INSTITUTO FEDERAL DE EDUCAÇÃO, CIÊNCIA E TECNOLOGIA
GOIANO – CAMPUS RIO VERDE
DIRETORIA DE PÓS-GRADUAÇÃO, PESQUISA E INOVAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE E
CONSERVAÇÃO

# Convergent gall structures induced by a single insect species across multiple plant body parts of *Sapium glandulosum* (L.) Morong **(L.)** (Euphorbiaceae)

Discente: Daniela Maria Wickert
Orientador: Dr. Vinícius Coelho Kuster

RIO VERDE – GO
SETEMBRO - 2025

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Dissertação apresentada como parte das exigências para obtenção do título de MESTRE EM BIODIVERSIDADE E CONSERVAÇÃO no Programa de Pós-Graduação em Biodiversidade e Conservação do Instituto Federal de Educação, Ciência e Tecnologia Goiano – Campus Rio Verde - Área de Concentração: Conservação dos Recursos Naturais.

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## ATA Nº 104

## BANCA EXAMINADORA DE DEFESA DE DISSERTAÇÃO

Aos trinta dias do mês de outubro do ano de dois mil e vinte e cinco, às 09h00min (nove horas), reuniram-se os componentes da banca examinadora em sessão pública realizada, de forma remota no Instituto Federal Goiano - Campus Rio Verde, para procederem a avaliação da defesa de Dissertação, em nível de mestrado, de autoria de **Daniela Maria Wickert** discente do Programa de Pós-Graduação em Biodiversidade e Conservação do Instituto Federal Goiano – Campus Rio Verde. A sessão foi aberta pelo presidente da Banca Examinadora, Prof. Dr. Vinicius Coelho Kuster, que fez a apresentação formal dos membros da Banca. A palavra, a seguir, foi concedida à autora para, em 30 min., proceder à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a examinada, tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, os membros da banca reuniu-se para deliberar a respeito da apresentação da dissertação, do documento escrito e das respostas proferidas no momento da arguição. Com base nisso, procedeu-se a avaliação da defesa. Tendo-se em vista as normas que regulamentam o Programa de Pós-Graduação em Biodiversidade e Conservação, a Dissertação foi APROVADA, portanto cumpriu integralmente este requisito para fins de obtenção do título de **MESTRE EM BIODIVERSIDADE E CONSERVAÇÃO,** na área de concentração em Conservação dos Recursos Naturais, pelo Instituto Federal Goiano – Campus Rio Verde. A conclusão do curso dar-se-á quando da entrega na secretaria do PPGBio da versão definitiva da Dissertação, com as devidas correções. Assim sendo, a defesa perderá a validade se não cumprida essa condição, em até **60 (sessenta) dias** da sua ocorrência. A Banca Examinadora recomendou a publicação do artigo científico oriundo dessa dissertação após procedida as modificações sugeridas. Cumpridas as formalidades da pauta, a presidência da mesa encerrou esta sessão de defesa de Dissertação de Mestrado, e para constar, foi lavrada a presente Ata, que, após lida e achada conforme, será assinada eletronicamente pelos membros da Banca Examinadora.

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**Biografia**

Daniela Maria Wickert, filha de Ginésio Arthur Wickert e Inês Maria Führ Wickert, nasceu em 30 de março de 1997, na cidade de Jataí, estado de Goiás. Seu interesse pela Biologia iniciou-se no Ensino Médio, durante as aulas da Profª Dr.ª Luciene, e se consolidou ao ingressar, em maio de 2019, no curso de Licenciatura em Ciências Biológicas da Universidade Federal de Jataí. Encantou-se pela Botânica nas disciplinas de Morfologia Vegetal, Anatomia Vegetal e Fisiologia Vegetal, cujos professores foram fundamentais para despertar sua vocação científica. Em 2021, atuou como monitora da disciplina de Anatomia Vegetal e, em 2022, participou de um projeto de Iniciação Científica no Laboratório de Anatomia Vegetal. No mesmo ano, concebeu e desenvolveu integralmente um jogo educacional, apresentado em seu Trabalho de Conclusão de Curso intitulado "Snake News: realidades e mitos. Um jogo para informar sobre o ofidismo", sob a orientação da Prof.ª Dr.ª Mirian Machado Mendes. Concluiu a graduação em 2023. Em setembro do mesmo ano, ingressou no Mestrado em Biodiversidade e Conservação no Instituto Federal Goiano – Campus Rio Verde, sob a orientação do Prof. Dr. Vinícius Coelho Kuster, onde desenvolveu a dissertação intitulada "Convergent gall structures induced by a single insect species across multiple plant body parts of *Sapium glandulosum* (Euphorbiaceae)".

**Summary**

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**Abstract**

WICKERT, DANIELA MARIA. Instituto Federal Goiano – Campus Rio Verde-GO, setembro de 2025. **Convergent gall structures induced by a single insect species across multiple plant body parts of *Sapium glandulosum* (L.) Morong (Euphorbiaceae).** Orientador: Prof. Dr. Vinícius Coelho Kuster.

Galls are anomalous structures formed in plants in response to induction by insects, mites, or other organisms. In reproductive organs, they generally develop from ovules, often resulting in the formation of false fruits, whereas galls in fruits are rarely documented. This study investigates the galls induced by *Neolithus fasciatus* Scott, 1882 (Hemiptera) on *Sapium glandulosum* (L.) Morong, both in the floral nectary and in the fruit pericarp, with emphasis on the anatomy and pectic composition of the cell walls. Anatomical analysis was performed using historesin embedding and sectioning with a rotary microtome, whereas immunocytochemistry was used to assess homogalacturonans (HGs) and rhamnogalacturonans I (RG-I) in the galls and their corresponding ungalled organs. Inflorescence galls originate from the cellular redifferentiation of the floral nectary, which loses its sugar-secreting and pollinator-attracting functions and assumes a new structural identity aimed at protecting the gall. In contrast, pericarp galls form from the exocarp and mesocarp, primarily from the parenchyma. Structurally, both the floral nectary galls and the pericarp galls are similar, exhibiting a uniseriate epidermis with a thin cuticle and a cortex composed externally of chlorophyllous parenchyma and internally of fundamental parenchyma, as well as collateral vascular bundles. Immunocytochemical analysis revealed strong labeling of methyl-esterified HGs in the similar galls induced in different organs, indicating the maintenance of elasticity and active growth. Pericarp galls also showed marked labeling for RG-I with (1→4)-β-D-galactan side chains, which are associated with cell hypertrophy and plasticity. These pectins were also intensely labeled in the phloem cell walls, suggesting increased flexibility and support for the elevated flow of photoassimilates required to sustain the inducing insect, which has a sucking feeding apparatus. The maintenance of a complex pectic matrix, distinct among host organs, reveals the influence of the host tissue's organization, whereas the structural similarity of the gall tissues highlights the central role of the inducer in phenotypic convergence.

**Keywords**: floral nectary galls, pericarp galls, immunocytochemistry.

**Resumo**

WICKERT, DANIELA MARIA. Instituto Federal Goiano – Campus Rio Verde-GO, setembro de 2025. **Estruturas convergentes de galhas induzidas por uma única espécie de inseto em múltiplas partes da planta *Sapium glandulosum* (L.) Morong (Euphorbiaceae).** Orientador: Prof. Dr. Vinícius Coelho Kuster.

As galhas são estruturas anômalas formadas em plantas como resposta à indução por insetos, ácaros ou outros organismos. Em órgãos reprodutivos, elas geralmente se desenvolvem a partir dos óvulos, com frequente formação de frutos falsos; já galhas em frutos são pouco documentadas. Este estudo investiga as galhas induzidas por *Neolithus fasciatus* Scott, 1882 (Hemiptera) em *Sapium glandulosum* (L.) Morong, tanto no nectário floral quanto no pericarpo do fruto, com ênfase na anatomia e composição péctica das paredes celulares. A análise anatômica foi feita com inclusão em historesina e cortes em micrótomo rotativo, enquanto para imunocitoquímica foram avaliados homogalacturonanos (HGs) e ramnogalacturonanos-I (RGI) nas galhas e órgãos originais. As galhas do nectário floral originam-se do processo de rediferenciação celular do mesmo, que perde sua função secretora de açúcares e atração de polinizadores, assumindo nova identidade estrutural, que protege a galha. Já as galhas do pericarpo formam a partir do exocarpo e mesocarpo, principalmente do parênquima. Estruturalmente, as galhas de nectário floral e do pericarpo são similares, apresentando epiderme unisseriada com cutícula delgada e córtex formado externamente por parênquima clorofiliano e fundamental interno, além de feixes vasculares colaterais. A imunocitoquímica mostrou alta marcação de HGs metil-esterificados nas galhas que são similares e induzidas em órgãos diferentes, indicando manutenção de elasticidade e crescimento ativo. As galhas do pericarpo destacaram-se também pela marcação de RGI com cadeias laterais de (1→4) β-D-galactanos, relacionadas à hipertrofia e plasticidade celular. Essas pectinas também foram intensamente marcadas nas paredes celulares do floema, sugerindo maior flexibilidade e suporte ao aumento do fluxo de fotoassimilados necessário para alimentar o inseto indutor, que é sugador. A manutenção da matriz péctica complexa, distinta entre os órgãos hospedeiros, revela a influência da organização do tecido hospedeiro, enquanto a similaridade estrutural dos tecidos das galhas evidencia o papel central do indutor na convergência fenotípica.

