



Anther glands in Mimosoideae (Leguminosae) are emergences with a conserved meristematic origin



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ABSTRACT

The six distinct gland types described in Mimosoideae anthers vary from simple projections to robust and vascularized structures. The origin of these glands is attributed to an extension of connective. However, except for an illustrative recording of some developmental stages, nothing is known about the origin and gland development, which prevents their correct classification. This study aimed to elucidate the ontogeny of four of the six gland types detected in the anthers of Mimosoideae. The intention was to understand whether the morphological diversity results from different ontogenetic processes. For this, flower buds of various sizes of four Mimosoideae species with different types of glands were collected: *Stryphnodendron adstringens* (Piptadenia subtype Piptadenia), *Tetrapleura tetraptera* (Piptadenia subtype Adenantha), *Adenantha pavonina* (Piptadenia subtype Entada), and *Pentaclethra maculosa* (Pentaclethra type). The samples were processed for surface (scanning electron microscopy) and anatomical analyses (light microscopy). Despite their morphological differences, the glands share a common meristematic origin. They arise from simultaneous divisions in the first three layers of meristematic cells that cover the apical portion of the young anther. After the formation of the protuberance, the developing glands undergo different specialized processes that include (1) elongation of the epidermal cells in Piptadenia subtype Adenantha and Piptadenia subtype Entada, (2) degradation of central gland cells in Piptadenia subtype Entada, (3) change from a rounded to a triangular shape in the Pentaclethra type, and (4) cell differentiation into a procambial meristem and subsequently into vascular tissue in the Pentaclethra type, resulting in the diversity encountered in the group. Their origin from protodermal and fundamental meristem cells characterizes the anther glands as emergences. Our data indicate a conserved meristematic origin of glands, favoring the hypothesis of homology of these structures and supporting the monophyly of the Mimosoideae clade.

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1. Introduction

The term gland is extensively used to designate various types of secretory structures in plants, such as trichomes, salt glands, colleters, digestive glands, and nectaries (see Lüttge, 1971; Fahn, 1979, 1990). They are multicellular structures that take on different shapes and act in the interaction of plants with the environment by secreting exudates (Fahn, 1979, 2002).

Gland classification can be based on different criteria such as location of the structures in the plant body, function, and nature of the secreted exudate, among others. These classification systems have not been considered to be fully satisfactory (Werker, 2000). Comparative ontogeny of the glands showing their meristematic origin and developmental stages can contribute to a more natural classification. For example, determining whether epidermal projections are trichomes or emergences can be very difficult without ontogenetic studies (Fahn, 1990; Werker, 2000; Souza et al., 2013). If we consider a classification according to the meristematic origin of the glands, these projections are defined as trichomes if they originate from protoderm cells and as emergences if they originate from protoderm cells and underlying tissues (Ramayya, 1964; Fahn, 1979; Souza et al., 2013).

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In particular, the glands present on the anthers of Mimosoideae species (Leguminosae) show wide morphological diversity and provide traits of taxonomic value (Luckow and Grimes, 1997; De Barros and Teixeira, 2016) and of potential phylogenetic significance in the clade since glands with structural similarities occur in closely related groups (De Barros and Teixeira, 2016). However, little is known about the origin and developmental stages of these glands, a fact that impairs their natural and appropriate classification. In addition to permitting structural characterization, results obtained in ontogenetic studies provide evidence for the definition of homologies and synapomorphies in the taxonomic groups in which they occur, thus being of fundamental importance for a correct classification of the glands (Souza et al., 2013).

At least six types of anther glands have been described for Mimosoideae species (Luckow and Grimes, 1997; De Barros and Teixeira, 2016): (1) the Piptadenia type subtype Piptadenia, a pedunculated gland with a rounded apex consisting of isodiametric cells; (2) the Piptadenia type subtype Adenantha, a pedunculated gland with a rounded apex consisting of an epidermis of radially elongated cells that delimit central isodiametric cells; (3) the Piptadenia type subtype Entada, a pedunculated gland with a rounded apex consisting of an epidermis of radially elongated cells that delimit a lumen; (4) the Pentaclethra type, a robust gland of triangular shape with a vascularized peduncle with an apex consisting of palisade epidermis that delimits central isodiametric cells; (5) the Prosopis africana type, a robust, sessile and vascularized gland consisting of a poorly voluminous epidermal cells delimiting central isodiametric cells, and finally (6) the Gagnebina type, a gland of acuminate shape consisting of elongated cells.

The origin of these glands has been attributed to an extension of connective tissue (Chaudhry and Vijayaraghavan, 1992; Luckow and Grimes, 1997), information that has been documented in the literature only with a scheme of the developmental stages of the gland on the anther of *Acacia catechu* (= *Senegalia catechu*) (Rao, 1954), and with few images of the developing gland of *Prosopis juliflora* (Chaudhry and Vijayaraghavan, 1992), which are insufficient to explain the morphological diversity of the anther glands occurring in Mimosoideae.

