inflorescências. *Lepidagathis* Willd. serve como exemplo, apresentando três tipos de inflorescências e morfologias florais divergentes que tem dificultado sua sistemática. Assim, explorando a morfologia, anatomia, vascularização e desenvolvimento das inflorescências e flores, foi possível encontrar homologias entre as espécies estudadas a especular sobre sua evolução. Descobriu-se que os padrões das inflorescências são formas enriquecidas ou escassas da mesma arquitetura. Em algumas espécies, existem mais ou menos meristemas reprodutivos nas axilas das brácteas e, portanto, mais ou menos possibilidades de desenvolvimento de flores e inflorescências parciais. A filogenia disponível para o grupo sugere que há uma probabilidade igual de ganho ou perda dos meristemas reprodutivos nas inflorescências. O desenvolvimento dos verticilos florais nas espécies estudadas é igual, apesar das diferenças na morfologia externa. No entanto, a vascularização revelou aspectos importantes sobre a evolução floral no gênero, mostrando que a anatomia pode reter características ancestrais que relacionam as espécies. Portanto, a disposição e o volume de flores por inflorescência e o tamanho e arranjo das flores tem mais chances de estarem relacionadas com a síndrome de polinização de cada espécie. Os resultados corroboram a circunscrição atual de *Lepidagathis* e encorajam mais investigações com as espécies de Acanthaceae que possam levar a descobertas importantes sobre homologias e ajudar nos estudos filogenéticos com a família.

**Palavras-chave:** anatomia, Barlerieae, desenvolvimento, evolução, Lamiales, vascularização.

## ABSTRACT

The phylogeny of Acanthaceae, chiefly based on molecular data, confirms the monophyly of the family, however, a morphological synapomorphy to characterize it is still unknown. Apart from being well represented in our flora, the identification of its species is quite difficult due to taxonomic problems and lack of morphological studies. The family presents many morphological instabilities within genera, for example with the pattern of inflorescences. *Lepidagathis* Willd. serves as an example, presenting three types of inflorescence and divergent floral morphologies that have challenged its systematics. Therefore, exploring the morphology, anatomy, vascularization and development of the inflorescence and flowers, it was possible to find homologies between the studied species and speculate around its evolution. The patterns of the inflorescence were discovered to be enriched or depleted forms of the same architecture. On some species, there were more or less reproductive meristems on the axil of bracts, and therefore, more or less possibilities of developing flowers or partial inflorescences. The available phylogeny for the group suggests an equal probability of gain or loss of such reproductive meristems on the inflorescences. The development of the floral whorls on the studied species was the same, despite their different external morphology. Nevertheless, the vascularization of the flowers revealed important aspects of the floral evolution of the genus, showing that the anatomy may retain ancestral characteristics that relate the species. Thus, the display and volume of flowers of each inflorescence, and the size and arrangement of the flowers are more likely related to the pollination syndromes of each species. The results corroborate the current circumscription of *Lepidagathis* and encourages further investigations with Acanthaceae species that may lead to interesting discoveries on homologies and assist the phylogenetic studies with the family.

**Key words:** anatomy, Barlerieae, development, evolution, Lamiales vascularization.

## INTRODUCTION

### **Acanthaceae Juss.**

Acanthaceae has approximately 200 genera and over 3500 recognized species distributed throughout the tropics and sub-tropics, rarely reaching the temperate zones (Olmstead, 2012). Around 40 genera and 449 species are estimated to occur with a broad distribution through Brazil, mainly on the Semideciduous Seasonal Forests inland (Profice *et al.*, 2015). However, their natural habitats are in a process of degradation, and, despite the family's abundance in the Brazilian flora, a great number of non-catalogued New World species are endangered (Wasshausen, 1975; Giulietti *et al.*, 2005, McDade *et al.*, 2008; Wanderley *et al.*, 2009).