**Palavras-chave:** galhas de nectário floral, galhas de pericarpo, imunocitoquímica.

## Introduction

Gall formation is triggered by chemical and/or physical stimuli from inducing organisms, which may include fungi, bacteria, viruses, mites, nematodes, or insects, the latter being the main inducing agents (MANI, 1964). These stimuli cause cyto-histological alterations in host plant tissues, such as hyperplasia, cell hypertrophy, and cell differentiation (MANI, 1964; DIAS et al., 2013; MILLER; RAMAN, 2019). The relationship between the host plant and the gall inducer is generally species specific (REDFERN; ASKEW, 1992), with the formation of different morphotypes depending on the taxon of the inducer. An example is the superhost *Croton floribundus* Spreng (Euphorbiaceae), in which eight gall morphospecies have been recorded, each induced by a distinct species of galling insect (TEIXEIRA et al., 2022).

In general, the organs most frequently affected by galls are leaves, whereas flowers and fruits are among the least affected (FERNANDES; CARNEIRO; ISAIAS, 2012; CARVALHO-FERNANDES et al., 2016; MAIA; SILVA, 2016; GOETZ et al., 2018). In *Alstonia scholaris* (Apocynaceae), galls are found on leaves, flowers, and pericarps induced by the same galling insect, identified as *Pauropsylla tuberculata* (Hemiptera). In flowers, the galls cause complete sterility (CHAUHAN; SINGH; CHAUHAN, 2019). When galls occur in flowers, they usually promote structural modifications that resemble, to some extent, those observed in vegetative organs, with reports of reduced reproductive success in some host plants (BOMFIM et al., 2020). For example, galls induced in the flowers of *Haloxylon aphyllum Iljin* (Amaranthaceae) and *Heracleum persicum* (Apiaceae) by *Caillardia robusta*, *C. azurea*, *C. nana*, and *C. notata* (Hemiptera: Psyllidae) resulted in structures resembling flowers or floral buds (ZHAO et al., 2021). In *Miconia chamissois Naudin* (Melastomataceae), galls induced by *Allorhogas uberlandiensis* Joele & Zaldívar-Riverón, 2019 (Hymenoptera: Braconidae) give rise to structures that mimic seeds and false fruits, are larger than the true ones and form from the ovary (BOMFIM et al., 2020). In flowers of *Alstonia scholaris* (L.) R.Br., galls induced by *Pyromaia tuberculate* (Lockington, 1877) cause significant damage to all floral parts, including stamens and pistils, resulting in complete floral sterility (CHAUHAN; SINGH; CHAUHAN, 2020). With respect to floral glands, such as floral nectaries, no studies have reported on gall formation or its impact on these structures. For fruits, galls generally develop in the pericarp (CHAUHAN; SINGH; CHAUHAN, 2020; HIRANO et al., 2020), a stage characterized by intense meristematic activity (CASTRO;

PEREIRA; VIEIRA, 2006). An example is the case of galls induced by *Pauropsylla tuberculata* Crawford, 1912 (Hemiptera: Psyllidae) in the fruits of *Alstonia scholaris* (L.) R.Br., which develop through cell hypertrophy and hyperplasia processes in the pericarp parenchyma (CHAUHAN; SINGH; CHAUHAN, 2020).

The term superhost refers to a complex system of interactions between gall inducers and host plants, in which several galling species may coexist on the same individual, including within the same organ (MANI, 1964; OLIVEIRA et al., 2013; ARAÚJO et al., 2019; GRANDEZ-RÍOS; PIZANGO; ARAÚJO, 2020). These multiple inductions can generate galls with different morphologies, colors, and anatomies, highlighting the potential of insects to drive morphogenesis in distinct ways (CORNELL, 1983; FERNANDES; SANTOS, 2014; MAIA; MASCARENHAS, 2023; ISAIAS et al., 2024; MARTINEZ et al., 2024).

In general, each insect inducer species tends to generate only a single gall morphotype (CORNELL, 1983; YUKAWA; TOKUDA, 2021). However, variables such as insect sexual dimorphism (GONÇALVES et al., 2022) and the position of the gall on the host organ (MISHIMA et al., 2014) may result in distinct morphologies and anatomies. Galls induced by the same insect in different plant organs may show small or large morpho-anatomical variation, depending on the host organ and the characteristics of the inducer (OLIVEIRA; ISAIAS, 2010; MAIA; MASCARENHAS, 2023; ISAIAS et al., 2024). In the case of aphids, *Schlechtendalia chinensis* Bell, 1851, *S. peitan* Tsai & Tang, 1946 and *Nurudea shiraii* Matsumura, 1917 form galls on *Rhus chinensis* Mill, while *Kaburagia rhusicola* Takagi, 1937 produces galls on *Rhus potaninii* Maxim. In both cases, the galls show clear differences in shape and anatomy, arising in several organs of the host plants (LU et al., 2019). However, a notable example is found in *Alstonia scholaris* L. (Apocynaceae), in which the gall-inducing insect *Pauropsylla tuberculata* Crawford (Hemiptera) induces galls on leaves, flowers, and fruits. The galls formed in these different organs are similar to each other, developing as numerous light-green conical structures (CHAUHAN; SINGH; CHAUHAN, 2019).

With gall formation, the cell walls of plant tissues undergo structural and compositional remodeling (GUEDES et al., 2025; SANTOS et al., 2024; SOUZA et al., 2024). Composed of cellulose, hemicelluloses, glycoproteins, and pectins (WESSELS, 1986; HEATH, 1990; XU et al., 2011; VOINICIUC et al., 2018), cell walls stand out particularly for the presence of pectins, which are associated with cell growth, water retention, and tissue rigidity (WILLATS et al., 2001; CAFFALL; MOHNEN, 2009;

VORAGEN et al., 2009). Homogalacturonans (HGs), the main pectic polymers (VINCKEN et al., 2003; CAFFALL; MOHNEN, 2009; DU; ANDERSON; XIAO, 2022), are generally demethylesterified by pectin methylesterases during cell maturation, which alters the rigidity and porosity of the cell wall (JOLIE et al., 2010; ALBERSHEIM et al., 2010; COSTA, 2019), as observed in galls of *Psidium cattleianum* Sabine (Myrtaceae) induced by *Nothotrioza cattleiani* (Triozidae) (CARNEIRO; BURCKHARDT; ISAIAS, 2013). Rhamnogalacturonans (RGs), which possess side chains composed of neutral carbohydrates (ALBERSHEIM et al., 2010; DANG et al., 2024), have functions that are modulated by β-D-galactans and α-L-arabinans, which promote cell wall elongation or adhesion (JONES et al., 1997; MCCARTNEY et al., 2003; BRUMMELL et al., 2004; O'DONOGHUE; SUTHERLAND, 2012). These components were detected, for example, in mature and senescent galls induced by *Nothotrioza myrtoidis* Burckhardt, 2013 (Hemiptera: Triozidae) on *Psidium myrtoides* O. Berg, 1857 (Myrtaceae) (CARNEIRO; OLIVEIRA; ISAIAS, 2014).

In *Sapium glandulosum* (L.) Morong (Euphorbiaceae), *Neolithus fasciatus* Scott, 1882 (Hemiptera: Triozidae) induces globoid, green leaf galls with cortical compartmentalization and a high concentration of carbohydrates (ROSA et al., 2024). Morphologically similar galls on leaves, also induced by *N. fasciatus*, have been reported in inflorescences of *S. glandulosum*, where they interfere with the fruiting process and prevent the natural abscission of inflorescences after the senescence of staminate flowers (CARDOSO, 2016). In addition, globoid galls have been observed in the pericarp of mature fruits of this species (personal observation), a phenomenon still scarcely documented in the literature. In this context, the present study aims to evaluate the morphology, histology, and immunocytochemistry of the cell walls associated with gall formation in the floral nectaries and in the fruit pericarp of *S. glandulosum*, both induced by *Neolithus fasciatus*. We hypothesize that the same insect inducer is capable of generating structurally similar galls in different regions of the host plant, reflecting a convergent anatomical pattern. Furthermore, immunocytochemical analyses are expected to reveal variations in the cell walls that are related to the specific organ of origin.

## Materials and Methods

*Galling insect–host plant systems and sampling*

*Sapium glandulosum* (Figure 1A–D) is a tree species typical of the Cerrado (Figure 1A) (ANDRADE et al., 2017). Its inflorescences, located on the terminal branches, are

spike-shaped (Figure 1B) and consist of reduced flowers accompanied by bracts and two glands present at the base of both staminate and pistillate flowers (Figure 1C). The pistillate flowers, yellow-green in color, are positioned at the base of the inflorescence, whereas the staminate flowers, located at the apex, have two stamens with reddish extrorse anthers and orange pollen (CARVALHO, 2010; CARDOSO, 2016). Globoid, green galls are found on the leaves of *S. glandulosum* (ROSA et al., 2024), whereas similar galls, ranging from green to pinkish, occur on the nectaries of the inflorescences (Figure 1D). Both are induced by the galling insect *N. fasciatus* (CARDOSO, 2016).

The fruits of *S. glandulosum* are dry and dehiscent (Figure 1E), of the tricocca capsule type, simple, septicidal, loculicidal, and globose in shape (PSCHEIDT; CORDEIRO, 2012; ROCHA, 2013). The seeds have a fleshy red testa, lack a well-developed caruncle, and possess a white aril when the fruits are still closed, which turns red after dehiscence (PSCHEIDT; CORDEIRO, 2012; ROCHA, 2013). The inflorescence occurs between September and April (PSCHEIDT; CORDEIRO, 2012). In the present study, globoid, green galls induced by *N. fasciatus* were observed on the pericarp of mature fruits (Figure 1F).

Floral glands from inflorescences, non-galled mature fruits, and mature galls originating from these structures were collected from six *S. glandulosum* individuals for morphological, anatomical, and immunocytochemical analyses. In this study, we considered as “mature” the tissues that had reached the final stage of structural development, as also described by Gómez, Vera-Sirera, and Pérez-Amador (2014). Collections were carried out in Cerrado phytophysiognomies and in urban areas of the city of Jataí, Goiás, Brazil (17°55’32’’S; 51°42’32’’W).

