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The flower structure of *Solanum caavurana* Vell. (Solanaceae) and aspects of the pollination biology

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Abstract

Aspects of the pollination biology and floral characteristics of *Solanum caavurana* Vell. Were investigated in a semidecidual seasonal forest fragment in Paraná, Brazil. Anthesis was diurnal and the *Pseudaugochlora* bees have visited the flowers with more frequency than other species. Sepals and petals had homogeneous parenchymatous mesophyll. The young anther wall was composed of epidermis, two or three layers of endothecium, two middle layers and secretory tapetum. Anthers were poricidal and there was no functional longitudinal stomium. Ovary structure was simple and there was compitum with septum split. Ovules were hemicampylotropous, unitegmic and tenuinucellate with hypostase. The flower of S. caavurana followed the *Solanum* pattern described in the literature, and the pollination should be made by bees.

Keywords: Bees; Compitum; Floral anatomy; Hypostase

1 Introduction

The knowledge about the biology of flowers in the widest sense is urgent, facing the threats to biodiversity, especially in the tropics [1]. The author considers that "the understanding of flowers is a central theme for the phylogenetic reconstruction of the angiosperms at all levels". Better knowledge of phylogenetic history and interactions between animals and plants is vital for evaluation of conservation actions [1].

Forest coverture in Paraná has reduced from 87.41% to approximately just 7% presently, most of which is concentrated in the "Serra do Mar" and Iguaçu National Park. In the northwest region of Paraná, the situation is even more critical, with less than 1% of the forest remnants located in units of conservation and on the islands in the Upper Paraná River which are subject to flooding [2,3].

In the present work, we selected for study the *Solanum caavurana* Vell. (Solanaceae) belonging to the subgenus *Solanum*, section *Geminata* (G. Don) Walp. That has a distribution confined to the secondary formations of humid forests in Brazil, and it is found from Ceará to Paraná (Brazil), Argentina and Paraguay [4]. It is a shrubby species that occurs in forest remnants of the northwest region of Paraná, Brazil. Solanaceae accounts for about 102 genera and 2460 species in its great concentrated majority in South America [5]. Most members of the family are poisonous or the source of several pharmaceutical drugs, and some are powerful narcotic; surprisingly, the family also provides edible fruits [6].

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The floral morphology and biology are basic knowledge for the understanding of the reproduction process of plants. The study of floral anatomy has so far remained a comparatively neglected, but the floral morphology is well known [7,8,9,10,11,12,13,14,15,16]. Also, the floral biology of Solanaceae species has aroused the interest of different researchers [17,18,19,20,21,22,23,24,25,26,27].

Faced with the need to carry out research with forest species, the present study pertains to the flower structure, the anthesis, and the behavior and identification of the floral visitors of *S. caavurana*.

2 Material and methods

The study was performed in a forest fragment (23º 57'S; 51º 57'O and altitude close to 550m), situated in Maringá, Brazil (state of Paraná). The vegetation area is classified as semidecidual seasonal forest. According to the Köeppen system, the climate is humid temperate with hot and rainy summers and dry winters (mean annual temperature of 22.6ºC). Thirteen specimens of *S. caavurana* were previously marked and were used for observations and collection of botanical material (floral buds and flowers). Voucher material was deposited at the UEM Herbarium, collection number 20286.

Aspects of the pollination biology were studied from February to March, 2011, totaling 40 hours. Flowers were examined morphologically, being analyzed the characters: form, size and disposition of the floral elements. Flower color was determined with the aid of the color guide of Kornerup and Wanscher [28]. The process of anthesis was recorded in inflorescences with mature and unopened buds at night and during the day. Another dehiscence and stigma receptivity (hydrogen peroxide test of Robinsohn [29]) were made. The osmophore detection was made in flowers submitted to the aqueous solution of red neutral at 1:10.000, for ten minutes and later washed in distilled water. Odor concentration test was accomplished in floral parts of five flowers maintained in closed container by twenty minutes, for identification of volatile composts [30]. Observation of insect activity was made during the day to determine the period of greatest visitation. The insects were photographed, collected and identified.

