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Laticifers and Secretory Ducts: Similarities and Differences

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Abstract

During the evolution of terrestrial plants, many protective strategies have emerged, guaranteeing the survival of plants in the most varied environments. Among these strategies, we highlight the chemical defense of plants given by secretory structures, such as laticifers and secretory ducts. These glands are responsible for the production of viscous exudates that can be toxic, deterrent or repellent to herbivores, in addition to acting against microorganisms and sealing wounds. The similarities between latex and resin produced by certain ducts led several researchers to misinterpret their characteristics and generated a great number of divergences in the literature. This chapter aims to review the similarities and differences between laticifers and ducts and to demonstrate the structure, secretory activity and chemical composition of the secretion of each one, as well as the evolutionary and ecological aspects that can be associated with the high rate of survival and diversification of the plants that contain laticifers and/or ducts.

Keywords: evolution, latex, resin, tubular secretory systems, protection

1. Introduction

The huge biological diversity is responsible for relations between different species of plants, animals and microorganisms, with emphasis on the correlation between plants and insects. The interrelationships between these two groups of organisms are already well established in the evolutionary history of both. In addition, they may account for more than 75% of the current biodiversity [1] in both beneficial associations, such as pollination, and adverse relationships, such as herbivory [2–4].

Herbivory has important implications for the evolutionary processes of the plant community. Its analysis reveals a continuous evolutionary adaptation [5] in which the plants developed physical and chemical defense mechanisms, just as the insects co-evolutionarily improved molecular, physiological and behavioral components in response to these mechanisms [2, 4, 6–10].

Herbivory generates a negative impact on the plant and minimizes its growth, reproduction and its adaptability to the environment [11, 12]. Therefore, several defensive strategies are observed in different groups of plants that protect them against herbivores and pathogens. These strategies may be (1) physical defenses, like trichomes, calcium oxalate crystals and sclerenchyma, which provide greater hardness to plant tissue and prevent it from penetration and degradation [13–15] and (2) chemical defenses, through the production of secondary metabolites by secretory cells [3, 6, 16–21]. The secondary metabolites found in the different secretions (or natural products) include a great diversity of alkaloids, terpenoids, cyanogenic glycosides and phenolic compounds that are toxic and play a selective role in relation to the enemies, mainly against herbivory [10, 17, 19, 22, 23], thus enhancing the plant adaptive success in many environments [10, 18, 24].

2. Defensive secretory structures

Secretions are present in all groups of vascular plants and may be composed of a high diversity of secondary and/or primary metabolites [16, 19, 21, 25, 26] and have a well-defined ecological role. Although a single metabolite may predominate within a taxon, especially in the case of some alkaloids [19], when we consider the totality of compounds produced by plant secretory structures (or glands), they usually vary even within a species due to genotypic variations and abiotic conditions [25].

Different secretions are produced by specialized cells and can be directly released to the environment or stored in the plant in intracellular or intercellular sites [16, 21]. Secretory structures vary enormously in relation to their structural complexity, and may be composed of a single cell (e.g., idioblasts and some laticifers) or many cells, as in the case of more complex structures such as trichomes, colleters, nectaries, osmophores, secretory cavities and ducts, among others [2, 16, 20, 21, 27–29]. Some of these secreted compounds can be profoundly affected, with their production being increased or reduced when the plant is subjected to some form of stress, such as wounds, infections or variations of climatic or edaphic factors [19, 25, 30].

Among the defensive glands, we highlight the tubular secretory systems that can form an anastomosed and branched network throughout the plant, a similarity that has generated numerous errors of identification between laticifers and resin ducts due to the production of similar secretions [6, 17, 25, 29, 31]. What are the similarities and differences between these two secretory structures?

3. Laticifer and resin duct

Laticifers and ducts can occur as single structures that often anastomose forming an interconnected network through all organs of the plant, whose viscous and mostly terpenic secretion

is only released to the outside by the rupture of the secretory system. However, these are the only similarities. Misidentifications are mainly due to the observation of the appearance and color of the secretion in the field, since latex and resin possess predominantly the same classes of chemical compounds. On the other hand, laticifers and ducts are very different in terms of structure and secretory activity.

3.1. Laticifer

A laticifer is a single cell or a row of specialized cells that contain latex [16] (**Figure 1A**). When the laticifer is composed of a single cell, it is classified as non-articulated; when it is formed by a row of cells (**Figure 1B**), it is classified as articulated [32]. Although their classification and morphological variations are very subtle, the identification of the laticifer must be made in the light of an ontogenetic study of the structure, since some articulated laticifers observed in Apocynaceae and Euphorbiaceae can differentiate rapidly next to the promeristem (**Figure 1C**). In these cases, few cell layers away from the promeristem, the laticifer cells completely dissolve their terminal walls, becoming a continuous tube without border remains between the different cells that compose it (**Figure 1D**). Thus, this type of articulated laticifer resembles a single cell at maturity, which may or may not be branched (**Figure 1E**). This has generated numerous divergences in the literature over time, and more detailed studies of the apical portion of the laticifer have tried to unravel its mode of growth among the meristems.

Apparently, the non-articulated laticifer has a more complex development. Several researchers have reported a predetermined number of laticifer initials present in the embryo, which theoretically develop and branch through the entire body of the plant, regardless of its size [8, 33]. This unlimited elongation would result from an intrusive autonomous growth of the laticifer tip between meristematic cells. This way, this type of laticifer would present cell division without the occurrence of cytokinesis, forming a long multinucleated, coenocytic tube [9, 33–36] (**Figure 1F**). Although this type of growth has also been recorded for a few articulated laticifers [35, 37], several studies have demonstrated the impossibility of its occurrence due to the absence of a subcellular apparatus capable of constantly producing cell wall at the laticifer tip [38], besides the lack of records of karyokinesis within laticifers in the main families of latexiferous plants [7, 39, 40]. Thus, the possible unlimited growth of the laticifer needs to be reviewed, and the record of articulated and non-articulated laticifers in the same genus and even in the same species should be re-evaluated ontogenetically [7, 33, 35, 39–41], since the current data point to the absence of non-articulated laticifers in all the families in which they were described.