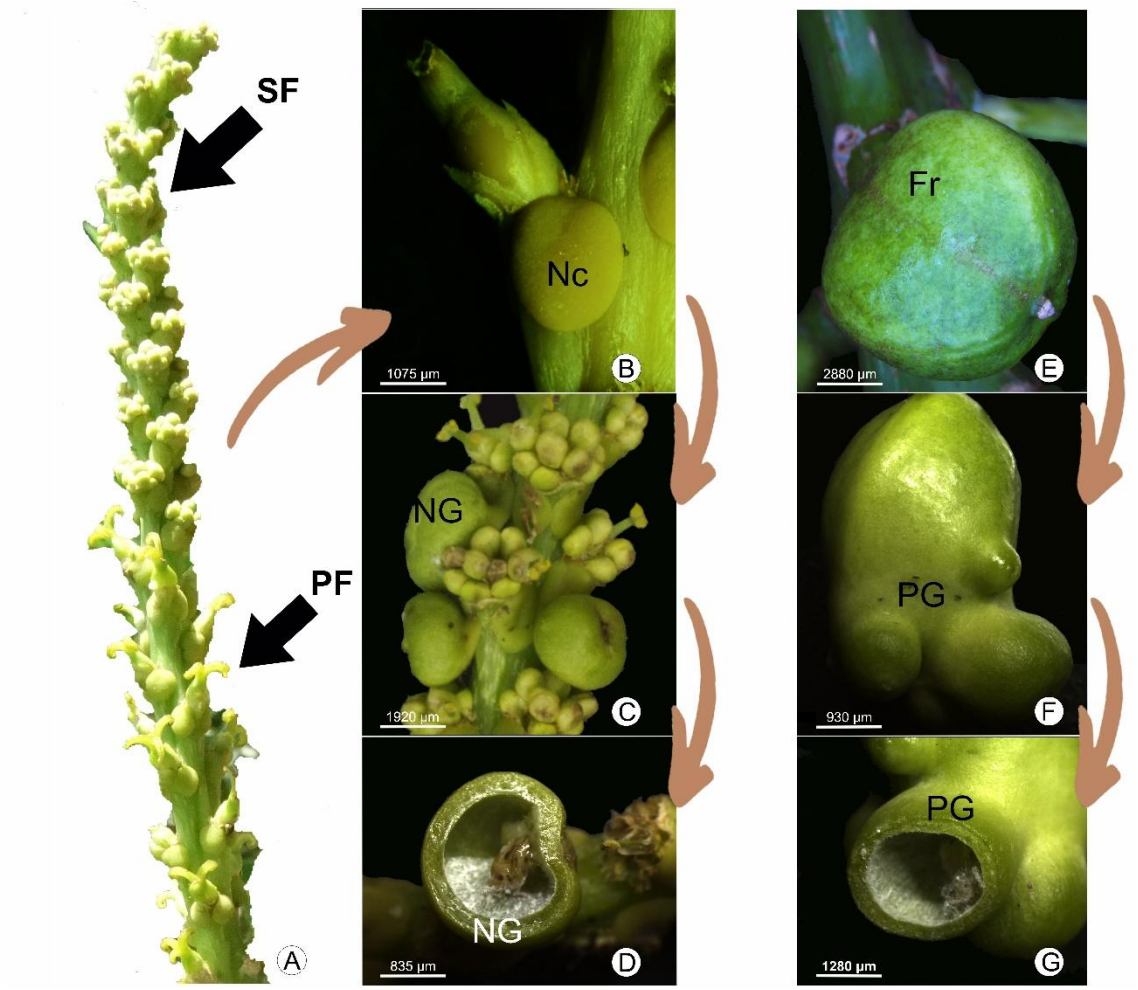


**Figure 1**. *N. fasciatus–S. glandulosum* gall-inducer–host plant system. A- Inflorescence; B- Non-galled floral nectary; C- Nectary gall; D- Open gland gall; E- Non-galled fruit; F- Fruit with galls on the pericarp; G- Open pericarp gall. Abbreviations: Fr – Fruit; Nc – Nectary; NG – Nectary gall; PF – Pistillate flower; PG – Pericarp gall; SF – Staminate flower.

*Morphological analyses*

Fifteen samples of pericarp and floral gland galls, as well as their non-galled counterparts, were randomly collected from six individuals of *S. glandulosum.* After that, the samples were dissected and photographed via a Leica® M165C stereomicroscope coupled with a Leica® DFC295 digital camera.

*Histological analyses*

Samples of galls and non-galled structures (n = 6 for each structure) were fixed in FAA solution (formaldehyde, acetic acid, and 70% ethanol at a 1:1:18 v/v ratio) for 48 hours and subsequently transferred to 70% ethanol (JOHANSEN, 1940). The samples were then embedded in 2-hydroxyethyl methacrylate (Historesin®, Leica Instruments,

Heidelberg), sectioned transversely and longitudinally on a rotary microtome (Leica® RM2235) at a thickness of 5 μm, and stained with 0.05% toluidine blue, pH 4.7 (O'BRIEN; FEDER; MCCULLY, 1964). For the glands located at the base of *S. glandulosum* flowers, samples (n = 6) were left unstained and subjected to the periodic acid–Schiff (PAS) test to label total polysaccharides (MCMANUS, 1948). All the slides were mounted with Entellan®, and the sections were photographed under a light microscope (Leica® DM750) coupled to a digital camera (Leica® ICC50 HD).

*Immunocytochemical analyses*

Fixation, embedding, and rotary microtome sectioning were carried out similarly to the procedures described for the histological analyses, with the sections (n = 6 for each structure) chosen for pectin immunolocalization in the cell walls. Initially, the samples were immersed in a blocking solution of Molico® powdered milk and 3% phosphate-buffered saline (PBS) for 30 minutes. The sections were subsequently incubated with primary monoclonal antibodies against LM5, LM6, JIM5, and JIM7 (Centre for Plant Sciences, University of Leeds, UK) (Table 1) for 2 hours. The sections were then washed in PBS and subsequently incubated with anti-rat IgG FITC antibody (Sigma–Aldrich) in blocking solution (1:100 in 3% milk/PBS) for 2 hours in the dark. The control was conducted by omitting the primary antibody incubation. After being washed in PBS, the sections were mounted in 50% glycerol and analyzed via a Leica® DM4000 LED fluorescence microscope coupled with a monochromatic HD camera (DFC3000 G) and imaging software. A FITC filter and a DAPI filter, which marks autofluorescence, were used with excitation wavelengths of 450–490 nm and an emission filter of 515 nm. The overlay function in the microscope software was selected, generating positive results in green and negative results in blue. Fluorescence intensity was measured in triplicate via ImageJ® version 1.54 g (http://rsb.info.nih.gov/ij) with grayscale (Gy) methodology in the following categories: (-) negative (= 0 Gy); (+) weak (≤ 10 Gy); (++) moderate (10–20 Gy); and (+++) strong (≥ 20 Gy).

**Table 1.** Recognition of primary monoclonal antibodies and their respective epitopes.

| **Monoclonal Antibodies** | **Epitopes** | **References** |
|---|---|---|
| | **Rhamnogalacturonan-I** | |
| **LM5** | (1→4) β-D- galactans | JONES et al. (1997) |

| | | |
|---|---|---|
| **LM6** | (1→5) α-L- arabinans | WILLATS et al. (2001) |
| | **Homogalacturonans** | |
| **JIM5** | Partially methyl-esterified HGs up to 40% | KNOX et al. (1990), WILLATS et al. (2000), CLAUSEN et al. (2003) |
| **JIM7** | HGs 15–80% methyl-esterified | KNOX et al. (1990), WILLATS et al. (2000), CLAUSEN et al. (2003) |

## Results

*Morphology*

*Sapium glandulosum* has a spike-shaped inflorescence positioned on the terminal branches, with pistillate flowers at the base (Figure 2A) and staminate flowers at the apex (Figure 2B), both of which are small in size and associated with two glands at the base (Figure 2A, B). The pistillate flowers are yellow to greenish in color, with a central pistil and a bifurcated stigma (Figure 2A). The staminate flowers have two stamens composed of reddish to yellowish anthers (Figure 2B). After fertilization, during fruit development, the fruit is generally green and rounded and of the capsule type, usually containing one to three seeds (Figure 2C).

Gall induction in the inflorescence occurs from the base to the apex of the structure without directly affecting the flowers. Galls are formed from the glands located at the base of both types of flowers, showing typical hypertrophy of the structure during the early stages of gall formation (Figure 2E). The gall is globoid and green (Figure 2F) and maintains a clear connection with the inflorescence at the site where the gland is positioned (Figure 2G). The gall has a single nymphal chamber containing only one inducer (Figure 2H) and exhibits a floral-like appearance after the senescence and departure of the inducer (Figure 2I). Gall formation in inflorescences leads to the abscission of pistillate and staminate flowers, preventing fruit and seed formation (CARSOSO, 2016).

Gall formation in the fruit occurs exclusively in the pericarp, which is classified as globoid, with a single nymphal chamber containing only one inducer (Figure 2D).