Anatomical preparations of flowers were made from fixed material in glutaraldehyde (1% in 0.1M phosphate buffer, pH 7.2), dehydrated through alcohol series, embedded in hydroxymethacrylate [31], sectioned via rotary microtome (cross- and longitudinal sections, and stained in toluidine blue 0.05% in phosphate buffer pH 4.7 [32]. Specific microchemical tests were carried out for lipid substances (using Sudan IV and Sudam Black dyes) [33], starch (iodine-potassium test), lignin (phloroglucin test) [34], and phenolic composts (ferric chloride) [35]. Anatomical illustrations were prepared using Leica ICC50 and Leica EZ4D optical microscopes with a digital camera.

Micromorphological analysis of the flowers was performed on fixed material in a Karnovsky solution [36]. Samples were processed and then mounted on aluminum stubbs, gold-coated, and subsequently examined using scanning electron microscopy (Shimadzu SS-550 Superscan), obtaining digital images.

3 Results

3.1 Aspects of floral biology

The blooming period has occurred from October to April, with pick in February and March. Flowers were pendent (Fig. 1D) with umbellate inflorescences. Flowers (Fig. 1A) were pedicellate, actinomorphic, hypogynous, dichlamydeous, heterochlamideous and bisexual. Calyx (Fig. 1A,B) was white, pentamerous, gamosepalous with ovate sepals of acute apex. Corolla (Fig. 1A,B) was also white, pentamerous, gamopetalous with lanceolate-ovate petals of acute apex. Androecium had 5-stamens with epipetalous filaments, yellow and sagittate anthers (Fig. 1C) with two tecae consisting of two pollen sacs; the filaments were united into a ring in the base which surrounded the ovary. Gynoecium (Fig. 1B) had 2-carpels and 2-locules, connate, with superior globose ovary, axile placentation, long white style, green 2-lobed stigma with a central rift. The flowers did not emit scent for the human sense, but in contrast of they had areas in the calyx and in the corolla, (mainly the leaf margin), that were stained with neutral red indicating the osmophore presence.

The anthesis began about 6 o'clock with the stigma exhibition in the corolla apex. Soon afterwards, the opening of corolla began with the separation of the petals from the apex towards the base, and the stamens extend out of the corolla. The flowers were completely open between 08:00am and 08:30am showing the petals in horizontal position or gone back to the base of the flower. The stigma receptivity began about 8 o'clock and it lasted between 24 and 36 hours. The anthers dehisced by means pores and the dehiscence occurred between 09:00 and 9:30. After anthesis, the petals as well as the stamens had already fallen but the calyx persisted in the young fruit.

The *Exomalopsis*, *Augochlora* and *Pseudaugochlora* (Fig. 1E) bees have visited the flowers, but the *Pseudaugochlora* species (Fig.1D) were more frequent than the other species, with more than 40% of visits in the flowers. Two fly species, *Salpingvgaster nigra* and *Ornidia obesa*, visited the flowers but with less than 15% of visits in the flowers. The bees flew over the inflorescences in zigzag in the morning and afternoon periods, and the visits to the flowers lasted around six seconds in the morning and three seconds in the evening. The bees held the anthers with the buccal pieces, vibrated the abdomen on the anthers and accomplished rotative movements on the flower, collecting the pollen and depositing it in the last pair of legs.

