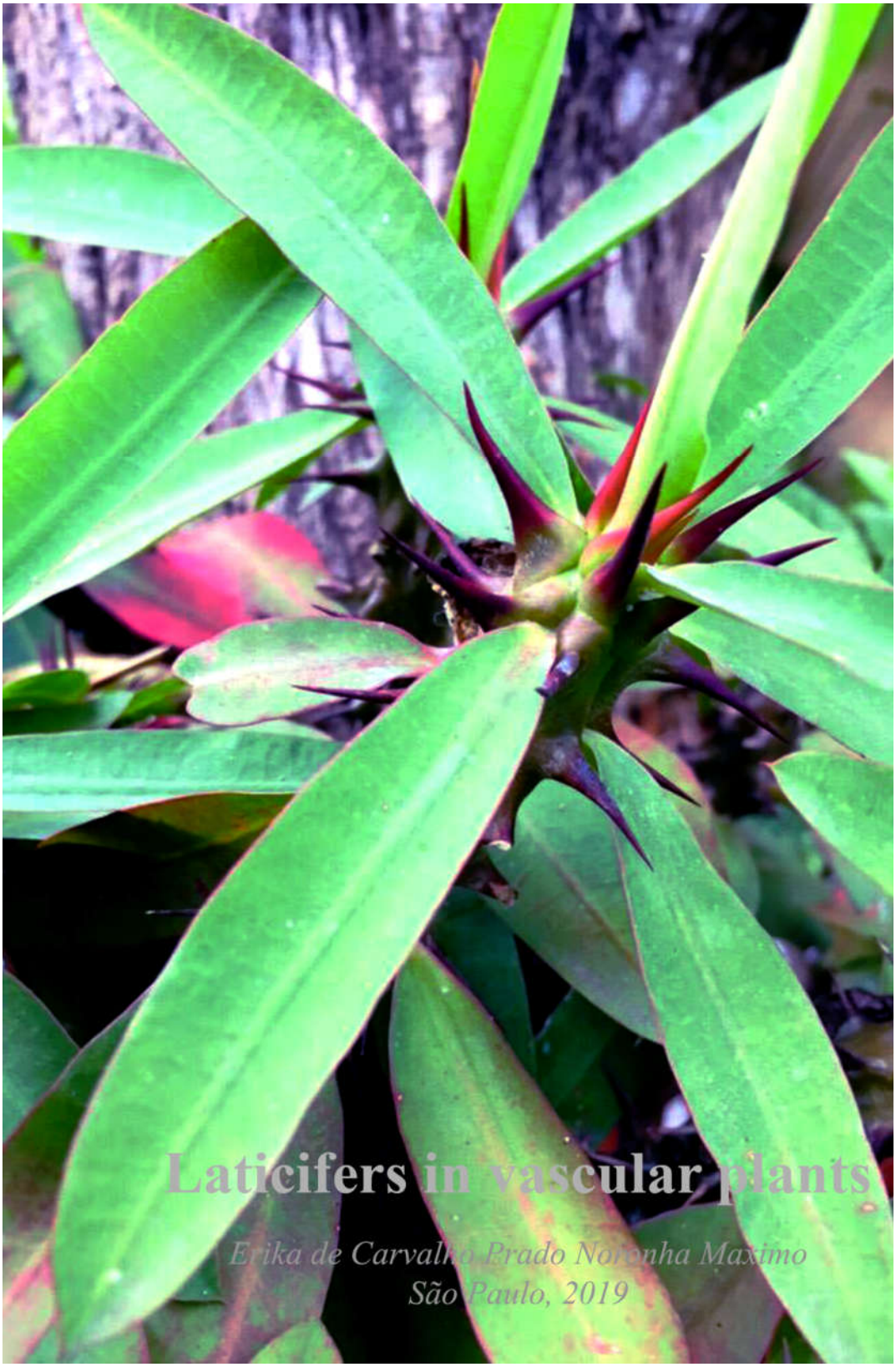

Laticifers in vascular plants

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São Paulo, 2019

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Laticíferos nas plantas vasculares

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção do título de Mestre em Ciências, área de concentração em Botânica