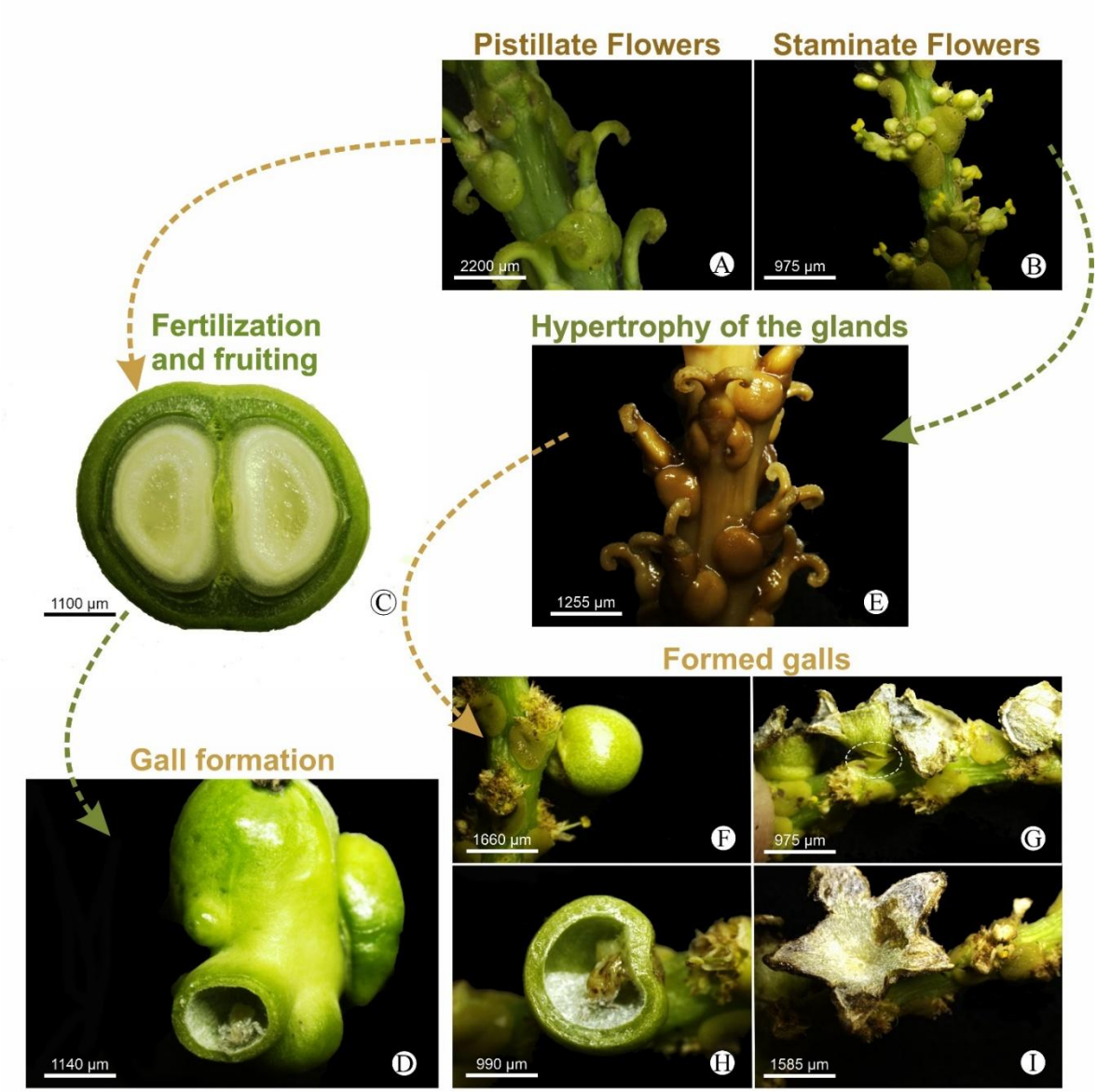


**Figure 2**. Flowchart with photos showing the formation of galls induced by *N. fasciatus* from fruits and nectaries at inflorescences of *Sapium glandulosum*. A- Pistillate flower; B- Staminate flower; C- Fruit formed after fertilization; D- Fruit with galls formed from the pericarp containing a single nymph; E- Onset of hypertrophy of the glands at the base of the flowers (fixed material); F- Mature globoid galls formed on nectaries; G- Connection (white circle) of the gall at the base of the flowers; H- Open gall containing a single nymph; I- Senescent gall without the gall-inducing insect.

*Histology – Floral nectaries and nectary galls*

The glands present at the base of the flowers are T shaped and possess a peduncle (Figure 3A). The adaxial epidermis is secretory and composed of palisade cells (Figure 3B), which secrete a polysaccharide solution (Figure 3C) and are thus classified as nectaries. These cells are covered by a thin cuticle and have a large and evident nucleus positioned in the median or basal region (Figure 3B). The cytoplasm of the epidermal

cells is dense, and the vacuole usually occupies approximately one-third of the cell volume (Figure 3B). Other regions of the nectary have epidermal cells that are square to rectangular in shape and are nonsecretory. The fundamental parenchyma predominates in the interior of the nectary and is composed of isodiametric, multifaceted cells, forming a nectariferous parenchyma (Figure 3D). In these cells, the nucleus is large and evident, located in the peripheral region and associated with the cytoplasm (Figure 3D). Most cells possess a single central vacuole occupying up to 90% of the cell volume (Figure 3D), which occasionally contains diffuse crystals (Figure 3E). Laticifers occur intrusively among the parenchyma cells (Figure 3F). Vascularization is represented by xylem and phloem, which extend from the base of the nectary and may reach 5 to 8 cells below the secretory epidermis.

Galls originating from floral nectaries are predominantly parenchymatous and possess a single nymphal chamber (Figure 3G). The epidermis is composed mainly of rectangular cells, covered by a thin cuticle, displaying a uniform structure throughout the gall and lacking secretory function (Figure 3H). The cortex is predominantly formed by chlorophyllous parenchyma and fundamental tissue, with isodiametric, multifaceted cells without diffuse crystals (Figure 3G, H). The outer and median cells of the cortex (Figure 3H) are larger than the inner cells (Figure 3J), with some cells exhibiting large and evident nuclei. In the region of the outer cortex cells, the vacuole occupies approximately 90% of the cell volume, whereas the cytoplasm, which contains chloroplasts, is located peripherally. In the inner part of the cortex, the cytoplasm is dense and contains multiple vacuoles (Figure 3J). The vascular bundles are collateral (Figure 3I) and are located in the median portion of the cortex. Laticifers occur intrusively among the parenchyma cells (Figure 3K).

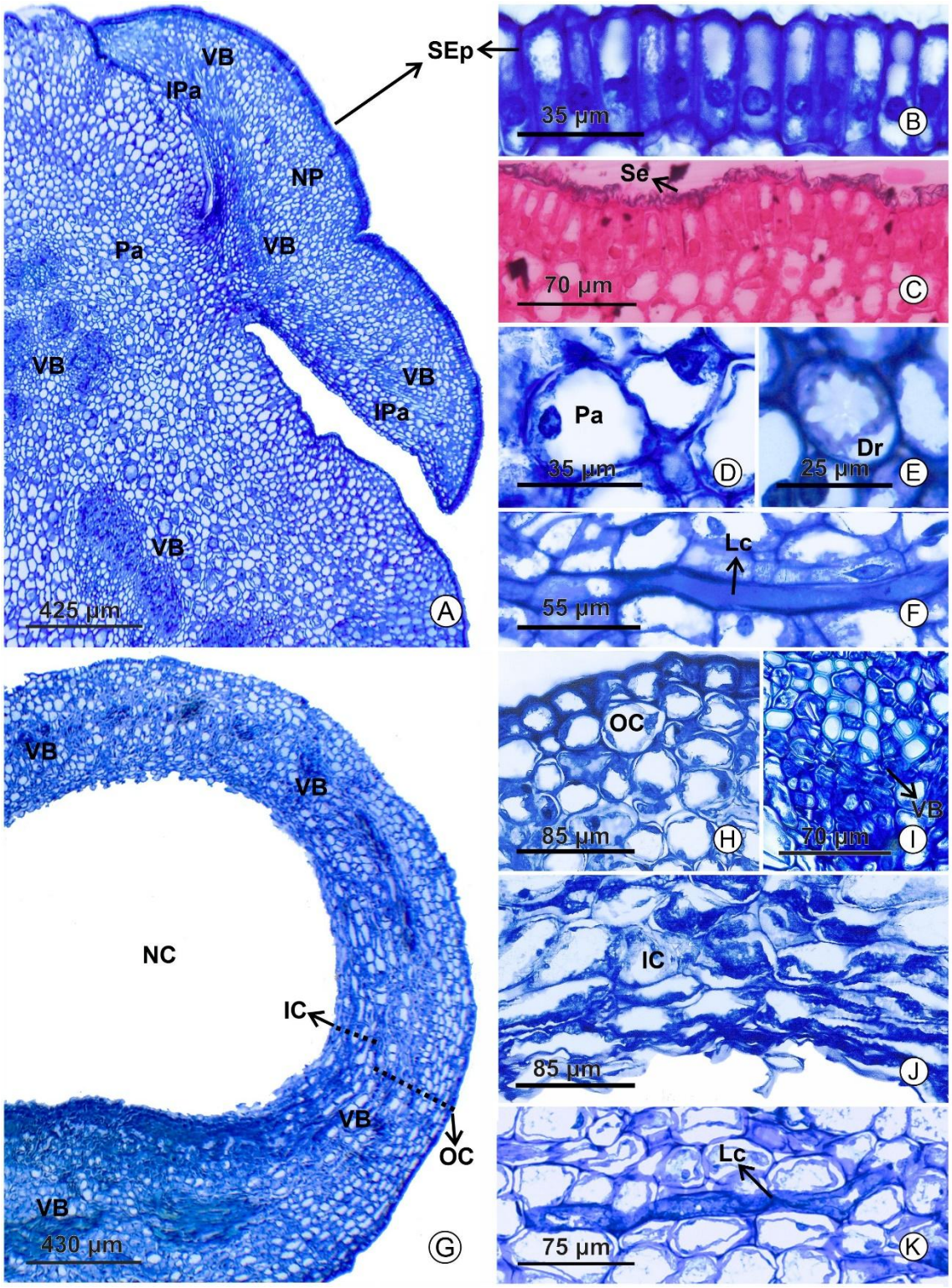


**Figure 3**. Anatomical structure of the non-galled floral nectary (A–F) and the nectary gall induced by *N. fasciatus* (G–K) of *Sapium glandulosum*. A- General view; B- Secretory epidermis; C- Secretory epidermis with PAS test; D- Parenchyma cells; E- Druses; F- Laticifers; G- General view; H- Outer epidermis and outer cortex; I- Collateral vascular bundle; J- Inner cortex; K- Laticifer. Abbreviations: Dr – Druse; IC – Inner cortex; IPa – Internal parenchyma; Lc – Laticifer; NC – Nymphal chamber; NP – Nectariferous parenchyma; OC – Outer cortex; Pa – Parenchyma; Se – Secretion; SEp – Secretory epidermis; VB – Vascular bundle.