The Acanthaceae are herbs, plants with climbing habits, shrubs, often growing extensively tall, and even small trees. The phyllotaxis is mainly decussate, with some species presenting a congest whorled phyllotaxis, and the leaves are simple with entire or, less frequently, toothed margins. The flowers are pentamerous, gamosepalous and gamopetalous, usually with a bilabiate corolla showing different degrees of zygomorphism. The androecium has four functional stamens, or two functional stamens and two staminodes, or, less frequently, a fifth staminode or only two functional stamens. The gynoecium is syncarpic, bicarpellary, superior, the style is terminal, and the ovary is bilocular, each locule with 2-10 ovules attached to the central septum. There is usually an annular nectary around the base of the ovary. The fruit is a loculicidal capsule, or, less often, a berry. Another common feature of these plants is the spike or thyrses inflorescence, made by decussate conspicuous bracts and a pair of bracteoles before each flower (Braz *et al.* 2002, Wasshausen & Wood 2004, Souza & Lorenzi 2012). Other frequent morphological aspects are the presence of cystoliths on vegetative organs (Solereder 1908, Patil & Patil 2011) and the presence of a retinacula (lignified funicle) sustaining the

seeds on the explosive capsules (Tieghem 1908, Wortley *et al.* 2005). Both are key features that help identify subfamilies and tribes (Scotland & Vollesen 2000, McDade *et al.* 2008). Since the relations amongst the families of the Lamiales are not yet clearly defined, other families related to Acanthaceae also share these characteristics (Stevens, 2001 onwards; Schäferhoff *et al.* 2010; Refulio-Rodriguez & Olmstead, 2014). Therefore, the family lacks a morphological synapomorphy to characterize it (McDade *et al.* 2012).

Driven by the need for new approaches to resolve the family's and its taxa delimitation, some researchers have been concentrating their analysis on phylogenetic studies based on molecular data. It has helped define and support infra-familiar relations (Schwarzbach & McDade 2002, McDade *et al.* 2005, McDade *et al.* 2012) and the monophyly of the family (Scotland *et al.* 1995, McDade & Moody, 1999, Scotland & Vollesen 2000, McDade *et al.* 2008).

The association of the molecular data and studies of the external morphology, like type of corolla aestivation and pollen morphology, have resulted in the recognition of three subfamilies in Acanthaceae (Scotland & Vollesen 2000). Nelsonioideae is the subfamily with more symplesiomorphies that reappear in later groups (Wenk & Daniel 2009). Thunbergioideae has species with climbing habits, flowers with reduced calyx and only two prophylls preceding them, amongst other characteristics which are autapomorphic of this clade (Borg *et al.* 2008, Borg & Schönenberger 2011). Acanthoideae, referred to as Acanthaceae *s.s.*, has as synapomorphy the presence of the retinacula on the explosive capsule (Scotland & Vollesen 2000, McDade *et al.* 2008).

## Morphology, anatomy and ontogenetic studies

In Acanthaceae the external morphology of the vegetative organs is highly variable, for instance the size of leaves, which suffer changes according to environmental pressures and chromosome variations (Kameyama, 1995). It is usual that, within species belonging to the same genus, the inflorescences suffer small changes relative to the size of internodes and bracts, creating congest or sparse architectures. Such variations in morphology were also observed among specimens of a single population (Ramsey & Schemske 2002).

Acanthaceae presents a great diversity of inflorescence types, even within a single genus, such as *Lepidagathis* Willd. (Kameyama 2008). Spikes are a common inflorescence structure in the family, and are made of monochasia, usually sessile or sub-sessile, preceded by two small bracteoles and subtended by a conspicuous and colored bract, arranged around an indeterminate main axis (Wasshausen & Wood 2004, Souza & Lorenzi 2012). Eventually, on the axil of the bracteoles, there is the formation of floral buds, evidencing the determinate nature of this unit of the inflorescence (Sell 1969, Moylan *et al.* 2004). This kind of increment on the structure creates a thyrse, as in *L. alopecuroidea*, where the flowers are organized in decussate dichasia around an indeterminate axis.