Latex is the laticifer's protoplast itself, which has most of the metabolites stored inside a large, central vacuole [7] (**Figure 1G and H**). This highly heterogeneous content forms a suspension or emulsion of many small particles in a fluid [16], whose typical color is milky white; however, depending on the latex composition, it may be red, orange, yellow, green and even colorless [7, 9, 10, 23, 30, 33, 34, 39, 42].

Although latex is a mixture of many distinct compounds, there is always a predominance of terpenoids in its composition [10, 40, 43] (**Figure 2A–C**). In general, these terpenoids are triterpenes or tetraterpenes, but rubber tree has up to 45% polyisoprenes (rubber) in its latex composition [30, 43, 44]. In addition, fatty acids, phytosterols, alkaloids, phenolic compounds, proteins, cardenolides, starch grains, among other compounds, have already been identified in the latex of many species [7–10, 30, 39, 42] (**Figure 2**).

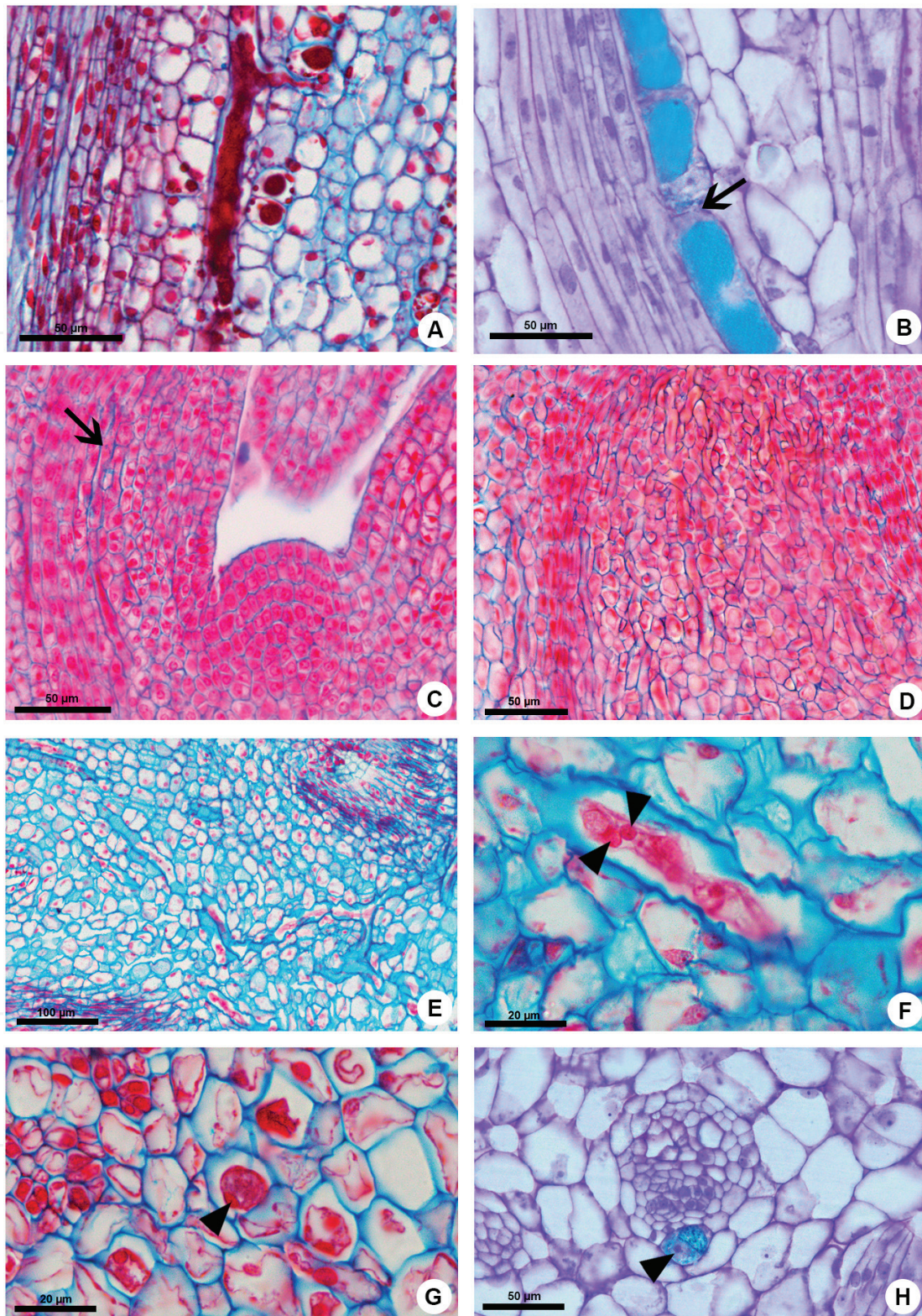


Figure 1. Laticifers. A, E–G. *Euphorbia milii* (Euphorbiaceae). B, H. *Musa paradisiaca* (Musaceae). C, D. *Thevetia peruviana* (Apocynaceae). A. Latex within the laticifer. B. Articulated laticifer. C. Laticifer ontogeny near the promeristem. D. Laticifer network. E. Branched laticifers. F. Multinucleated laticifer. G, H. Latex metabolites within the vacuole and peripheral nucleus. Arrow, terminal wall; arrowhead, nucleus.