*Histology – Non-galled pericarp and pericarp gall*

The non-galled pericarp is composed of exocarp, mesocarp, and endocarp (Figure 4A), classified according to the tissue position, with the exocarp as the outermost layer, the endocarp as the innermost layer, and structurally similar layers, and the mesocarp as the tissue in between. The exocarp consists of a single epidermal layer with square to rectangular cells, lacking trichomes, possessing stomata, and being covered by a thin cuticle (Figure 4B). The mesocarp is predominantly composed of three regions and two tissue types: the outer mesocarp consists of fundamental parenchyma with 20 to 30 layers of compact cells (Figure 4A-C), occasionally containing diffuse crystals. Collateral vascular bundles occur in the median region of the outer mesocarp (Figure 4D), and laticifers are intrusively throughout the tissue (Figure 4G). The inner mesocarp contains large, lignified cells composed of 4 to 6 layers of compact cells (Figure 4C). Between the two mesocarp tissues lies the median mesocarp, which is composed of cells with primary and secondary walls elongated anticlinally (Figure 4C). The endocarp consists of approximately 3–5 layers of lignified cells, with the innermost layer being the epidermis (Figure 4E). The dehiscence zone is represented by a reentrance in the endocarp that suppresses the presence of the lignified layer of the mesocarp (Figure 4F). Laticifers occur intrusively among the parenchyma cells (Figure 4G).

The pericarp gall is predominantly parenchymatous and possess a single nymphal chamber (Figure 4H), formed from modifications of the exocarp and parenchymatous mesocarp tissue. The gall epidermis consists mainly of rectangular cells covered by a thin cuticle that is structurally uniform throughout the gall (Figure 4I). The cortex is predominantly composed of parenchyma, with outer chlorophyllous parenchyma and inner fundamental parenchyma, with isodiametric, multifaceted cells lacking diffuse crystals (Figure 4H). The outer cortical cells are larger than the inner ones, with a few cells exhibiting large and evident nuclei (Figure 4I). In this region, the vacuole occupies approximately 90% of the cell volume, whereas the cytoplasm containing chloroplasts is located peripherally (Figure 4I). The vascular bundles are collateral and occupy the median portion of the cortex (Figure 4H). In the inner cortex, the cells exhibit dense cytoplasm and multiple vacuoles (Figure 4J). Laticifers occur intrusively among the parenchyma cells (Figure 4K).

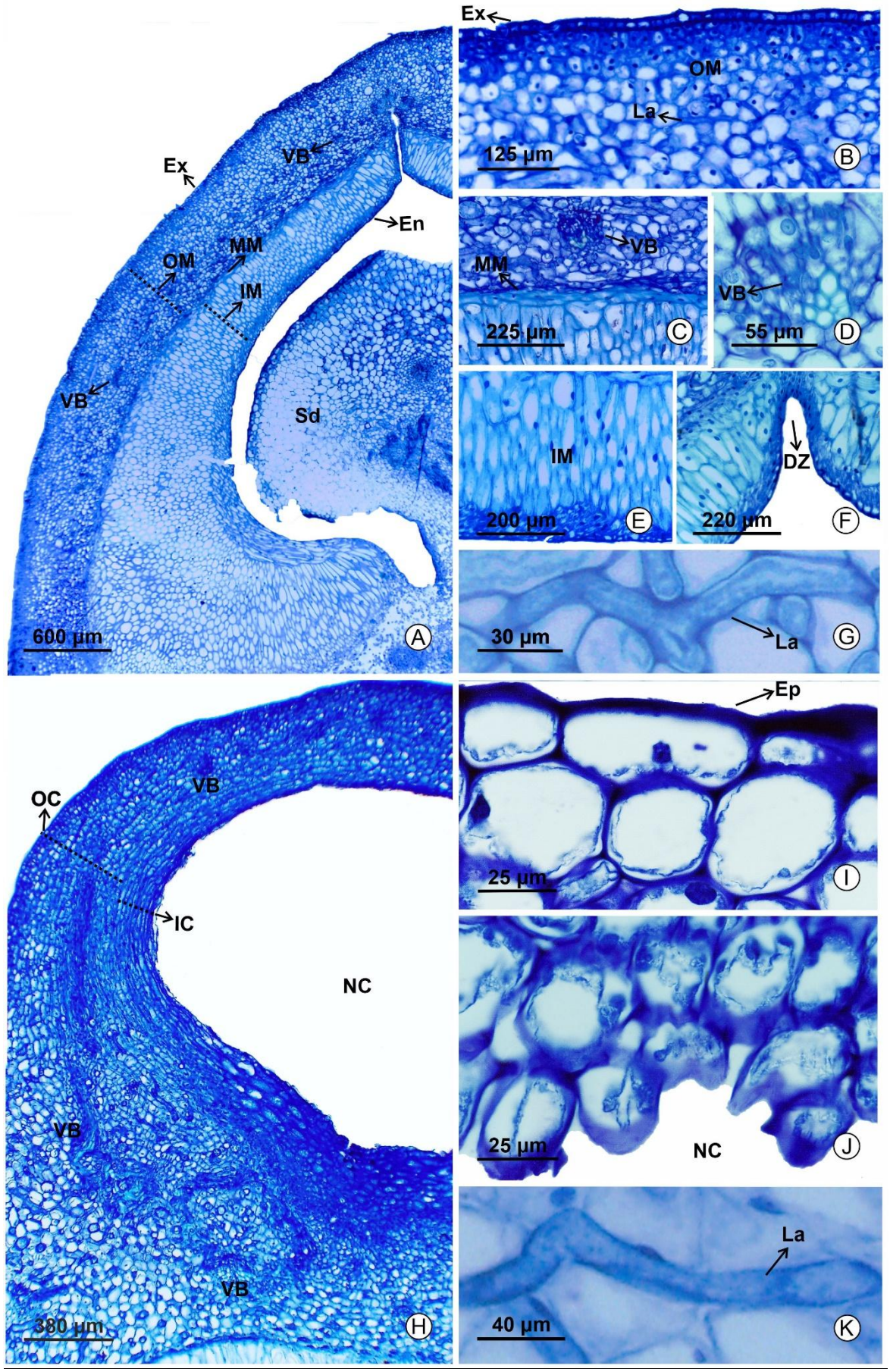
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**Figure 4.** Anatomical structure of the non-galled pericarp (A–G) and the pericarp gall (H–K) of *Sapium glandulosum*. A- General view; B- Exocarp; C- Mesocarp tissues; D- Collateral vascular bundle; E- Endocarp; F- Dehiscence zone; G- Laticifer; H- General view; I- Outer epidermis and subepidermal parenchyma; J- Inner cortex; K- Laticifer. Abbreviations: DZ – Dehiscence zone; Ep – Epidermis; En – Endocarp; Ex – Exocarp; IC – Inner cortex; IM – Inner mesocarp; La – Laticifer; MM – Median mesocarp; NC – Nymphal chamber; OC – Outer cortex; OM – Outer mesocarp; Sd – Seed; VB – Vascular bundle.

*Immunocytochemistry*

Gall formation from the floral nectary and the fruit pericarp of *S. glandulosum* occurred through the remodeling of pectic components in their cell walls, primarily involving changes in the degree of methyl esterification of HGs and modifications of the side chains of RGI (Figure 5).

