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Research Article

Croceous glands are oil secretory cavities in fruits of *Senega longicaulis* (Polygalaceae)

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Abstract – Croceous glands are yellowish glands that occur exclusively in some species of *Senega* Spach (Polygalaceae). These glands are especially conspicuous in reproductive organs, such as the fruits, but their structure, origin, and secretion are still uncertain. The objective of this study is to determine the nature of the croceous glands in *Senega* from an analysis of the fruits of *Senega longicaulis* (Kunth) J.F.B. Pastore. Flowers and fruits at different developmental stages were analysed through light microscopy and scanning electron microscopy to investigate the origin, structure, and composition of the secretion of the glands. Croceous glands of the pericarp are cavities that originate early, while still in the ovary, through a schizolysigenous process. In addition, new glands are formed *de novo* during fruit development, and the persistent calyx observed surrounding the fruit, also has such cavities. The secretory tissue is constituted by a single layer of epithelial cells, lining a spheroidal lumen that stores the secretion. The exudate is composed of essential oils, indicating functions related to protection against herbivory and microbial attacks. Our results partially diverge from previous reports, and further comprehensive analyses of Polygalaceae glands are essential to understand the nature of croceous glands and the evolution of defence strategies within the family.

Keywords: cavities, defence, ovary, Polygalaceae, schizolysigeny, *Senega longicaulis*, terpenes

Introduction

Croceous glands are conspicuous yellowish glands observed in the vegetative and reproductive organs of some Neotropical species of Polygalaceae (Chodat 1893). Their occurrence has taxonomic importance and has already been used to delimit a section of *Polygala* – *Timutua* DC. (Pastore and Harley 2009, Pastore 2018). Recently, the Neotropical species of *Polygala* were segregated to the genus *Senega* Spach, now the only genus in which the croceous glands occur, being reported for the new sections *Cruciatae* J.F.B. Pastore & J.R. Abbott, *Galioidae* (Chodat) J.F.B. Pastore, *Incarcanatae* (Chodat) J.F.B. Pastore & J.R. Abbott and *Trichospermae* (Chodat) J.F.B. Pastore & J.R. Abbott (Lüdtke et al. 2013, Pastore 2018, Pastore et al. 2023). The genus *Senega* comprises 229 chiefly Neotropical species (Pastore et al. 2023).

The nature and function of croceous glands have intrigued researchers since they were first described, but they have only recently been analysed for the first time in *Senega adenophora* (DC.) J.F.B. Pastore (= *Polygala adenophora*) by Jorge et al. (2024), who observed that these glands are cavities and ducts present in both vegetative and reproductive organs. The secretory spaces (cavities and ducts) are widely used in the characterisation of numerous other genera within Fabales (Teixeira and Rocha 2009, Milani et al. 2012, Duarte-Almeida et al. 2015, Mendes et al. 2019). Despite the taxonomic potential of these glands for Polygalaceae (Chodat 1893, Holm 1929, Metcalfe and Chalk 1950, Aguiar-Dias and Cardoso-Gustavson 2011, Jorge et al. 2024), there is little information in the literature about them.

Internal glands, such as idioblasts, laticifers, cavities and ducts, generally have a defensive function (Fahn 1979, Costa

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et al. 2021, Tölke et al. 2021, 2022, Freitas et al. 2024). However, analysis of the structure of the gland alone is not sufficient to identify it, as its function depends, at least in part, on the composition of its secretion (Fahn 1979, Demarco 2023). In this context, to determine the nature of croceous glands, we selected *Senega longicaulis* (Kunth) J.F.B. Pastore, a species in which these glands had previously been observed in the fruits (pers. obs.). This species belongs to *Trichospermae*, a section characterised by the presence of bilocular capsule-type fruits with a persistent calyx, in which croceous glands are present in both the perianth and pericarp (Pastore et al. 2023).

The glands of Polygalaceae may provide data on potential functions, insights into ecological relationships, as well as anatomical novelties with taxonomic and evolutionary significance. Therefore, this study aimed to understand (1) what type of gland croceous glands correspond to, (2) the origin and anatomical structure of these glands, and (3) the composition and potential function of their secretion.