Thus, the objective of the present study was to elucidate the origin and the main developmental stages of four of the six gland types previously described in Mimosoideae in order to determine whether the morphological diversity of the glands results from distinct ontogenetic processes. The following species were chosen as models considering their gland types: *Styphnodendron adstringens* (Mart.) Coville (Piptadenia subtype Piptadenia), *Tetrapleura tetraptera* (Schumacher & Thonn.) Taub. (Piptadenia subtype Adenantha), *Adenantha pavonina* L. (Piptadenia subtype Entada), and *Pentaclethra macroloba* (Willd.) Kuntze (Pentaclethra type).

2. Materials and methods

Buds of various sizes and flowers of *Styphnodendron adstringens* (Piptadenia subtype Piptadenia), *Tetrapleura tetraptera* (Piptadenia subtype Adenantha), *Adenantha pavonina* (Piptadenia subtype Entada) and *Pentaclethra macroloba* (Pentaclethra type) were collected and immediately fixed in buffered formalin for 48 h (Lillie, 1954). The samples were dissected under a stereomicroscope and the anthers were processed for surface analysis of the developing gland by scanning electron microscopy (SEM) and for anatomical analysis by light microscopy (LM).

Voucher material was deposited in the SPFR Herbarium (FFCLRP-USP, Ribeirão Preto, USP) under the following access numbers: SP Teixeira 73 & TC Barros for *Adenantha pavonina* (Fig. 1A), SP Teixeira 72 & TC Barros for *Pentaclethra macroloba* (Fig. 1B), SP

Teixeira 68 & TC Barros for *Styphnodendron adstringens* (Fig. 1C), and TC Barros 05 for *Tetrapleura tetraptera* (Fig. 1D). The samples for SEM and the anatomical sections are stored in the Botany Laboratory, Faculty of Pharmaceutical Sciences of Ribeirão Preto, University of São Paulo.

For surface analysis (SEM) the fixed samples were dehydrated in an ethanol series (Tucker, 1993), submitted to critical point drying in a Bal Tec CPD 030 dryer, mounted on a metal support on an adhesive carbon strip and sputtered with gold with a Baltec SCD 050 sputter for 360 segundos. A Zeiss IVO-50 scanning electron microscope was used for the observations at 15 kv.

For the anatomical study, the samples were dehydrated in an ethanol series, embedded in historesin (Gerrits, 1991) and cut lengthwise into 2 to 3 µm-thick sections with a Leica RM2245 rotary microtome. The serial sections were stained with 0.05% Toluidine Blue in phosphate buffer, pH 5.8 (O'Brien et al., 1964), mounted in water, and observed and recorded under a Leica DM 4500 B light microscope coupled to a Leica DFC 320 digital camera.

3. Results

3.1. Meristematic origin of anther glands

The glands arise during intermediate stages of stamen development and their complete development is concomitant with stamen development (Figs. 2A–F).

They originate from simultaneous divisions in the first three cell layers (L1, L2 and L3 – see Fig. 3A–C) that cover the apical portion of the young anther (Figs. 3B, 3Ca and 3Cb), before the differentiation of androspore mother cells (pre-meiosis) in the gametangium.

L1 cells undergo anticlinal mitotic divisions (Fig. 3Cc), L2 cells undergo anticlinal and periclinal mitotic divisions, with the periclinal divisions frequently occurring in the more apical region of the young anther (Fig. 3Cd), and L3 cells undergo mitotic divisions on many planes (Fig. 3Ce). The young gland is characterized as a small protuberance on the apical region of the developing anther.

3.2. Intermediate and final stages of gland development

After the onset of the protuberance on the young anther, the apical cells continue to show high mitotic activity and the protuberance takes on a slightly acuminate shape followed by a rounded shape.

3.2.1. Piptadenia type glands

3.2.1.1. subtype Piptadenia. After the formation of the rounded protuberance (Fig. 4 A and B), the peduncle starts to differentiate (Fig. 4C) while the apex of the gland concomitantly becomes increasingly rounded. The gland continues to develop by mitotic division without changing its format or undergoing any other process of cell specialization, resulting in a pedunculated gland with a spherical apex consisting of isodiametric cells (Fig. 4D).

3.2.1.2. subtype Adenantha. After the formation of the initial protuberance (Fig. 4E), the peduncle starts to elongate in parallel to an increase in volume and to the radial elongation of epidermal cells (Fig. 4F). The epidermal cells become more voluminous and more distinct from the central cells of the gland, which continue to be isodiametric (Figs. 4G and 4H). This process results in a pedunculated gland with spherical apex consisting of a layer of radially elongated epidermal cells delimiting the central isodiametric cells.

3.2.1.3. subtype Entada. This gland type develops like the Piptadenia type gland subtype Adenantha. However, after the increase in volume and the radial elongation of the epidermal cells (Fig. 4I),

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