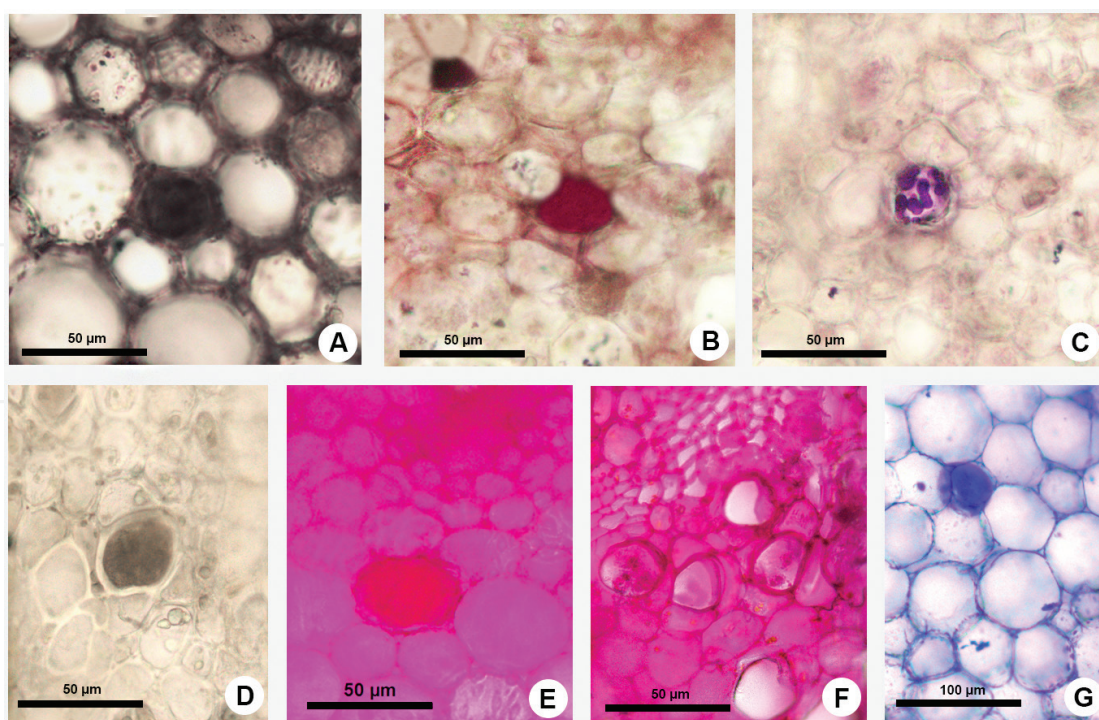


Figure 2. Histochemistry of the laticifers of *Hura crepitans* (Euphorbiaceae). A. Detection of lipids with Sudan black B. B. Resins identified within the laticifer using NADI reagent. C. Globules of essential oils and resins in the latex. NADI reagent. D. Detection of phenolic compounds with ferric chloride. E. Mucilage identified using ruthenium red. F. Polysaccharides within laticifers detected by PAS reaction. G. Proteins in the latex identified with coomassie blue.

The function of such compounds is, either individually or synergistically, to protect plants against herbivory and penetration of pathogens; further, they have the ability to seal wounds, since latex polymerizes when in contact with the air [6, 7, 10, 23, 25, 30, 33, 39, 40, 45, 46].

The protective function of the latex is reflected in the time of laticifer differentiation, since all the secretory defense structures originate early in the organogenesis. Laticifers are present from the younger portions of the plant and are widely distributed in almost all tissues (**Figure 1**), but there is a higher frequency of laticifers associated with vascular tissues, especially with the phloem [40, 41] (**Figure 1H**). This proximity allows a direct transference of the transported nutrients to the laticifer, supplying the intense biosynthetic demand of this cell. This fact becomes even more relevant when it is considered that a single laticiferous cell can produce all the major classes of secondary metabolites [10]. These compounds, which can be extremely toxic, are isolated from the rest of the plant tissues remaining inside the laticifer and will only be released to the environment if there is a rupture of the secretory system [8, 23, 38].

3.2. Resin duct

Ducts are glands formed by a secretory tissue called epithelium that delimits an intercellular space, the lumen, where the secretion is stored (**Figure 3A**). The ducts are always elongated (**Figure 3B**) and can remain individualized or anastomose laterally (**Figure 3C**) forming a