The basic spike pattern often goes through reduction of flower production, with the extreme form becoming the solitary flower, like in *Thunbergia* Retz. and *Mendoncia* Vell. ex Vand., whose inflorescences are basically a single flower preceded by two prophylls (Schönenberger & Endress 1998). The extreme increase in flower production may also happen, developing complex and, many times, congest inflorescences with repeated units along the axis. The reduction of internodes and great amount of flowers grant the inflorescence a glomerulate aspect that is difficult to interpret, leading to vague or confuse descriptions, as for *Dicliptera* Juss. (Sell 1969).

When the flowers appear in opposite pairs, 90° across at each node on the axis of the inflorescence, this is considered a decussate spike, like that of *L. diffusa*. However, one of the bracts of the decussate pair might become sterile, characterizing a secundiflorous spike, such as in *L. floribunda*. As in *Lepidagathis*, other non-related genera of Acanthaceae have secundiflorous spikes where the sterile bract suffers a displacement in relation to the flower-bearing, or fertile, bract. Thus, the pairs turn alternate along the inflorescence axis, with the sterile bract of one pair becoming close to the fertile bract of the next pair (Kameyama 2008, Indriunas & Kameyama 2012).

The leaves of Acanthaceae are generally hypostomatic with diacitic stomata and subsidiary cells transverse to the pores. Non glandular and glandular trichomes are always present, and the head of the glandular trichomes is composed by a single or multicellular disk with vertical walls (Ahmad 1978, Patil & Patil 2011, Larcher & Boeger 2006). The xylem rays are narrow, the perforation plates of the vessel elements are simple, and the fibers might be septate and have simple pitting (Solereder, 1908).

The stem wood anatomy of the climbing species of Thunbergioideae is well studied because of the cambial variants. On these plants there are successive cambia, internal phloem, and new vascular bundles appearing at the boarder of the pith (Carlquist 2007, Angyalossy *et al.* 2012). Bicolateral bundles were observed in stems and leaves of species not related to the Thunbergioideae, like the African lineages of the Barlerieae tribe (Solereder 1908, Patil & Patil 2012).

The presence of cystoliths on the epidermis is an important characteristic of Acanthaceae *s.s.*, and was well characterized by Larcher & Boeger (2006) and Patil & Patil (2011, 2012). There are many studies with species used in popular medicine (Bhogaonkar & Lande 2012) and ornamental species (Zuffellato-Ribas *et al.* 2005). Other studies focus on the tropical species



that live under high temperatures, investigating the xeromorphic characteristics (Akhani *et al.* 2008; O'Neill 2010; Muhaidat *et al.* 2012).

Few developmental studies have been published with Acanthaceae, mostly focusing on the corolla ontogeny to resolve taxonomic issues, or its shape, correlating it with the clades evolution and pollination syndromes. Some studies have revealed important aspects to the taxonomy of groups, like the work of McDade & Turner (1997), who studied a group of species of *Aphelandra* R. Br. that present dark spots at the base of the bracts, classified as nectaries. Through anatomical investigations, the authors verified that these nectaries vary in number and size of glands, and thus serve as taxonomic identification characters.

The corolla of mature flowers of Acanthaceae have a constant morphology, apart from a few taxa that are characterized by peculiar floral features. An analysis of the aestivation of the corolla can reveal different patterns that help with classification and delimitation of taxa (Scotland & Endress 1994). Ontogenetic studies evidence evolutionary steps that are different or camouflaged on mature structures. It is the case of the corolla of *Avicennia* L., which is tetramerous at anthesis phase. However, at the beginning of development, five distinct primordia are found on the floral meristem, the upper two, later, connating and growing together (Nadia *et al.* 2013).

Scotland & Vollensen (2000), assisted by molecular biology, conducted one of the first general revisions of the classic phylogeny of Acanthaceae, since the Works of Lindau (1895 *apud* Scotland & Vollesen 2000) and Bremekamp (1965), which were based on corolla aestivation and pollen morphology. The general conclusion is that the lack of profound morphological studies to elucidate the nature of certain structures makes it difficult to position certain groups, despite the molecular techniques.