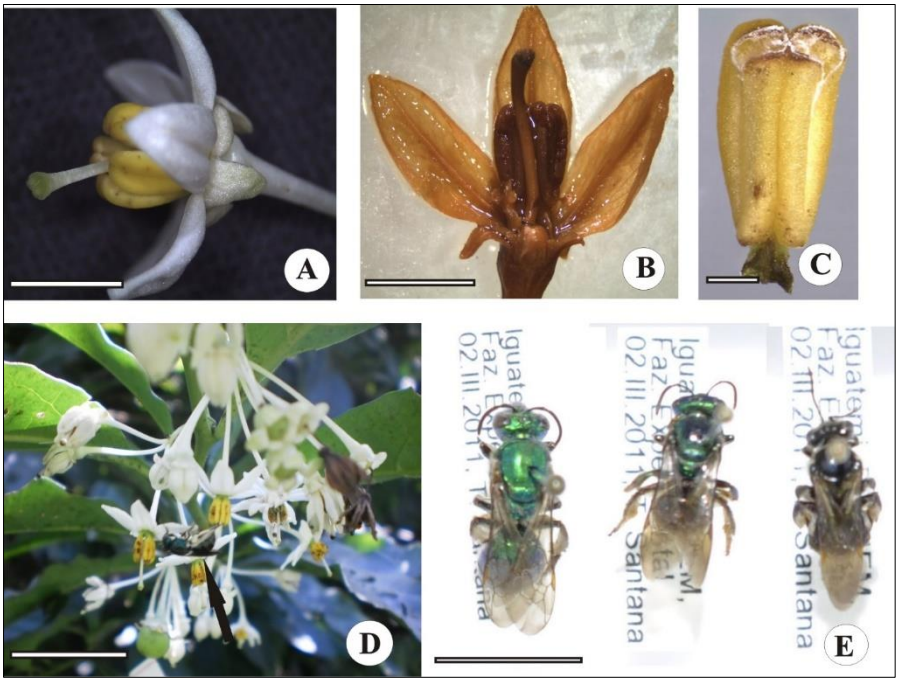

Figure 1 Morphology and aspects of the floral biology of *S. caavurana* Vell. A) Flower. B) Flower in longitudinal section. C) Mature anther showing pore. D) Inflorescence showing *Pseudaugochlora* sp. (arrow). E) Floral visitants: *Pseudaugochlora* sp, *Augochloropsis sp.* and *Exomalopsis sp.*, respectively. Scale bars = 0,1cm (B), 0,5cm (A, H), 1cm (E), 2cm (D)

3.2 Floral anatomy

Sepals consisted of uniseriate epidermis in both surfaces, but they presented trichomes in the adaxial face and stomata in the abaxial one (Fig. 2A). Trichomes were secretory, pluricellular and capitate; they were short or long with simple stalk and the head consisting of two rows of cells. The sepals were pubescent in the base and the upper part had only a few scattering trichomes (Fig. 2B,C). Mesophyll is parenchymatous and homogeneous (Fig. 2A). The vasculature consisted of bicollateral and collateral bundles.

The lobes of the petals consisted of epidermis in which the cells of both surfaces were elongated to form papillae (Fig. 3A). In floral buds, adhesion of the lobes was carried out by epidermal papillae (Fig. 3D). Pluricellular trichomes occurred in the margin (Fig. 3C) and on the adaxial surface, and may be classified as simple or ramified non-glandular, and glandular. The mesophyll was spongy (Fig. 3A) in the most part of the petals. A large bicollateral vascular bundle and smaller bundles occurred in each petal lobe; and the base of the corolla consisted of ten bicollateral bundles. Protuberances (Fig. 3B) consisting of epidermis with papillae and trichomes, and parenchyma were present on the surface of the corolla.

The young anther wall (Fig. 4A) in the dehiscence region was composed of uniseriate epidermis, two or three layers of endothecium with thin-walled cells, two middle layers and secretory tapetum. The mature wall anther (Fig. 4B) had epidermis and endothecium which consisted of one to three cell layers with fibrous thickened ridges in the cell wall. The stomium (Fig. 4C) was not limited to the region of the pore, also occurring along the anther in the furrow between the pollen sacs. However, the endothecium along the anther did not present fibrous thickening in the wall cell, being formed a longitudinal slit in the anther although not enough for the pollen liberation. There was a single amphicribral vascular bundle in the filament.