Material and methods

Plant material

Flowers and fruits of *Senega longicaulis* (Kunth) J.F.B. Pastore at different developmental stages were collected in Marapanim (Pará, Brazil), and voucher specimens were deposited in the MG Herbarium of the Museu Paraense Emílio Goeldi (MG 248141). The analysis of reproductive organs was based on previous observations of croceous glands in this species.

Structural and ontogenetic analyses

Ovaries with the persistent calyx and samples of developing and mature fruits were isolated, fixed in formalin–acetic acid–alcohol (FAA) solution for 24 h (Johansen 1940) and buffered neutral formalin in 0.1 M sodium phosphate buffer (pH 7.0) for 48 h (Lillie 1965). Part of the material was dehydrated through a tertiary butyl alcohol series (Johansen 1940), embedded in Paraplast® (Leica Microsystems Inc., Heidelberg, Germany) and serially sectioned on a Leica RM2245 rotary microtome at 11 μm thickness. The sections were stained with astra blue and safranin O (Gerlach 1984), and the slides were mounted with Canada balsam. The other part of the fixed material was dehydrated in an ethanol series, embedded in Leica Historesin®, and serially sectioned at 5 μm thickness. The sections were stained with toluidine blue pH 4.8 (O'Brien et al. 1964). Observations and photographic register were performed using a Leica DM6 B light microscope.

Analysis of secretion composition

The composition of the croceous gland secretion was investigated using the histochemical tests: Sudan black B for lipids (Pearse 1985), Nile blue for acidic and neutral lipids (Cain 1947), Nadi reagent for terpenoids (essential oils and resin; David and Carde 1964), periodic acid–Schiff's (PAS) reaction for polysaccharides (Jensen 1962), ruthenium red for acidic mucilage (Gregory and Baas 1989), tannic acid and ferric chloride for mucilage (Pizzolato 1977), Lugol's reagent for starch (Johansen 1940), fixation in ferrous sulphate–formalin for phenolic compounds (Johansen 1940), and Dragendorff's reagent for alkaloids (Svedsen and Verpoorte 1983). Standard control procedures were carried out according to Demarco (2023).

Micromorphological analysis

For the micromorphological study, the FAA-fixed samples were dehydrated in a graded ethanol series, dried by the critical point method, mounted on aluminium stub, and sputter-coated with gold, with subsequent observation in a Tescan Mira3 scanning electron microscope (Tescan, Brno, Czech Republic).