The curious inclusion of *Avicennia* in the family, attested by molecular studies, could have been less intriguing if the morphology of this mangrove genus and its sister clade, the

Thunbergioideae, were better understood. The construction of the clade was tested by Schwartzbach & McDade (2002), based on three genetic sequences of DNA from the nucleus and chloroplast, and the analysis showed the clade to be well supported. However, the authors point to morphological evidences that would position *Avicennia* closer to the Acanthoideae subfamily. Anatomically, *Avicennia* is recognized by the presence of successive cambia on the stem (Zamski, 1979; Carlquist, 2007), besides other characteristics resulting from its convergent evolution with other woody species from the mangrove. Nevertheless, cambial variants are also present on lianas from the Thunbergioideae subfamily (Angyalossy *et al.* 2012). In this case, ecological and ontogenetic studies can acknowledge which are homologous characteristics, supporting the molecular analysis and requesting new studies with different groups and structures. Following this lead, Borg & Schönenberger (2011) analyzed the floral development in *Avicennia* and the Thunbergioideae. They found many synapomorphies regarding the ovules, and similarities between the androecium and the corolla aestivation that endure the clade. The authors call attention to the fact that other morphological aspects could establish the relations between the taxa, like the inflorescence structure, however the evolution of these traits is not known for the family, and, thus, can guide to misleading conclusions.

An opposite case, the segregation of *Thomandersia* Baill from Acanthaceae, was supported by studies with the fruits development. Wortley *et al.* (2005) verified that the retinacula from the *Thomandersia* fruits are homoplastic to those characteristic of the Acanthoideae subfamily, presenting an example of parallel evolution within the Lamiales. Therefore, the genus was elevated to the rank of family, as Thomandersiaceae Sreem. Other particular structures have interested new researches, like on the Ruellieae tribe where the connated basal portion of the stamens' filaments create a "filament curtain", partitioning the corolla tube (Manketlow 2000, Moylan *et al.* 2004, Tripp *et al.* 2013). Thus, on account of such discoveries, the knowledge of the morphology and anatomy of Acanthaceae must continue to

grow. Analysis that investigate the true nature of structures on this family collaborates with other areas of study, not only for the family, as for the Lamiales.

### *Lepidagathis* Willd.

*Lepidagathis* has approximately 100 species with pantropical distribution (Durán & Ramírez 2011). In Brazil there are 16 known species, mainly on semideciduous and tropical rain forests on the middle west and southwest of the country (Silva & Nogueira 2012, Profice *et al.* 2015). This genus is located in the Barlerieae lineage, characterized by the quincuncial aestivation of the corolla, inside a clade within the Acanthoideae subfamily that has as sinapomorphy the presence of cystoliths on vegetative organs (Fig. 1) (Scotland & Vollesen 2000; McDade *et al.* 2008).

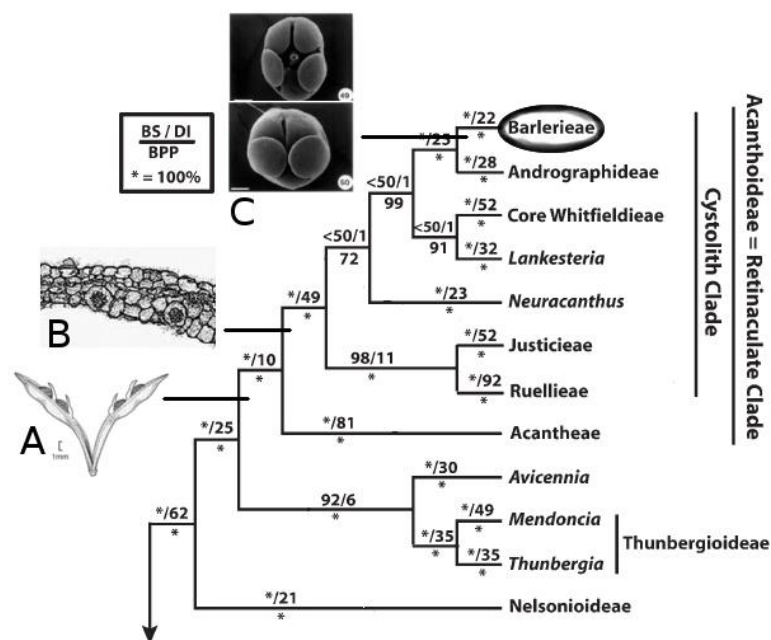


Fig. 1. Simplified phylogenetic tree of Acanthaceae (adapted from McDade *et al.* 2008). (A) Capsule fruit of *Stenostephanus lyman-smithii* Wassh. (Wasshausen & Wood 2004). (B) Cystoliths on the leaf epidermis of *Hemigraphis alternata* (Burm. f.) T. Anderson (Moylan *et al.* 2004). (C) Developing corolla of *Crabbea velutina* S. Moore (Scotland & Endress 1994).