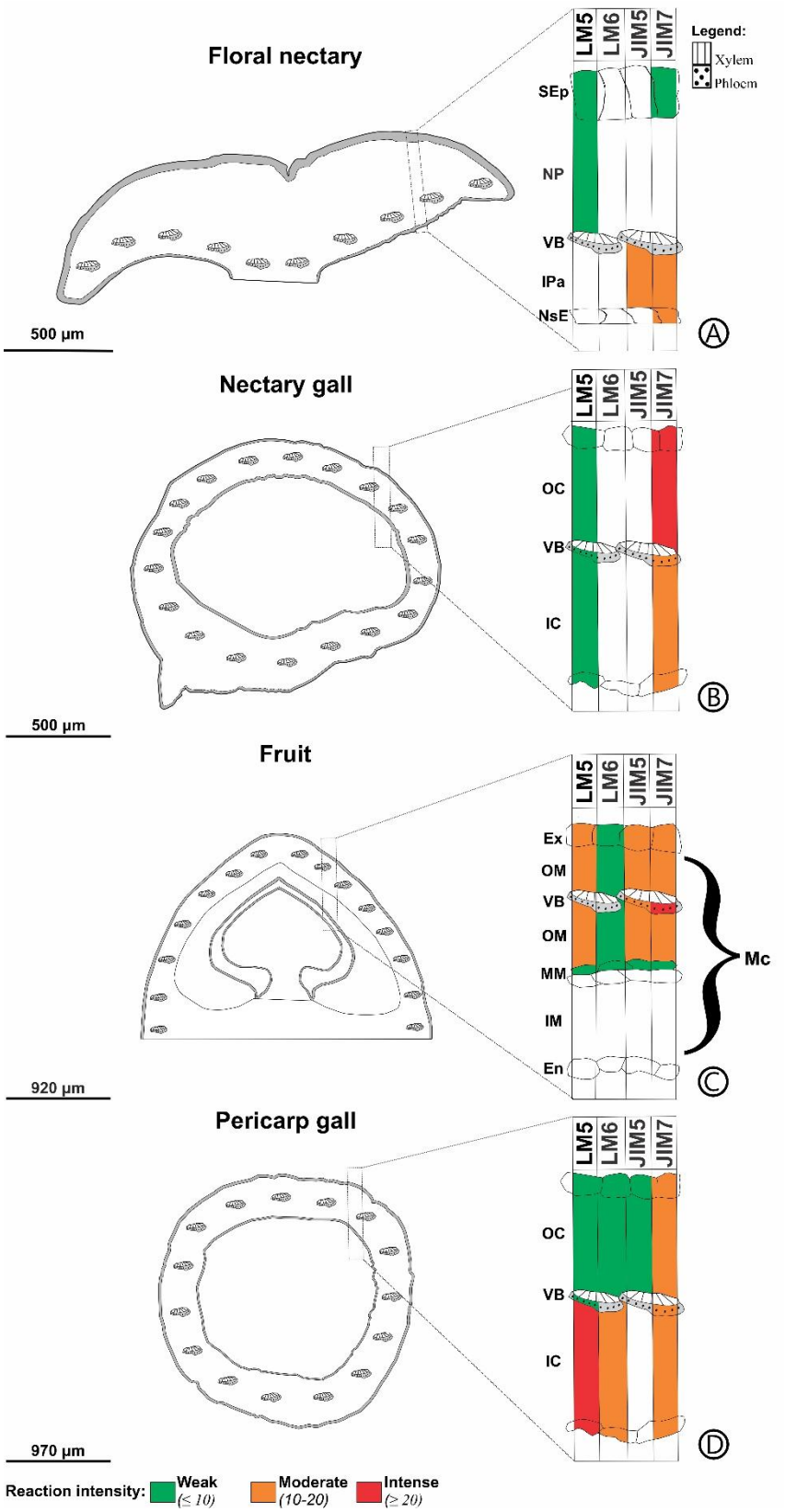


**Figure 5.** Diagram of the non-galled nectary (A), nectary gall (B), non-galled pericarp (C) and pericarp gall (D), showing immunocytochemistry results of *Sapium glandulosum*. Abbreviations: En – Endocarp; Ex – Exocarp; Ic – Inner cortex; IM – Internal mesocarp; IPa – Internal parenchyma; Mc – Mesocarp; MM – Median mesocarp; NP – Nectariferous parenchyma; NsE – Nonsecretory epidermis; Oc – Outer cortex; OM – Outer mesocarp; SEp – Secretory epidermis.

*Immunocytochemistry–Floral nectaries and nectary galls*

In the nectary (Figures 6A–B), LM5, which recognizes β-D-(1→4) galactans, showed weak labeling, primarily at the cell junctions of the secretory epidermis and the nectariferous parenchyma (Figure 5A), whereas LM6 did not detect α-L-(1→5) arabinan epitopes in any of the tissues (Figure 5A). JIM5 moderately labeled partially methyl-esterified homogalacturonans (HGs) only in the cell walls of the inner parenchyma (Figure 5A; Figure 6A), with stronger labeling in the nectary peduncle, suggesting greater structural support for the nectary. Conversely, JIM7 weakly recognized methyl-esterified HGs in the outer periclinal wall of the secretory epidermis (Figure 5A) and in the inner parenchyma and moderately recognized HGs in the inner epidermis (Figure 6B).

In the galls derived from the floral nectary, LM5 labeled the cell walls throughout the cortex and phloem (Figure 5B; Figure 6C). LM6 and JIM5 did not immunolocalize to their respective epitopes. JIM7 showed moderate to strong labeling throughout the cortex and in the phloem (Figure 5B; Figure 6D).

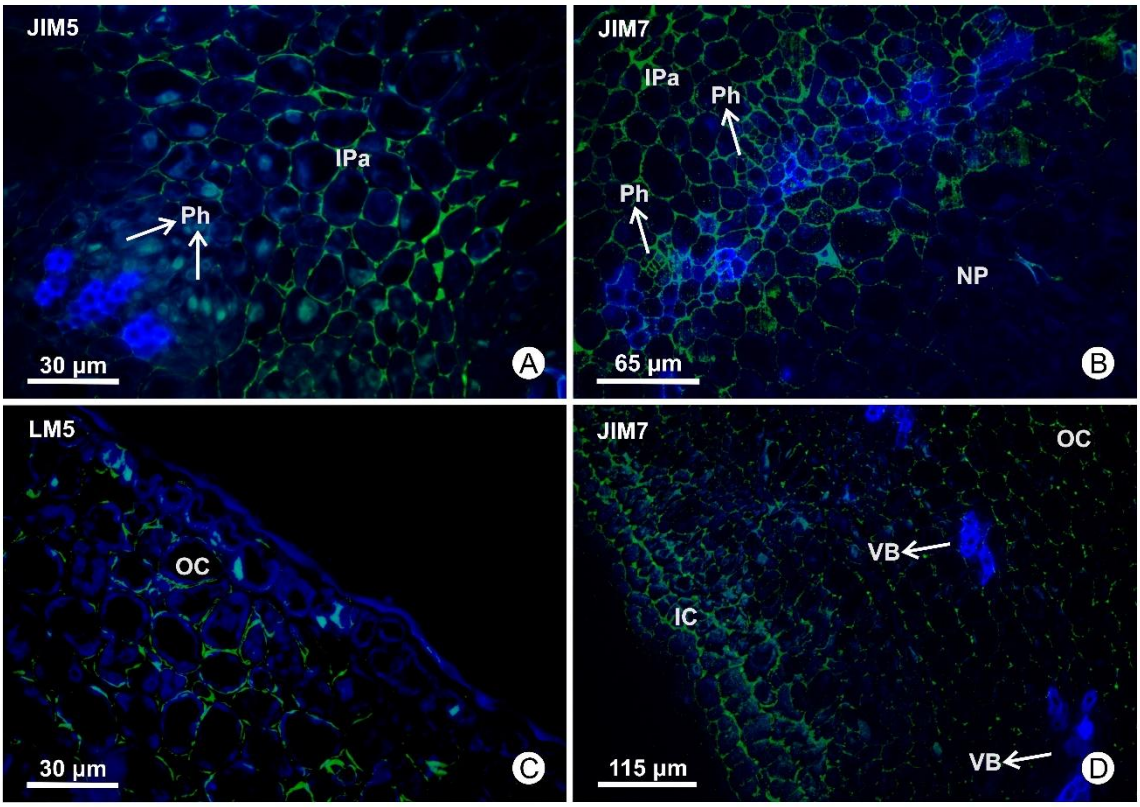


**Figure 6.** Immunocytochemistry of the non-galled floral nectary (A, B) and the nectary gall (C, D) of *Sapium glandulosum*. A – Partially methyl-esterified HGs recognized by JIM5; B, D – Methyl-esterified

HGs labeled by JIM7; C – (1→4)-β-D-galactans recognized by LM5. *Green labeling in the cell wall indicates a positive result for the epitope. Abbreviations: IC – Inner cortex; OC – Outer cortex; Pa – Parenchyma; Ph – Phloem; VB – Vascular bundle.

*Immunocytochemistry – Non-galled pericarp and pericarp gall*

The non-galled pericarp (Figures 5C; 7A–C) exhibited weak to moderate labeling with the LM5 antibody, which recognizes (1→4) β-D-galactans, in the cell walls of the exocarp, outer mesocarp, and median mesocarp, with the latter showing weak labeling (Figures 5C; 7A). LM6, which recognizes (1→5) α-L-arabinans, displayed weak labeling, in the exocarp as well as in the outer and median mesocarp (Figure 5C). JIM5 moderately to weakly recognized partially methyl-esterified homogalacturonans (HGs) in the cell walls of the exocarp, outer mesocarp, and phloem and weakly recognized HGs in the median mesocarp (Figures 5C; 7B). JIM7 moderately to strongly labeled methyl-esterified HGs in the cell walls of the exocarp, outer mesocarp, and phloem (Figures 5C; 7C), as well as weakly in the median mesocarp.

The pericarp gall (Figures 5D; 7D–E) exhibited weak LM5 labeling in the cell walls of the parenchyma of the outer cortex and strong labeling in the inner cortex, as well as weak labeling in the phloem (Figures 5D; 7D). LM6 also showed weak labeling in the outer cortex and moderate labeling in the inner cortex (Figure 5D), mainly at cell junctions. JIM5 showed weak labeling, whereas JIM7 displayed broad, moderate labeling throughout the cortex and in the phloem (Figures 5D; 7E).