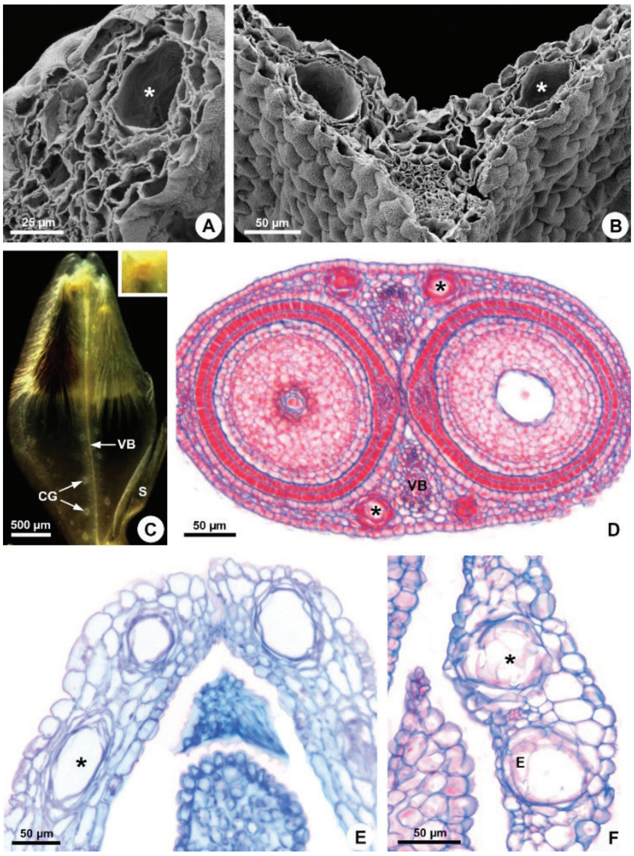

Fig. 1. Croceous glands (secretory cavities) in fruits (pericarp) and calyx of *Senega longicaulis*. Ellipsoidal cavity in the pericarp close to the septum (A), secretory cavities in the sepal near the vascular bundle (B), croceous glands forming two rows along with the pericarp vascular bundle, extending from the top to the base of the fruit (C); note the yellow secretion within the croceous gland (inset) and the presence of a persistent calyx with the fruit. Secretory cavities in the ovary near the synlateral vascular bundles (D), longitudinal rows of secretory cavities in the pericarp (E), secretory cavities in the sepal (F); note the presence of epithelium: CG – croceous gland, E – epithelium, S – sepal, VB – vascular bundle, asterisk – secretory cavity. Longitudinal sections (A, E). Transversal sections (B, D, F). Translucent fruit after fixation (C). Scanning electron microscopy (A-B). Stereomicroscopy (C). Light microscopy (D-F).

Results

The yellowish croceous glands of *Senega longicaulis* occur in the pericarp (Fig. 1A, C) and in the persistent calyx (Fig. 1B) that surrounds the fruit (Fig. 1C). These glands are cavities arranged in longitudinal rows following the main vascular bundles (Fig. 1C-F). Their shape varies from spherical to ellipsoidal (Fig. 1A-F), and, in the latter case, the major axis never exceeds twice the length of the minor axis (Fig. 1A). Although the cavities are aligned and close to each other, they are not adjacent and never merge (Fig. 1C, E).

Pericarp

In the pericarp, the cavities occur only in the septum and are arranged in four rows, close to the synlateral/synventral vascular bundles (Fig. 1C-D), extending from the top to the base of the fruit (Fig. 1C). These cavities are formed early in the ovary (Fig. 2A-J), but new cavities are originated *de novo* during fruit development, increasing the number and extension of the cavity rows along with the fruit expansion (Fig. 2K). In the ovary, they originate from the ground meristem (Fig. 2A) and are observed in the ovarian mesophyll (Fig. 1D), whereas in the pericarp (Fig. 1E) the new cavities are formed by meristematic cells of the mesocarp.

Calyx

The cavities found in the persistent calyx are located in the mesophyll and are arranged in rows along the sepals, near the midrib (Fig. 1F). As the cavities formed during floral development, these are also originated from ground meristem. There is no formation of new cavities during fruiting.

Structure and ontogeny

The cavities in the calyx, ovary, and pericarp are similar, formed by a uniseriate secretory epithelium composed of globose secretory cells during the secretory phase (Fig. 1F, Fig. 2J), which become flattened in the post-secretory phase (Fig. 2K).

The ontogeny of the cavities begins with a meristemoid (Fig. 2A), a cell rich in cytoplasm that expands, becoming much larger than the others. Successive divisions of the meristemoid form a cluster of cells (Fig. 2B), and periclinal divisions (in relation to the location of the future lumen) form a peripheral layer that will give rise to the epithelium (Fig. 2C). The central cell remains much larger than those that surround it. After multiple divisions (Fig. 2D-F), the cluster assumes a spherical or ellipsoidal shape, and the cells split away (schizogeny), leaving the large central cells more or less loose in the centre (Fig. 2G). The surrounding cells, which will become the secretory epithelium, continue to move away, and large vacuoles are observed in the central cells, marking the beginning of the programmed cell death (Fig. 2H). Subsequently, the vacuole ruptures, and the walls of the central cells dissolve, causing the complete lysis of these cells, which disintegrate (lysigeny), originating the cavity lumen (Fig. 2I).