Orientador: Prof. Dr. Diego Demarco

São Paulo
2019

RESUMO

Os laticíferos são células especializadas que secretam látex, uma complexa mistura de metabólitos que tem como principal função a defesa contra a herbivoria. Os laticíferos estão presentes em diversas famílias de plantas vasculares e sua ocorrência é considerada um indicador taxonômico e, muitas vezes, filogenético. Há inúmeras interpretações equivocadas na literatura, atribuindo a presença de laticíferos em famílias que não os possuem. Desta forma, uma ampla revisão sobre esta estrutura e sua real distribuição e evolução se faz necessária. Os objetivos do presente trabalho são caracterizar e distinguir os laticíferos de outras estruturas secretoras, avaliar comparativamente a composição do látex nas diferentes famílias de plantas latescentes e identificar o tipo de laticífero em cada família com base em sua ontogênese. Verificamos que, embora haja semelhança de cor e diversidade de metabólitos na secreção dos laticíferos e de alguns ductos resiníferos, o látex é uma secreção intracelular que corresponde ao próprio protoplasto dos laticíferos, enquanto a resina dos ductos é uma secreção extracelular que não possui componentes estruturais em sua composição. Além disso, látex é uma secreção específica dos laticíferos e laticíferos são conceitualmente fileiras de células, enquanto ductos são formados por um epitélio que delimita um lume, não se enquadrando em sua classificação. Quanto aos metabólitos presentes no látex, identificamos lipídeos, proteínas, compostos fenólicos, carboidratos e alcalóides nas diferentes famílias de plantas latescentes, evidenciando a grande convergência evolutiva que ocorreu nas diferentes linhagens de plantas vasculares. Em relação à distribuição dos laticíferos, verificamos que das 63 famílias analisadas, apenas 34 possuem látex em pelo menos um de seus representantes. Muitas dessas famílias não têm relação filogenética, demonstrando que os laticíferos surgiram múltiplas vezes na evolução das plantas vasculares. Demonstramos que 18 famílias ditas latescentes, na verdade, possuem ductos resiníferos ou idioblastos secretores. Também verificamos que todos os laticíferos são articulados, podendo ser classificados como anastomosados ou não anastomosados, ramificados ou não ramificados, refutando a existência dos laticíferos classificados como não articulados. Por fim, também refutamos a teoria do crescimento autônomo intrusivo por não haver indícios de sua ocorrência em nenhuma das dezenas de famílias analisadas. Esse estudo traz uma contribuição muito significativa para o entendimento dos laticíferos quanto a sua identificação, composição do látex, distribuição, modo de crescimento e evolução nas plantas vasculares.

Palavras-chave: laticíferos, látex, distribuição, ductos resiníferos, idioblastos fenólicos, plantas vasculares.

ABSTRACT

Laticifers are specialized cells that secrete latex, a complex mixture of metabolites whose main function is defense against herbivory. Laticifers are present in several families of vascular plants and their occurrence is considered as a taxonomic and often phylogenetic indicator. There are many misinterpretations in the literature attributing the presence of laticifers in families that do not have them. Thus, a comprehensive review of this structure and its actual distribution and evolution is necessary. The objectives of the present work are to describe laticifers structurally, distinguishing them from other secretory structures and correcting any description errors; to comparatively evaluate the composition of latex in the different families of latescent plants; to identify the type of laticifer in each family based on their ontogenesis; and to evaluate their actual distribution and evolution in vascular plants. Although the secretions of laticifers and resin ducts are similar in color and the diversity of metabolites, latex is an intracellular secretion that consists of the very protoplast of laticifers, while the resin of ducts is an extracellular secretion that has no structural components in its composition. In addition, latex is a secretion specific to laticifers and laticifers are conceptually rows of cells, while ducts are formed by an epithelium that delimits a lumen; therefore, they do not fall under this classification. As for the metabolites present in latex, we have identified lipids, proteins, phenolic compounds, carbohydrates, and alkaloids in the various families of latescent plants, evidencing the important evolutionary convergence that occurred in the various lines of vascular plants. With relation to the distribution of laticifers, we have found that of the 63 families analyzed, only 34 have latex in at least one of their representatives. Many of these families have no phylogenetic relationship, demonstrating that laticifers emerged multiple times in the evolution of vascular plants. We have demonstrated that 18 so-called latescent families actually have resin ducts or secretory idioblasts instead of laticifers. We have also ascertained that all laticifers are articulated and can be classified as anastomosed or non-anastomosed, branched or unbranched, thereby refuting the existence of laticifers classified as non-articulated. Finally, we also refute the intrusive autonomous growth theory since there is no evidence of its occurrence in any of the latescent families. This study makes a very significant contribution to the understanding of laticifers regarding their identification, latex composition, distribution, growth and evolution in vascular plants.

Keywords: laticifers, latex, distribution, resin ducts, phenolic idioblasts, vascular plants.

General Introduction

A laticifer is a specialized cell or a row of latex-containing cells (Fahn 1979). The definition of this secretion has changed over several decades of study; however, nowadays, the whole protoplast of the laticifer is taken into consideration because when the plant is injured the entire cell content is released (Demarco *et al.* 2006, Demarco 2015, Prado and Demarco 2018, Ramos *et al*, 2019).