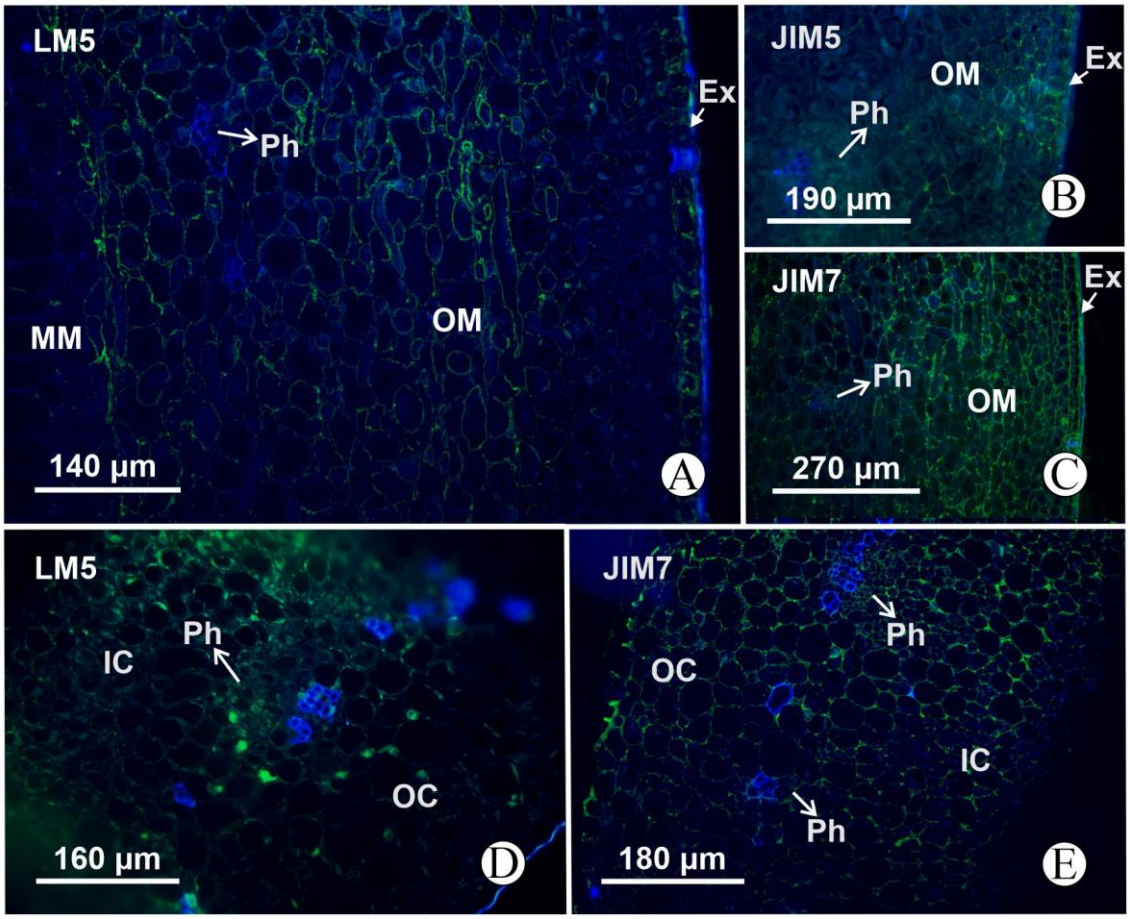


**Figure 7.** Immunocytochemistry of the non-galled pericarp (A-B) and pericarp gall (C-D) of *Sapium glandulosum*. A, C – (1→4) β-D-galactans labeled with LM5; B, D – methyl-esterified HGs recognized by JIM7. *Green labeling in the cell wall indicates a positive result for epitope detection. Abbreviations: Ex – Exocarp; IC – Inner cortex; MM – Median mesocarp; OM – Outer mesocarp; OC – Outer cortex; Pa – Parenchyma; Ph – Phloem; VB – Vascular bundle.

## Discussion

It was observed that the galls of *Sapium glandulosum* induced by *N. fasciatus*, formed both from floral nectaries and from the fruit pericarp, exhibit morphologically similar structures. The galls are globose and green, indicating that the morphogenesis of the affected organs was profoundly reprogrammed by the inducing insect, with alterations in cell division patterns, elongation, and metabolism. A similar process had already been documented in leaf galls of *S. glandulosum* induced by *N. fasciatus* (ROSA et al., 2024), which also exhibited comparable morphological characteristics. Analyses of the immunocytochemical composition of the cell walls in *S. glandulosum* (Euphorbiaceae) galls reinforce this recurrent pattern, highlighting the determining role of the inducer in producing a specific gall phenotype, regardless of the organ of origin, and revealing steps

in their formation and development. Notably, the formation of galls from floral nectaries constitutes a novel finding, with no similar records in the consulted literature.

The anatomical structural similarity among the galls induced in the pericarp and floral nectary was evident, demonstrating that both share a predominance of parenchymatic cells forming a uniform structure throughout the gall, collateral vascular bundles in both floral nectary and pericarp galls, and a single nymphal chamber housing the inducer *Neolithus fasciatus*. The structural resemblance among the different types of galls, including the leaf galls reported by Rosa et al. (2024), was supported by a pectic matrix with characteristic features in the cell walls, although exhibiting convergent functionalities, particularly regarding the maintenance of cellular responsiveness. Immunocytochemical data indicate that, despite the structural convergence observed among the galls, the composition of the cell walls still reflects, to some extent, the particularities of the organ of origin in *S. glandulosum*. This suggests that, although the inducer exerts strong control over gall morphogenesis, constraints imposed by the genotype and the nature of the host organ tissues also influence the outcome of the induced structure.

*Floral nectary and pericarp galls: same inducer and structural convergences*

Galls are structures that originate from the response of host plant tissues to mechanical and/or chemical stimuli induced by an organism (MANI, 1964). In *Aspidosperma macrocarpon* and *A. tomentosum*, the galling insect *Pseudophacopteron longicaudatum* (Hemiptera) induces morphologically similar galls in different plant species, suggesting that the inducer exerts a strong influence on the morphology of the formed galls (MARTIN; GONÇALVES; OLIVEIRA, 2020). The development of these structures occurs under morphogenetic constraints imposed by the host plant genotype and the plasticity of the affected organs (ISAIAS et al., 2014; FORMIGA et al., 2013; OLIVEIRA et al., 2015).

In *Sapium glandulosum*, an influence of the galling insect *Neolithus fasciatus* can be observed across different plant organs, where the morphology and anatomy of the galls are structurally similar. In *Matayba guianensis* (Sapindaceae), galls induced by *Bystracoccus mataybae* (Eriococcidae) form on different organs and at distinct insect stages: stem galls are induced by first-instar nymphs, while leaf galls are formed by second-instar nymphs (SILVA et al., 2021). These galls exhibit distinct morphologies, indicating the influence of both the host organ and the developmental stage of the inducer

on gall formation (MARTINI; GONÇALVES; OLIVEIRA, 2020). Galls of *S. glandulosum* induced by *N. fasciatus* contain only one nymphal stage, with a single nymphal chamber in their structure. The gall morphotype results from the interaction between inducer specificity and the responsiveness of host plant tissues (FORMIGA et al., 2015). In *S. glandulosum*, the induction tissue primarily affected the pectic matrix composition of the gall cell wall, leading to compositional similarity among galls and revealing the high responsiveness of the galled tissue.

The gall inducers in *Croton floribundus* Spreng. (Euphorbiaceae) are Cecidomyiidae species that are not yet fully identified. In this species, four leaf gall morphotypes have been described: globose, lenticular, fusiform, and marginal-rolling (sensu ISAIAS et al., 2013). These galls are induced by at least eight distinct gall-inducing insect species, resulting in eight morphospecies that are morphologically and anatomically distinct (TEIXEIRA et al., 2022). This pattern highlights the species-specific relationship characteristic of galls (MOURA; SOARES; ISAIAS, 2008). Conversely, in *S. glandulosum*, the opposite condition is observed: *N. fasciatus* induces globoid galls with similar tissue profiles regardless of the part of the plant in which they form, whether in leaves (ROSA et al., 2024), floral nectaries, or pericarps. This finding indicates the relative indifference of the inducer to the morphological plasticity of the different galled organs.

The host plant *Psidium cattleianum* Sabine (Myrtaceae) presents globoid galls induced by *Nothotrioza cattleiani* Burckhardt, 2013 (Triozidae), which are morphologically similar to those observed in the congeneric dual system *P. myrtoides* O. Berg, 1857 – *N. myrtoidis* Burckhardt, 2013 (CARNEIRO; BURCKHARDT; ISAIAS, 2013). In addition to having a globoid shape, both galls project toward the abaxial leaf surface and have univoltine cycles (BUTIGNOL; PEDROSA-MACEDO, 2003; CARNEIRO; BURCKHARDT; ISAIAS, 2013). According to Carneiro et al. (2014), the two *Nothotrioza* spp. present phenotypes capable of inducing similar biochemical changes in the cells of their respective *Psidium* hosts. In the case of *N. fasciatus* in *S. glandulosum*, galls formed on leaves (ROSA et al., 2024), floral nectaries and pericarps presented a compartmentalized cortex composed of outer layers with large cells and an inner layer with small, highly metabolic cells, as well as collateral vascular bundles in the median portion of the cortex. These data reinforce that, in addition to the host plant genotype and environmental conditions, the inducing insect plays a key role in determining the specific gall phenotype.

In *S. glandulosum*, floral nectaries are located beneath staminate and pistillate flowers, appear as flattened discs, and are always arranged in pairs. These structures have secretory cells organized in palisades, a common pattern among Euphorbiaceae species (FREITAS et al., 2001; BERNADELLO, 2007; COUTINHO; VALENTE; MEIRA, 2010). Structurally, nectaries consist of nectariferous tissue formed by a secretory epidermis, usually overlaying parenchyma specialized in nectar synthesis and secretion (FAHN, 1972, 1988, 2000). Gall formation on the floral nectaries of *S. glandulosum* causes reorganization of the nectariferous tissue, with loss of its secretory function. This modification compromises nectar production, which likely reduces flower attractiveness to pollinators, and there is a tendency for premature flower abscission, which negatively impacts fruit and seed production. Indeed, the frequent absence of pollination in flowers and inflorescences can lead to floral abscission, interrupting the plant's reproductive cycle (VAN DOORN, 1997; JANSEN-GONZÁLEZ; TEIXEIRA; PEREIRA, 2024). This phenomenon was corroborated in an experimental study with *Thaumatophyllum bipinnatifidum*, where inflorescences with unpollinated flowers presented facilitated abscission (LARSON; WHITHAM, 1997; JANSEN-GONZÁLEZ; TEIXEIRA; PEREIRA, 2024).