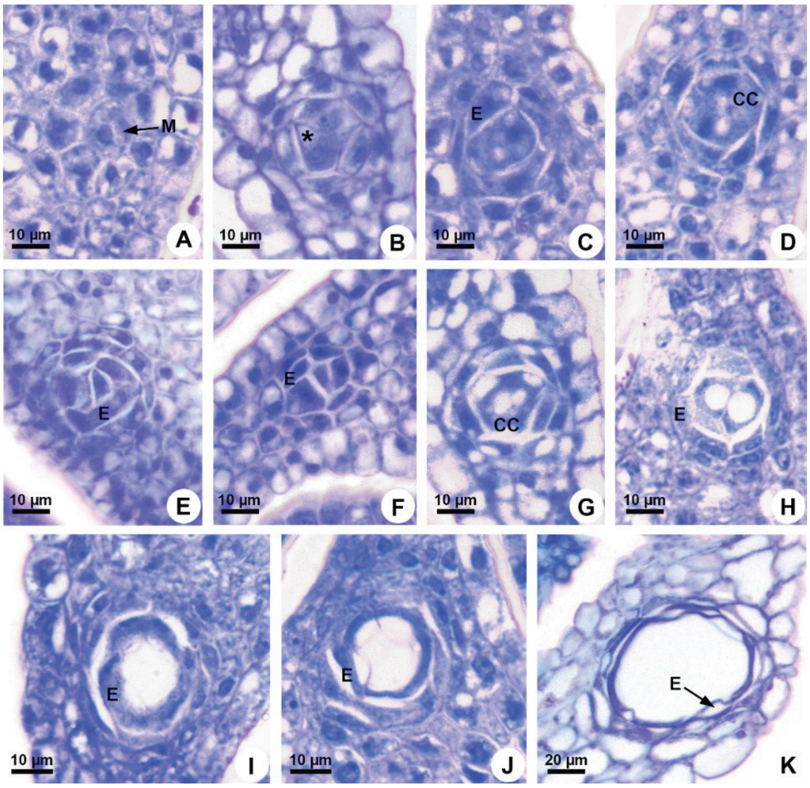

Fig. 2. Ontogeny of the croceous gland (secretory cavity) of *Senega longicaulis*. Meristemoid, *i.e.*, initial cell of the cavity (A), first division of the meristemoid (asterisk) (B), periclinal division giving rise to the layer that will originate the epithelium (C), subsequent cell divisions forming a cluster of meristematic cells (D-F), vacuolation of the central cells; beginning of the programmed cell death (G), separation (schizogeny) of the epithelium from the central cells, which are dying (H), epithelium in secretory activity after the lysis of the central cells (I-J). Epithelium in post-secretory phase (K), Ovary (A-J) and pericarp (K). M – meristemoid, CC – central cells, E – epithelium.

Then, the epithelial cells start their secretory activity (Fig. 2J), releasing the secretion into the lumen.

Since cavities are also formed during fruit development, their origin is asynchronous, and cavities at different developmental stages can be observed from the ovary to the mature fruit.

Secretion composition

The cavities are oleiferous (Tab. 1, Fig. 3).

Histochemical analysis revealed the exclusive presence of lipids in the secretion (Fig. 3A-B), identified as essential oils (Fig. 3C), *i.e.*, volatile terpenes.

stele corners of the stem (Holm 1929, Metcalfe and Chalk 1950). In addition, mucilaginous ducts have been observed in the same position in the stems of *Senega poaya* (as *Polygala angulata*; Aguiar-Dias and Cardoso-Gustavson 2011). Although these glands are not croceous, they demonstrate that secretory spaces are present in other species of the genus, and are distinguished by the composition of the secretion.

Internal secretory structures typically occur throughout the entire plant. On the other hand, when their occurrence is restricted to specific locations, this peculiar distribution usually has taxonomic potential, as previously noted for idioblasts and laticifers (Metcalfe and Chalk 1950, Demarco et al.

Tab. 1. Histochemical tests performed on the croceous glands (secretory cavities) of fruits of *Senega longicaulis* (+ = present; - = absent).