When present, laticifers generally occur in all vegetative and reproductive organs of the plant (Metcalfe and Chalk 1950; Demarco et al. 2006; Demarco and Castro 2008); however, there have been cases where their occurrence was restricted to certain organs of certain families (Metcalfe 1967, Lewinsohn 1991).

Latex is a complex mixture of metabolites such as lipids, proteins, carbohydrates, starch grains, mucilages, cardenolides, and alkaloids (Fahn 1979, Konno 2011, Demarco *et al.* 2013, Demarco 2015). Its primary function is defense against herbivory because many of its compounds are toxic. In addition, latex coagulates rapidly, thus sealing plant wounds and inhibiting the entry of pathogens such as bacteria and viruses (Wink 2008, Konno 2011, Bauer *et al.* 2014, Demarco 2015, Dussourd 2017).

Laticifers are present in several families of vascular plants, from ferns to the most derived angiosperm groups, often without phylogenetic relationship, demonstrating a polyphyletic origin (Metcalfe and Chalk 1950, Metcalfe 1967, Lewinsohn 1991, Prado and Demarco 2018). The occurrence of laticifers is considered as a taxonomic and often phylogenetic indicator in several groups.

The currently accepted classification of laticifers was defined by De Bary (1884), who divided them into articulated and non-articulated. Articulated laticifers are

rows of cells that can either keep their end walls intact (not anastomosed) or dissolve them (anastomosed). Non-articulated laticifers are individualized cells. Both types may or may not have ramifications (Esau 1977, Fahn 1979, Mahlberg 1993, Ramos *et al*. 2019).

Although the definition is simple, there are many misinterpretations in the literature attributing the presence of laticifers in families where they do not appear, often confusing them with resin ducts that produce a white secretion (Venning 1948, Mauseth 1978a, b, Wittler and Mauseth 1984).

Another point of divergence in the literature regards the growth of laticifers. Several papers support the theory of intrusive apical growth in non-articulated laticifers (Snyder 1955, Wilson and Mahlberg 1977, Mahlberg 1993) and in some articulated laticifers (Rudall 1994, Canaveze and Machado 2016, Canaveze *et al.* 2019). According to this theory, laticifers would develop in the intercellular spaces of plant tissues (Mahlberg 1993). Although this theory is hard to explain, many authors still support it (Canaveze and Machado 2016, Canaveze *et al.* 2019, Marinho and Teixeira 2018). However, this misconception stems from the observation of supposed acute apexes, often recorded as indications of this type of growth, but which are actually an oblique section to the apical cell of the laticifer due to the sinuous growth of this secretory structure (Demarco et al. 2006, 2013; Demarco and Castro 2008, Gama *et al*. 2017).

The objectives of this paper are to describe laticifers in a structural manner, distinguishing them from other secretory structures and correcting any description errors; to comparatively evaluate the composition of latex in the different families of latescent plants; to identify the type of laticifer in each family based on their ontogenesis; and to evaluate their actual distribution and evolution in vascular plants.

To meet these objectives, this dissertation has been divided into three chapters according to the manner in which it is intended to be published:

Chapter 1: Laticifers and secretory ducts: similarities and differences

Chapter 2: Plant latex and latex-borne defense

Chapter 3: Laticifers in vascular plants

General Conclusions

In our study, we have established that, although at times laticifers and resin ducts are similar in relation to the color of their secretion and the diversity of secretion compounds, latex is a secretion produced and stored inside the cell, both in the vacuole and in the cytoplasm. The latex is considered to be the entire laticifer protoplast, because when the plant is injured the entire cell content – that is, both the metabolites produced and the laticifers' membranes, organelles and nuclei – is released. On the other hand, resin ducts produce an extracellular secretion that has no structural components in its composition and is stored in an intercellular space called lumen. In addition, laticifers are conceptually rows of cells, while resin ducts are formed by an epithelium that limits the lumen.

The histochemical analysis of latex from plants of different families has also shown an important evolutionary convergence with latescent plants of different strains of vascular plants, and that the latex from any plant is composed of lipids (especially terpenes), proteins, phenolic compounds, carbohydrates and alkaloids, the latter being the only compound that might be absent.

Based on the correct identification of laticifers and the detection of latex, we have identified laticifers in 34 vascular plant families, distributed into 22 orders, often without phylogenetic relationship, showing that laticifers have emerged multiple times in the evolution of vascular plants. We also refute the occurrence of laticifers in 18 families considered latescent, which have only resin ducts or secretory idioblasts. Further, we have ascertained that all laticifers are articulated and can be classified as anastomosed or non-anastomosed, branched or unbranched, refuting the existence of laticifers classified as non-articulated. Finally, we also contest the intrusive autonomous growth theory since there is no evidence of its occurrence in any of the latescent families.

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