Most gall occurrences in angiosperms are concentrated on leaves (77%), followed by stems (10%), floral buds (7%), and fruits (3%) (MANI, 1964; MAIA; SILVA, 2016), with no records to date of galls specifically induced from nectaries. Nectar production by galls is a rare trait along the phylogenetic spectrum of insect-induced galls, recorded only in some cases involving cynipid galls (NICHOLLS et al., 2017). When present, this secretion can provide ecological advantages to inducers by attracting arthropods that protect galls against predators and parasitoids (FERNANDES et al., 1999; INOUYE; AGRAWAL, 2004; ARANDA-RICKERT et al., 2017; NICHOLLS et al., 2017; PIERCE, 2019). However, in the case of galls formed from the floral nectaries of *S. glandulosum*, there is a loss of secretory capacity associated with restructuring of the epidermis, which no longer presents palisade cells. These specialized cells, in their functional form, possess a complex network of cytoplasmic components, such as abundant mitochondria, a Golgi apparatus, and a rough endoplasmic reticulum, reflecting intense metabolic activity directed toward nectar production (PAIVA; MACHADO, 2008; ROY et al., 2017). The replacement of this structure highlights the remarkable capacity for structural and metabolic manipulation by *N. fasciatus*, which is capable of modifying complex and highly specialized tissues of the host plant.

Fruits of representatives of the Euphorbiaceae family exhibit wide morphological variation, with records of schizocarp, capsule, drupe, and berry types (BARROSO et al., 1999). In *Euphorbia* fruits, the pericarp is differentiated into three distinct regions: the exocarp, uniseriate, papillose, and glabrous; the mesocarp, composed of parenchymatous and fibrous regions with lignified macrosclereids arranged perpendicularly to the middle mesocarp; and the endocarp, formed by 2–3 layers of non-lignified fibers, with an epidermis bearing trichomes (GAGLIARDI et al., 2012). In *S. glandulosum*, the fruit shows a structure similar to that of *Euphorbia*, being a dehiscent capsule with sclerenchymatous tissues present in both the mesocarp and endocarp. In *S. glandulosum* fruits, the gall-induced alterations extend from the exocarp to the parenchymatous mesocarp tissue and occur through processes of hyperplasia and cell hypertrophy. This results in the formation of exclusively parenchymatous galls located at the periphery of the fruits. Parenchyma, the most plastic and totipotent plant tissue, is generally the most modified during gall induction (FERREIRA et al., 2019).

*The formation of nectary and pericarp galls is determined by changes in the pectic composition of the cell walls*

The tissue similarity found for nectary and pericarp galls of *Neolithus fasciatus* associated with *S. glandulosum* was not structured by the same pectic matrix in the cell walls, since highly methyl-esterified homogalacturonans (HGs) predominated in nectary galls, and rhamnogalacturonan-I (RGI) with a predominance of (1→4) β-D-galactan side chains associated with methyl-esterified HGs predominated in pericarp galls. The recognition of highly methyl-esterified HGs by JIM7 is generally associated with growth regulation and cell wall elasticity and is particularly evident in metabolically active and expanding cells (XU et al., 2011; COSTA, 2019). In association, RGI with (1→4) β-D-galactans, recognized by LM5, is also linked to cell hypertrophy, flexibility, and elongation, which are typically reported for newly formed tissues (XU et al., 2011). The pectic composition of the cell walls in nectary and pericarp galls indicates the maintenance of metabolically active cells with the capacity for expansion and responsiveness. Cosgrove (2005) and Wolf, Mouille, and Pelloux (2009) discuss the importance of pectins in maintaining cell wall integrity and flexibility, associating them with metabolically active cells. Silva et al. (2021) also highlight the role of pectins in metabolically active cells in galls induced by *Bystracoccus mataybae* on *Matayba guianensis*.

In *Sapium glandulosum* galls, epitope labeling was observed primarily in parenchymatous tissues, reflecting the totipotency of these cells, which can be redirected toward specific functions, such as providing nutrition for the inducer, a phloem-sap–sucking insect (GIRON et al., 2016; SILVA et al., 2021; ISAIAS et al., 2024). Highly methyl-esterified homogalacturonan pectins are frequently found in galls that contain metabolically active cells, as reported for the reserve and nutritive tissues of leaf galls of *Macairea radula* (Melastomataceae), which are induced during the larval stage of *Paleomystella oligophaga* (Lepidoptera) (SANTOS et al., 2024). In the case of galls produced by Hemiptera, such as aphids (Aphididae) and psyllids (Psyllidae), there is no typical nutritive tissue. Instead, a “nutritive-like tissue” has been observed surrounding the nymphal chamber, but it does not have a nutritive function for these inducers (DESNITSKIY et al., 2023).

Although the inner cortical cells of the leaf galls of *S. glandulosum* exhibit high metabolic activity, their cyto-histological profile differs from classical nutritive tissues (ROSA et al., 2024; CARNEIRO et al., 2013). Reserve cells and nutritive-like tissues have already been reported around the vascular bundles in Hemiptera-induced galls in *S. glandulosum* (CARNEIRO; ISAIAS, 2015). Salivary sheaths have been recorded for *Baccharopelma dracunculifoliae*, deposited by the inducers near the parenchyma, vascular bundles, and secretory cavities (ARDUIN et al., 2005). In these systems, the phloem is the main feeding site of the inducer (OLIVEIRA et al., 2020; FERREIRA et al., 2019; OLIVEIRA et al., 2015), and it has also been observed that nutrients from the nutritive-like tissue are indirectly harvested as the inducer feeds (OLIVEIRA et al., 2015).

In mature galls formed from floral nectaries and fruit pericarps of *S. glandulosum*, a low degree of HG demethylesterification was observed, which may indicate partial blockage of pectin methylesterase (PME) activity. This blockage limits the formation of the "egg-box" structure, reducing cell wall rigidity and favoring elasticity and cell hypertrophy (WOLF; MOUILLE; PELLOUC, 2009; HUANG et al., 2023). PME suppression may also represent a strategy of inducing insects to inhibit the defense systems of *S. glandulosum*, since lower demethylesterification of pectins reduces the accessibility of cell wall-degrading enzymes, favoring gall establishment and development (PAGORELKO et al., 2013; WOLF, 2022). This pattern of cell wall modulation, which promotes greater plasticity and expansion of parenchymatous cells, has been documented in other systems, such as the globose galls of *Clinodiplosis* sp. formed on *Croton floribundus* Spreng., 1826 (Euphorbiaceae) (TEIXEIRA et al., 2017).

These data reinforce the hypothesis that pectin dynamics play a central role in gall morphogenesis and functionality, especially because of their influence on cell architecture and the physiological response of the host plant.

The absence of rhamnogalacturonan I (RGI) with (1→5)-α-L-arabinans, recognized by the LM6 antibody, in galls formed from the floral nectaries of *S. glandulosum* indicates that the cells in these structures maintain high responsiveness. This component is associated with cell adhesion, making it a typical marker of late developmental stages of organs (PENHOAT et al., 1987; KUCZAK; KURCZYŃSKA, 2020). In contrast, this epitope was detected in galls formed in the pericarp, indicating greater restriction of cell expansion, maintaining the pattern observed in the non-galled pericarp. This result suggests conservation of the complexity of the pectic matrix between non-galled tissues and their respective galls. While galls induced in nectaries maintain low marking of pectic compounds in the cell walls, those formed in the pericarp preserve a more complex pectic matrix, similar to the original tissue. These data suggest that, despite the structural convergence among different gall types, which often exhibit similar morphologies even when originating from distinct organs, the cell wall composition of the galls reflects the characteristics of their organ of origin. This evidence highlights the influence of morphogenetic constraints imposed by the host tissues (MANI, 1964; FORMIGA et al., 2015; ISAIAS et al., 2024), which are herein determined by the genotype of *S. glandulosum*.

Another relevant aspect is the increased marking of pectic compounds in the cell walls of the phloem in galls compared with their respective non-galled tissues. This increase was especially evident for methyl-esterified homogalacturonans (HGs) and rhamnogalacturonan I (RGI) with (1→4)-β-D-galactans, compounds associated with greater cell wall flexibility. The active expansion metabolism and the flexibility influenced by highly methyl-esterified HGs result in metabolically active cells with the ability to expand (LIU et al., 2017). In the stems of *Malus pumila* galled by *Eriosoma lanigerum*, it was observed that the regions where the inducer fed on the plant's vascular bundles exhibited thinner and more elastic cell walls compared with non-galled regions, indicating an increase in the flow of photoassimilates that facilitates the insect's feeding (NOGUEIRA et al., 2025). A similar pattern was observed in the vascular bundles of galls of *Matayba guianensis* Aubl., 1775 (Sapindaceae) induced by *Bystracoccus mataybae* Hodgson, Isaias & Oliveira, 2013 (Hemiptera: Eriococcidae), where this flexibility facilitated growth and reorganization of the vascular system (SILVA et al.,

2021; OLIVEIRA et al., 2014). In galls of *S. glandulosum*, the increased flexibility of the phloem appears to be functionally related to the increased flow of photoassimilates toward the galls, promoting direct resource supply to the inducer *N. fasciatus*, an insect with a sucking feeding apparatus. This mechanism highlights the gall's capacity to redirect the host plant's metabolism in favor of the inducing organism.

## Conclusion

The results of this study reveal the formation of galls in two relatively uncommon organs: floral nectaries, reported here for the first time as a site of gall induction, and the fruit pericarp. In the floral nectaries, gall induction led to a complete structural reconfiguration, resulting in the loss of sugar-secreting function, whereas in the fruits the reorganization was restricted to the outer pericarp tissues, without affecting the endocarp or directly compromising the seeds. Despite originating from distinct organs, the galls exhibited remarkable structural similarity, highlighting the determinative role of *N. fasciatus* in producing the same globoid morphotype in galls induced from different organs of *S. glandulosum*. Analysis of the pectic matrix revealed compositional variations between similar galls induced in different host organs, particularly regarding the presence of methyl-esterified homogalacturonans (HGs) and rhamnogalacturonan I (RGI) with (1→4)-β-D-galactan side chains. Nevertheless, despite these structural differences in the composition of the cell walls, the labeling patterns indicated convergent functional traits, with a predominance of cells maintaining high responsiveness, an essential feature for gall development and metabolic maintenance.

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