Histochemical test	Target substance	Croceous gland
Sudan Black B	lipids	+
Nile blue	acidic and neutral lipids	+
Nadi reagent	essential oils and resin	+
PAS reaction	polysaccharides	–
Ruthenium red	acidic mucilage	–
Tannic acid and ferric chloride	mucilage	–
Lugol's reagent	starch	–
Ferrous sulphate-formalin	phenolic compounds	–
Dragendorff's reagent	alkaloids	–

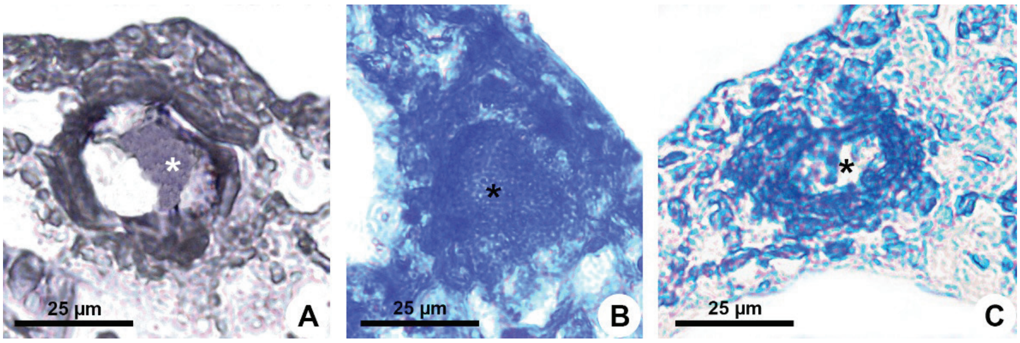

Fig. 3. Histochemical analysis of the croceous gland (secretory cavity) of *Senega longicaulis*. Lipids detected using Sudan black B (A), lipids stained with Nile blue (B), essential oils identified using Nadi reagent (C). Asterisk - secretion detected in the croceous gland lumen.

Discussion

Our study revealed that the croceous glands of *Senega longicaulis* are oil cavities whose yellow colour, typical of these glands, is due to their lipid secretion. This result partially diverges from previous findings for *Senega adenophora*, in which croceous glands can be either ducts or oil cavities (Jorge et al. 2024). Despite this, the nature of the croceous glands has been elucidated and they can be considered, in general terms, secretory spaces (*sensu* Fahn 1979), a generic term that encompasses both types of epithelial glands.

In Polygalaceae, cavities have been described in the leaves (mesophyll) of *Senega paniculata* (L.) J.F.B. Pastore & J.R. Abbott (= *Polygala paniculata* L.; Aguiar-Dias et al. 2012). Cortical oil ducts were also reported in some species of North American *Polygala*, which are almost always located in the

2013), and/or implications regarding their origin and function, as reported for ducts (Costa et al. 2021, Tölke et al. 2021). In *S. longicaulis*, we observed that the cavities of the ovary and pericarp occur only in the septum, forming four rows adjacent to the synventral bundles, and in the sepals only near the midrib. No croceous glands were observed in any other part of the fruit or calyx. This distribution is similar to that reported for the croceous glands in the same organs of *S. adenophora* (Jorge et al. 2024) and might have taxonomic and/or systematic significance, particularly considering that croceous glands are restricted to the genus *Senega*. Further studies are needed to evaluate the croceous glands present in vegetative organs as well (Jorge et al. 2024).

The co-occurrence of secretory cavities and ducts has already been described in leaves and stems of some North American species of *Polygala* (Holm 1929, Metcalfe and

Chalk 1950), and many other reports are found for Asteraceae, Boraginaceae, Combretaceae, Hypericaceae, Malvaceae, Polygalaceae, Rutaceae, Salicaceae, among others (Metcalfe and Chalk 1950, Aguiar-Dias and Cardoso-Gustavson 2011, Aguiar-Dias et al. 2012, Fernandes et al. 2018, Garcia et al. 2020, Tölke et al. 2022). Furthermore, cavities and ducts have been described as occurring side by side within the same organ in some species (Fernandes et al. 2018, Garcia et al. 2020, Tölke et al. 2022, Jorge et al. 2024). Considering that in many of these reports both structures have the same origin and secrete the same exudate, further studies are needed to verify the mode of formation of these epithelial glands. In Malvaceae, it was discovered that the ducts originate from the coalescence of aligned and contiguous cavities (Garcia et al. 2020), similarly to the findings of Jorge et al. (2024) for *S. adenophora*.