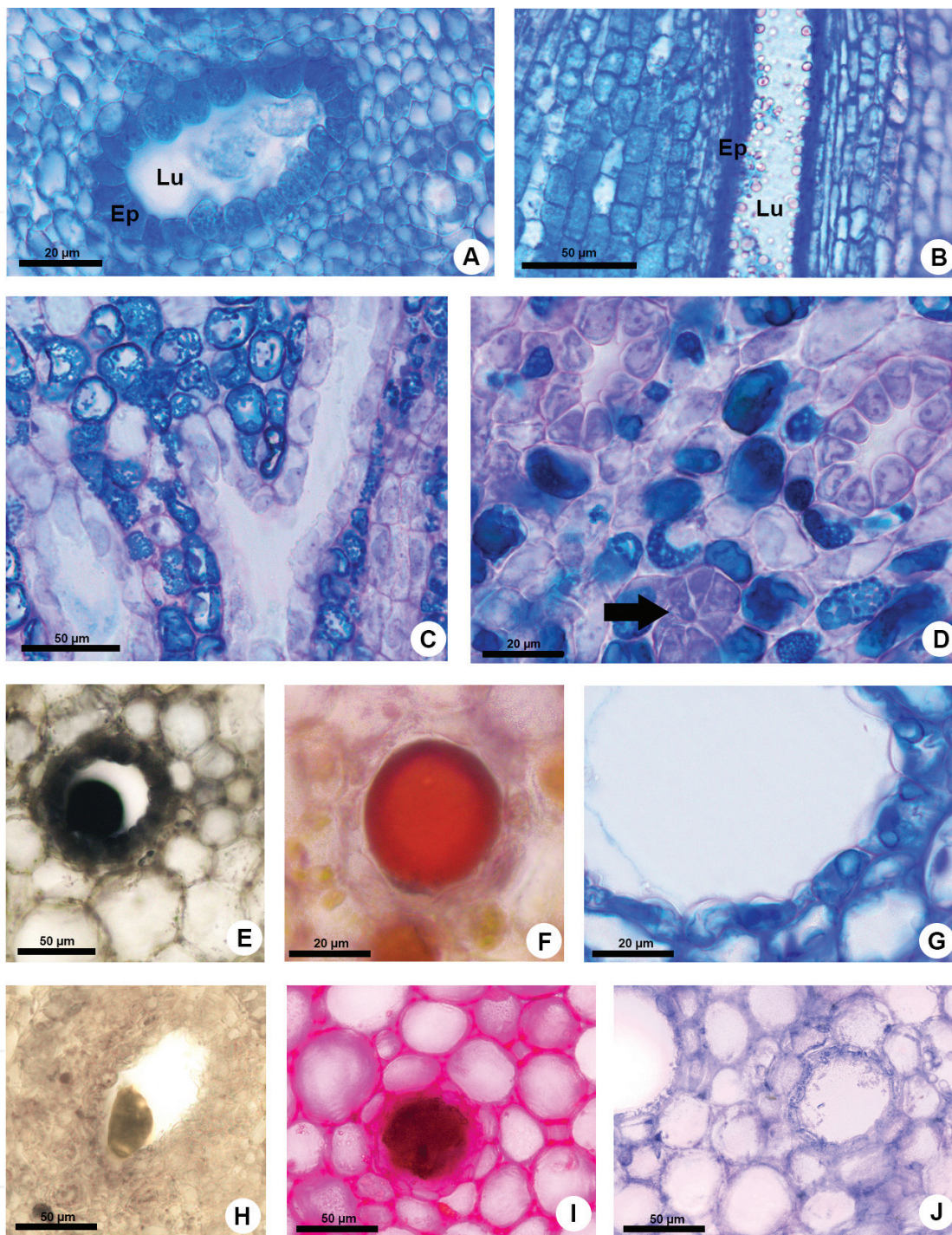


Figure 3. Resin ducts. A–D. General view. A, D–J. Transverse sections. B, C. Longitudinal sections. A, B, E, H. *Schinus terebinthifolius* (Anacardiaceae). C, D, F, I, J. *Clusia* sp. (Clusiaceae). G. *Protium heptaphyllum* (Burseraceae). E–J. Histochemistry. E. Lipids stained with Sudan black B. F. Resins identified using NAD1 reagent. G, H. Phenolic compounds detected by toluidine blue (G) and ferric chloride (H). I. Polysaccharides identified with PAS reaction. J. Proteins stained using coomassie blue. Arrow, duct initials rosette; Ep, epithelium; Lu, lumen.

complex network of ducts throughout the plant [9, 23, 25]. Although this branched duct system may superficially resemble some types of laticifers, ducts are never composed of a single cell or a single row of cells. Actually, the epithelium of some ducts may have dozens of cell rows lining the lumen.

In addition, ducts differ from laticifers in relation to the origin and the mode of secretion storage. The main event in duct morphogenesis is the process of lumen formation. Initially, we observe a set of meristematic cells called rosette (**Figure 3D**), which may form an intercellular space by means of three processes: (1) schizogeny, in which a space is formed by separation of the rosette initials through an active movement of the cells; (2) lysigeny, in which a space is formed by programmed cell death of one or more central cells of the rosette; and (3) schizolysigeny, where the lumen is initially formed by programmed cell death and then spread apart cells enlarging the intercellular space [9, 23, 25, 34, 47, 48].

After the formation of the lumen and concomitant differentiation of the epithelium, the secretory process is initiated by means of which the produced secretion will be stored extracellularly in the lumen [17, 25, 34, 49] (**Figure 3A and B**). This secretion's composition varies depending on the group and may be constituted of mucilage, gum or resin.

Despite all the differences between laticifers and secretory ducts, many divergences are found in the literature of some families for which some authors described the secretory structure as ducts, laticifers or latex ducts (=laticiferous canals). This confusion occurs exclusively in relation to the resin ducts, since the resin of some families may be white, especially in species of Anacardiaceae, Burseraceae, Cactaceae, Calophyllaceae and Clusiaceae [42, 47, 50–58].

Although resins are usually associated with the amber coloration, they may also be colorless [52, 59] or white. In the same way that latex varies in color, resins vary in color depending on their composition. By definition, resins are composed of phenolic compounds, terpenoids or a mixture of both [60] but what is observed in those five families is that the resin is composed of several classes of compounds [21, 59], although its constitution is mostly terpenic (**Figure 3E and F**), such as the resin of the gymnosperms and almost all angiosperms [60]. This fact led some authors to propose mixed terms, such as gum-resin to indicate the heterogeneity of the secretion. However, this term is not comprehensive enough, as this resin may have other compounds, such as phenolic compounds, alcohols, aldehydes, esters, gums, mucilage, proteins and alkaloids [16, 21, 23, 25, 48, 59, 61, 62] (**Figure 3G–J**).

The high chemical complexity of some resins confers functions similar to those of the latex, acting against herbivory and microorganisms, besides sealing wounds by the polymerization of their compounds when in contact with the air [6, 63]. The secretion is stored in the lumen and does not come into contact with any surrounding tissue. Its release to the environment occurs only by rupture of the secretory system. Ducts have an early formation during plant organogenesis but due to its more complex structure in relation to the laticifers, they are found in mature stage at a little longer distance from the promeristem than laticifers (**Figure 4A**). Ducts also occur preferentially in the vascular system (**Figure 4B**) or in the surrounding area (**Figure 4C**).