*Lepidagathis* has four didynamous stamens, the anterior pair bitheous and the posterior pair with monotheous or bitheous anthers, sometimes reduced to staminodes or completely missing. The fruit is a capsule with oblong outline, thin walls and the seeds are recovered by hygroscopic trichomes that expand when hydrated, secreting a mucilaginous substance (Schnepf & Deichgräber 1983, Wasshausen & Wood 2004, Kameyama 2008). In some species, the calyx appears to be tetramerous, with unequal sepals. However, a closer examination reveals that the anterior segment is constituted by the two anterior sepals that are connate with various degrees of fusion amongst the species (Benoist 1911).

The anterior sepals' fusion was used to separate two genera: *Lepidagathis*, with a pentamerous calyx where the anterior sepals were connate only at the base, and species mainly paleotropical; and *Lophostachys* Pohl, in which the anterior sepals could have more than  $\frac{1}{3}$  of its margins connate, so the calyx appeared to be tetramerous, and its species were restricted to the neotropics, with the diversity center in Brazil. Later, based on the different architectures of the inflorescences, about 10 neotropical species were attributed to a new genus *Teliostachya* Nees, with thyrses made by dichasia displayed around an indeterminate axis in opposition to the simple spikes of the other species (Kameyama 2008). Divergences and misinterpretations of the pollen morphology, number of stamens and geographical distribution were also taken in account to separate the three genera, but an analysis of these characters showed them to be too variable. Therefore, Kameyama (2008) put *Lophostachys* in synonymy with *Lepidagathis*. Some authors have been treating *Teliostachya* under *Lepidagathis* as well, but further studies with the development of its inflorescences may reveal and corroborate this inclusion (Wasshausen & Wood 2004; Kameyama 2008).

## AIMS

- Analyze the development of the three inflorescence architectures, the fusion of the anterior sepals and the androecium constitution;
- Hypothesize about the patterns of evolution of such traits in the genus, in account of reduction or enrichment of structures.

To achieve the proposed aims, the dissertation was divided into two chapters written in a manuscript format.

## CONCLUSIONS

Considering the diversity of inflorescence architectures and floral morphologies and the obscure taxonomy of the genus, *Lepidagathis* proved to be a prominent model for morphological and developmental studies to understand its evolution. The investigations of this dissertation provided base information, with which it is now possible to hypothesize about evolutionary trends. On the inflorescences, it was proposed that a reduction of reproductive meristems on the inflorescences, creating patterns like the secundiflorous spike, or an increment of reproductive meristems on the axil of bracteoles, that creates the thyrses pattern of inflorescence, have the same probability of having occurred on the evolution of the group. The constant tetramery of the androecium was proved by the presence of vascularization, even on flowers with only two stamens, and the probable extinction of the vascular traces, as a fifth trace was only found on one species. The study of the floral anatomy revealed an intriguing characteristic of the ovaries of *Lepidagathis*, and may be extended to Acanthaceae s.s. The recognition of a marginal fusion of the carpels is important considering phylogenetic homologies and proves that anatomical investigations have a critical value to botanical studies.

Therefore, studying the ontogeny of an organ, a solitary flower or a whole inflorescence, is important, for only then the activity of the meristems that will lead to its final morphology are able to be accompanied. By analyzing the origin and sequence of emergence of the primordia and its anatomy, it is possible to look for homologies and reflect about the fusions and reductions on the plant body. These factors are essential to comprehend the phylogenetic relations between the taxa and contribute with the knowledge of our flora.

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