Cavities and ducts are histologically and ontogenetically similar. The only difference between these two glands lies in their three-dimensional shape, which is more or less spherical in cavities and elongated in ducts (Fahn 1979). It is not yet possible to establish whether there is an anatomical pattern for the croceous glands of Polygalaceae since multiseriate epithelial cavities have been observed in *S. adenophora* (Jorge et al. 2024), whilst we found uniseriate epithelium cavities in *S. longicaulis*. However, there does seem to be an ontogenetic pattern. In both species studied so far, croceous glands are formed from the ground meristem in the same locations and have a lumen formed by a schizolysigenous process, in which the separation of cells occurs first and then the central cells disintegrate through programmed cell death. However, this developmental process does not always occur in this sequence. In the ducts of *Kielmeyera* Mart. & Zucc., the schizolysigenous formation of the lumen begins with the lysis of the central cells of the rosette, forming an initial space, followed by the separation of the remaining cells. This mixed lumen formation involves cytoskeletal rearrangement and various coordinated subcellular changes during programmed cell death (Costa and Demarco 2024).

The composition of the secretion of croceous glands and its mode of release into the lumen in *S. longicaulis* are also consistent with those observed in *S. adenophora* (Jorge et al. 2024), which seems to indicate a pattern for this type of gland within the family. In both species, the mode of release is merocrine, and the epithelium can be observed in mature glands in the post-secretory phase.

Based on the current data, the yellowish secretion, typical of croceous glands, is composed of volatile oils (terpenes). Similar oil cavities, visualised as pellucid dots, are characteristic of some families, such as Rutaceae and Myrtaceae. In both families, the cavities occur in vegetative organs, flowers and fruits, and their volatile oils are composed of terpenes with the role of defence (eventually, phenolic compounds; Metcalfe and Chalk 1950, Lange 2015, Paschoalini et al. 2022, Tölke et al. 2022, Ladd 2024). As described for those two families, the structure, distribution, and composition of the secretion of croceous glands indicate a protective function in *Senega*.

Volatile oils, produced by internal glands and released only when the tissue is disrupted, act in defence against herbivores and microorganisms (Waterman 1992, Bennett and Wallsgrove 1994, Lange 2015, Tölke et al. 2022). There are many examples of plant terpenes involved in resistance to insects and pathogens, showing an insecticidal effect due to their action as antifeedants (or deterrents), toxins, or as modifiers of insect development, and as inhibitors of fungal proliferation (Bennett and Wallsgrove 1994, and references therein). The presence of croceous glands in the pericarp and persistent calyx, which are largely formed in the flower, helps to protect the developing fruit and ensures the perpetuation of the species.

Our study revealed that croceous glands are secretory spaces that produce volatile terpenes with a probable protective function in *Senega*. Structurally, these glands are cavities in *S. longicaulis*, and the divergence in their typology, compared to other species of the genus, suggests the presence of transitional structures between cavities and ducts. Their specific distribution in organs has potential taxonomic and evolutionary value, but further studies are needed to assess the mode of formation and the systematic importance of croceous glands for Polygalaceae.

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Author contribution statement

L.K.C.L.: data curation, formal analysis, investigation, methodology, writing – original draft. A.C.A.A.D.: conceptualization, data curation, formal analysis, funding acquisition, project administration, supervision, writing – original draft, and writing, review, and editing. J.F.B.P.: writing, review, and editing. D.D.: conceptualization, data curation, formal analysis, supervision, writing – original draft, and writing, review, and editing. All authors contributed to the article and approved the submitted version.

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