In our study, we have analyzed the five families that have disagreements regarding the presence of resin or latex. In Anacardiaceae, Venning [64] reported the presence of ducts in *Schinus* as laticifers with schizogenous origin, and Fahn and Evert [47] attributed the milky white color of *Rhus* resin to the fact that the secretion contains carbohydrates in its constitution.

The tribe Protieae (Burseraceae) is recognized for presenting resinous latex or latex [50–52]. *Mammillaria* is a genus of Cactaceae described as latescent due to the presence of a milky

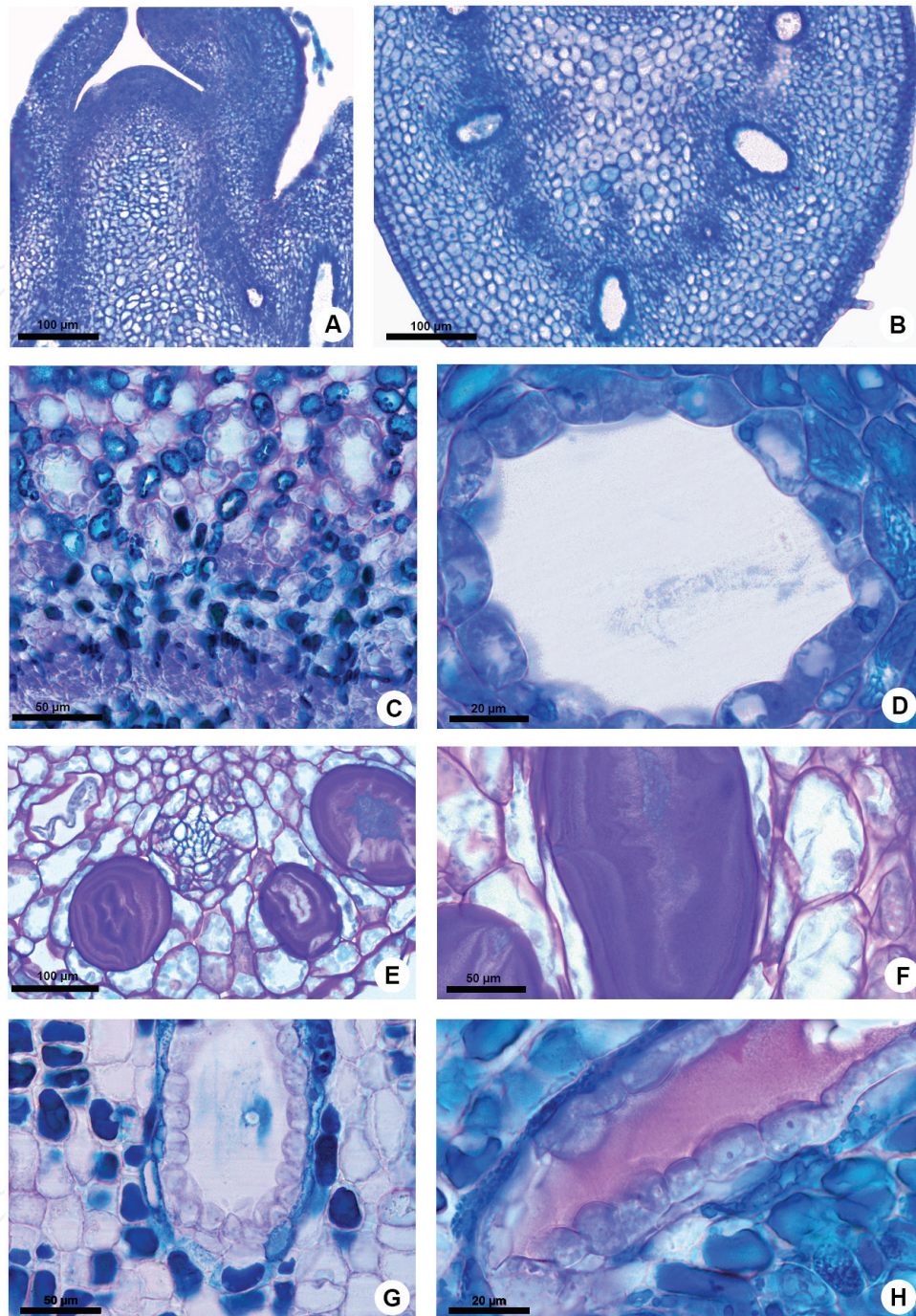


Figure 4. Resin ducts. A, B. *Schinus terebinthifolius* (Anacardiaceae). C. *Clusia* sp. (Clusiaceae). D. *Protium heptaphyllum* (Burseraceae). E, F. *Mammillaria* sp. (Cactaceae). G, H. *Kielmeyera apparicana* (Calophyllaceae). A, F, H. Longitudinal sections. B–E, G. Transverse sections.

white exudate [42, 53–57], and Mauseth [65] states that the *Mammillaria* laticifers would have evolved independently of all other latescent families, since their mode of formation is completely different. In addition, *Kielmeyera* (Calophyllaceae) and *Clusia* (Clusiaceae) are registered as latescent [42, 66, 67] due to the production of a white to yellowish exudate [58].

Our analyses showed that the genera of these five families, in which some authors suggested the presence of latex, actually have resin ducts (**Figures 3** and **4**). The white color of the secretion is due to the high heterogeneity of its composition, which is formed by several types of lipids, mainly terpenoids, phenolic compounds, polysaccharides and proteins (**Figure 3E–J**).

3.3. Occurrence of laticifers and resin ducts in plant taxa and their distribution according to the environment

The plant ability to produce latex or resin is not related to growth habit and seems to be related to a phylogenetic conserved trait or to a key evolutionary innovation that arose in a particular group, influenced directly or indirectly by the environment in which it lives.

Laticifers occur in about 10% of the angiosperm families and the resin ducts in other 10% of them. As they usually do not occur in the same groups, both together are found in about 20% of the flowering families (**Table 1**), being very common defensive secretory structures. Moreover, this number may be underestimated, and laticifers have been identified in several genera of Sapindaceae described as non-latescent due to the inconspicuous latex released when the plant is ruptured [68]. We have noticed that the amount of latex, as well as resin, depends on the gland density in the organ, the degree of anastomosis of the secretory system, climatic and edaphic conditions and even the injuries caused by microorganisms or environmental factors.

According to our updated survey, laticifers are found in Marsileaceae (fern), Gnetaceae (gymnosperm) and 38 families belonging to almost all major lineages of angiosperms. Similarly, resin ducts occur in seven families of gymnosperms, belonging to Ginkgoales and Pinales, and are widespread within angiosperms in which they are present in 40 families (**Table 1**). Both in terms of absolute and proportional estimates, latescent and resinous families predominate in tropical regions [42, 60] (**Table 1**). It is estimated that 14% of the tropical species produce latex compared to 6% of the species in temperate regions [42]. In addition, the largest number of resin-producing families which have numerous genera that produce copious resins occur in tropical areas [60].

The comparative analysis shows that 17 orders have both laticifers and resin ducts but generally in different families. The occurrence of both secretory structures in the same family was recorded only for Araceae, Salicaceae, Fabaceae, Cannabaceae, Moraceae, Cornaceae and Asteraceae, which are tropical families or have a wide distribution in tropical regions (**Table 1**).

3.4. Evolution of laticifers and resin ducts and ecological implications

The production of latex or resin is a highly convergent trait that has evolved independently multiple times (**Figure 5**). Despite the co-occurrence of laticifers and resin ducts being found in only 50% of the angiosperm orders which have these secretory structures (**Table 1**), the possible presence of laticifers or resin ducts in the ancestor of the same major lineages is noticeable (**Figure 5**). This fact may indicate the emergence of an ancestral metabolic capability to synthesize higher molecular weight terpenoids, which resulted in similar possibilities to

Groups	Order and families	Laticifer	Resin duct	Distribution
Ferns	Salviniales			<i>Regnellidium</i> , Southern Brazil and Argentina
	Marsileaceae	+	-	
Gymnosperms	Ginkgoales			China
	Ginkgoaceae	-	+	
	Pinales			Southern S. America, Malesia to Australia and New Zealand
	Araucariaceae	-	+	
	Cupressaceae	-	+	Northern and southern hemispheres
	Pinaceae	-	+	Northern hemisphere
	Podocarpaceae	-	+	Tropics and subtropics
	Sciadopityaceae	-	+	Japan
	Taxaceae	-	+	Northern hemisphere, scattered in south temperate regions
	Gnetales			Tropics
	Gnetaceae	+	-	
Angiosperms	Nymphaeales			World-wide, rather scattered
	Cabombaceae	+	-	
	Nymphaeaceae	+	-	World-wide
Magnoliids	Piperales			Tropics
	Piperaceae	-	+	
Monocots	Alismatales			Pantropical, also temperate
	Alismataceae	+	-	
	Aponogetonaceae	+	-	Old world tropics
	Araceae	+	+	American tropics, W. Indies
	Pandanales			<i>Cyclanthus</i> , Central and tropical South America
	Cyclanthaceae	+	-	
	Liliales			North Temperate
	Liliaceae	+	-	
	Asparagales			World-wide
	Amaryllidaceae	+	-	
Asparagaceae	-	+	World-wide	
Asphodelaceae	-	+	Xanthorrhoeoideae ; Australia	
Commelinids	Arecales			Indomalesia, esp. W. Malesia
	Arecaceae	-	+	
	Zingiberales			Africa, South Asia, Philippines and N. Australia
	Musaceae	+	-	

Groups	Order and families	Laticifer	Resin duct	Distribution
Eudicots	Ranunculales			East Asia, E. North America and South America
	Berberidaceae	-	+	
	Lardizabalaceae	+	-	South East Asia and Chile
	Papaveraceae	+	-	N. Temperate, S. Africa and South America
	Proteales			Temperate, E. North America and E. Asia
	Nelumbonaceae	+	-	
	Platanaceae	-	+	North Temperate, S.E. Asia
Superrosids	Saxifragales			Indomalesia, E. Mediterranean, E Asia, S.E. North America, Central America
	Altingiaceae	-	+	
	Peridiscaceae	+	-	S. America, tropical W. Africa
Fabids	Zygophyllales			Dry and warm temperate, also tropical
	Zygophyllaceae	-	+	
	Celastrales			World-wide
	Celastraceae	+	-	
	Malpighiales			Tropics
	Calophyllaceae	-	+	
	Clusiaceae	-	+	Tropics
	Euphorbiaceae	+	-	Pantropical
	Humiriaceae	-	+	Tropical America, W. Africa
	Malpighiaceae	+	-	Tropics and subtropics
	Salicaceae	+	+	Pantropical, temperate to Arctic
	Fabales			Tropics
	Fabaceae	+	+	
	Rosales			Central Asia, N. temperate zone
	Cannabaceae	+	+	
	Moraceae	+	+	Tropical to warm temperate
	Rhamnaceae	-	+	N. hemisphere to Brazil, S. Africa
Rosaceae	-	+	Temperate zones and tropical mountains	
Urticaceae	+	-	World-wide, esp. tropical	
Fagales			North Temperate to Andes and S.E. Asia	
Betulaceae	-	+		

Groups	Order and families	Laticifer	Resin duct	Distribution
Malvids	Myrtales			Worldwide, esp. tropical-warm temperate
	Myrtaceae	+	-	
	Sapindales			Tropical, also temperate
	Anacardiaceae	-	+	
	Bursaceae	-	+	Tropics
	Rutaceae	-	+	Largely tropical
	Sapindaceae	+	-	Tropics and subtropics, Australia
	Simaroubaceae	-	+	Largely tropical; a few temperate
	Malvales			Pantropical
	Bixaceae	+	-	
	Cistaceae	-	+	Mediterranean region, N. Africa, N. America, S. South America
	Dipterocarpaceae	-	+	Tropical, esp. Malesia
	Thymelaeaceae	-	+	World-wide, tropical Africa and Australia
	Brassicales			Tropical America and Africa
	Caricaceae	+	-	
Gyrostemonaceae	-	+	Australia, Tasmania	
Superasterids	Santalales			Tropics
	Loranthaceae	+	-	
	Olacaceae	+	-	Pantropical
	Caryophyllales			<i>Mammillaria</i> , America
	Cactaceae	-	+	
	Plumbaginaceae	-	+	Tropical, warm regions
Asterids	Cornales			N. temperate zone, S. America, Indomalesia
	Cornaceae	+	+	
	Nyssaceae	+	-	East Asia, Indo-Malesia and E. North America
	Ericales			Pantropical
	Sapotaceae	+	-	
	Styracaceae	-	+	Warm N. temperate to tropical
Campanulids	Aquifoliales			World-wide
	Aquifoliaceae	+	-	
	Cardiopteridaceae	+	-	Tropics
	Asterales			World-wide
	Asteraceae	+	+	
	Campanulaceae	+	-	World-wide
	Goodeniaceae	-		Australia
	Apiales			World-wide, esp. N. temperate
	Apiaceae	-	+	
	Araliaceae	-	+	Largely tropical, few temperate

Groups	Order and families	Laticifer	Resin duct	Distribution
Lamiids	Gentianales			Largely tropical to warm temperate
	Apocynaceae	+	-	
	Rubiaceae	-	+	World-wide, esp. Madagascar and the Andes
	Solanales			World-wide
	Convolvulaceae	+	-	
	Solanaceae	-	+	World-wide, esp. tropical America
	Boraginales			Largely north (warm) temperate, some on mountains in the tropics
	Boraginaceae	-	+	
	Lamiales			Epithemateae , tropics
	Gesneriaceae	-	+	
	Scrophulariaceae	-	+	World-wide
	Garryales			Central China
	Eucommiaceae	+	-	
Icacinales			Pantropical	
Icacinaceae	+	-		

Note: + = present; - = absent. The occurrence of laticifers or ducts in only one infra-familial group was highlighted with the taxon in bold. . Survey based on Metcalfe [41], Lewinsohn [42], Langenheim [60], Montes [68] and personal observation. (Occurrence not confirmed was not included. Classification *sensu* APG IV [69].)

Table 1. Occurrence of laticifers and resin ducts in vascular plants according to plant taxa and their distribution.

the evolution of laticifers and resin ducts. This hypothesis is strengthened by the correlation between the evolution of resin ducts and a remarkable chemical diversification of terpenoids [70]. However, this issue is not so simple. Many resinous families do not have resin ducts in all their members, and latescent families rarely possess all their representatives with laticifers. Apocynaceae stand up as an exception in which laticifers are ubiquitous [7, 40] but laticifers have apparently evolved multiple times within other families, such as Sapindaceae [68].

The multiple evolutions of these defensive secretory structures may be associated with a sharp increase in insect herbivory during Paleocene–Eocene [1]. In this epoch, angiosperms became the predominant plant group and coevolved with the insects that fed on these plants and pollinated them [71]. Although the first fossil records of plants with resin ducts were found in pteridosperms from the Carboniferous period of the Paleozoic era [71–74], laticifers were apparently first seen over 250 million years later in the beginning of Cenozoic era [71], when abrupt global warming seems to be related to an increase of both insect diversity and population density [1].

The emergence of laticifers and resin ducts during evolutionary history of vascular plants represents key innovations that have spurred adaptive radiation in plants. Farrell et al. [6] showed that plants that have laticifers or secretory ducts have more advantages in the environment in which they live in relation to those that do not have them or in which these secretory structures

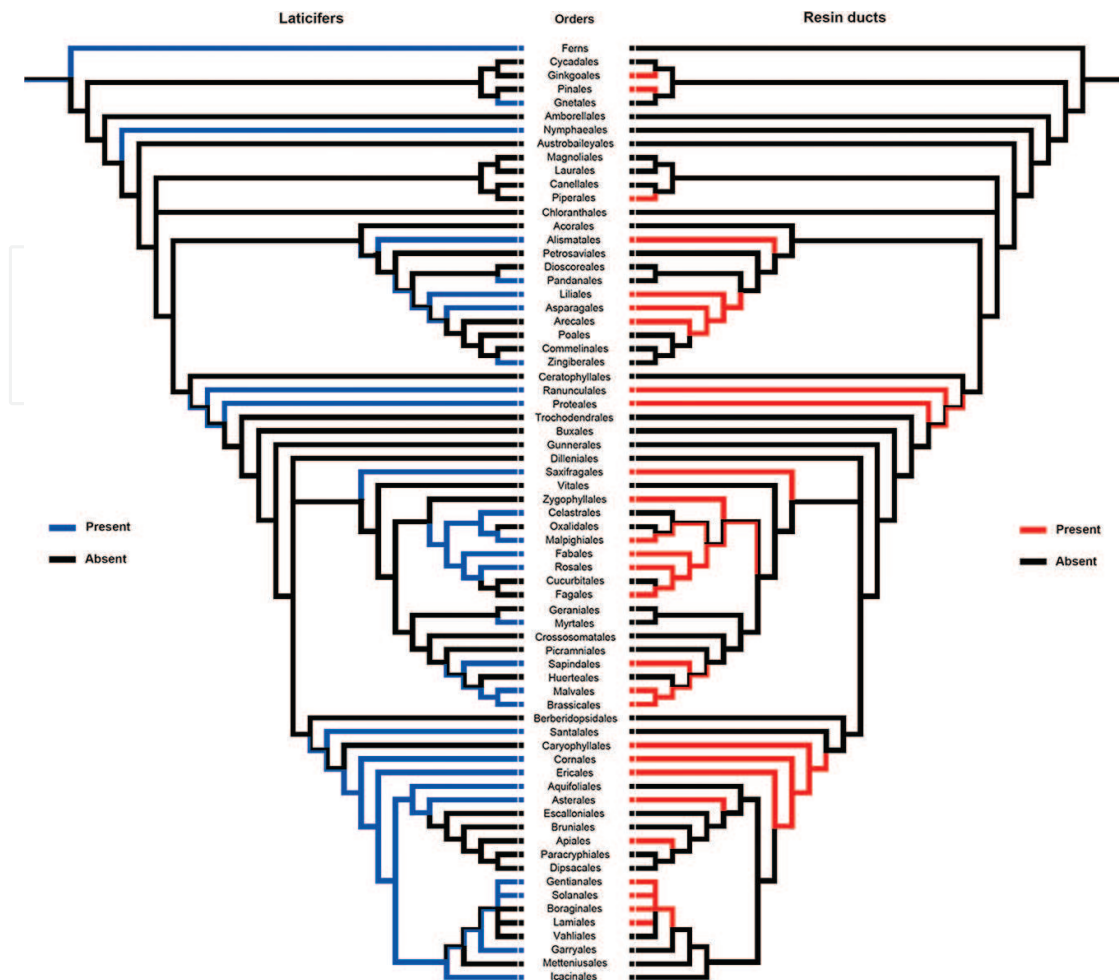


Figure 5. Comparative evolutionary analysis of the distribution of laticifers and resin ducts in vascular plants. All orders containing one laticiferous or resinous species, at least, were labeled. The data were obtained from the surveys of Metcalfe [41], Lewinsohn [42], Langenheim [60], Montes [68] and personal observation optimized on the current phylogeny [69] using parsimony analysis.

are reduced, promoting a greater diversity in both the reproductive capacity and individual fitness [7, 39]. This can be observed in the higher occurrence of resin and laticiferous species in tropical regions, where the herbivory rate is higher [40, 42, 60]. If, on the one hand, tropical environments provide better conditions for plant metabolism in terms of photosynthesis and water availability, on the other hand, they also favor a greater diversity of phytophagous insects and pathogenic fungi [6, 61, 75].

Although specialist insects can feed on some plants that produce latex or resin, generalist ones are highly affected by the properties of these secretions, which are either toxic or deterrent [2, 5, 23]. Strategies to reduce the intake of toxic plant secretions have appeared in multiple insect lineages, allowing to verify the convergent evolution of similar behaviors in several laticiferous or resinous plants, regardless of the plant morphology or phylogenetic relationships [3, 5, 6, 17, 23, 25, 26, 30, 76–79].

These specialized insects' ability to avoid the ingestion of toxic compounds involves leaf vein-trenching, vein-cutting, girdling and leaf clipping strategies, among others, reducing by up to 90% the ingestion of the exudate [17, 23, 30, 79, 80]. It is noteworthy that some specialist

insects have developed chemical defenses – such as digestive proteases – against latex compounds [81] and also sequester toxic components from the exudate to reuse them later in their own defense against predators [77].

4. Conclusions

Laticifers and resin ducts have similarities in relation to the secretion, which is mostly terpenic, function as protection against herbivory, present high viscosity and polymerize in contact with the air, and the resin, at times, is white. However, laticifers and ducts are structurally very distinct and have different origins and mode of secretion storage. It is also important to highlight that, since latex is the own protoplast of the laticifer, when it extrudes, there is not only metabolites in the exudate but also membranes, organelles and nuclei. As the resin is an extracellular secretion, these cellular remnants are not present, and when they are found in its composition, it is due to a completely different process related to a holocrine release of the secretion to the lumen.

Since the secretions are confused only when they are white, it should be noted that, although latex is typically white, and resin is typically amber, both secretions may have different colors and may even be colorless or change their color when in contact with the air. The concept of latex is linked to that of the laticifer and to its complex composition, rather than to its color. Thus, if a white secretion is produced by a duct, it must not be considered latex, and the structure cannot be a laticifer. We propose that the term resin be used in a broad sense for the secretions mainly composed of terpenoids (or phenolics in few cases) which are produced by secretary ducts, regardless of their color, as well as the term latex is used for all secretions produced by laticifers, even when it is not milky white.

The evolutionary analysis of both structures shows that they emerge multiple times in the phylogeny, often in the same order, although they are not usually present in the same plants. Our analyses indicate that the appearance of the higher molecular weight terpenoid metabolic route in the ancestral of some major lineages, associated with events of increased herbivory, leads to the emergence of either laticifers or resin ducts in distinct families. In some cases, the presence of both latex and resin within certain families, such as Fabaceae and Asteraceae, certainly conferred greater adaptive success in several environments.

5. Future perspectives

Much remains to be studied about laticifers and ducts. Although their structures have been known for more than a century, and we have clear and objective definitions of them, discrepancies in the descriptions still remain. Divergences about the origin, mode of growth and the lack of information about the chemical composition of latex and resin of several groups still prevent a series of evolutionary analyses that may clarify the factors that determined the emergence of these structures in different groups, especially considering that both appeared multiple times throughout the evolution of plants.

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Conflict of interest

The authors declare no conflict of interest.

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