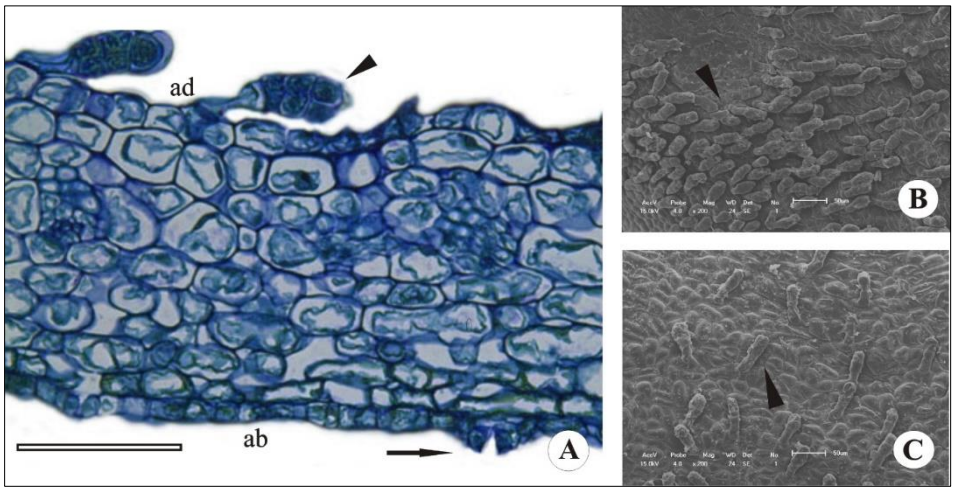

Figure 2 Calyx structure of *S. caavurana* Vell., in longitudinal section (A) and scanning electron microscopy (SEM) (B,C). A) Anatomical detail of the sepal. B) Basal region of the sepal. C) Apical region of the sepal. (ab) = abaxial surface, (ad) = adaxial surface, (arrow) = stomata, (arrow head) = glandular trichomes. Bars = 100 µm (A), 50 µm (B,C)

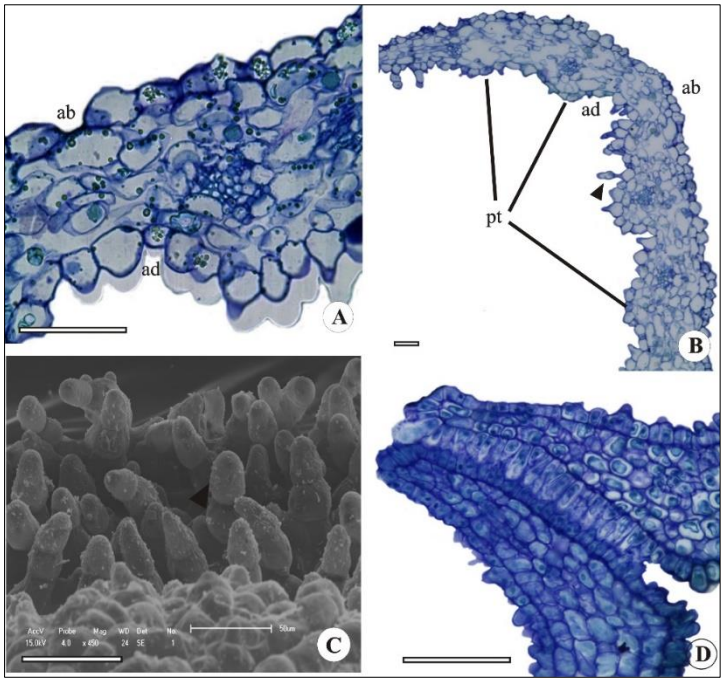

Figure 3 Corolla structure of *S. caavurana* Vell., in cross-section (A-B) and scanning electron microscopy (SEM) (C). A) Petal evidencing the nervure region.B) Petal detail showing protuberances.C) Petal trichomes.D) Region of interlocking of the petal margin by papillae. (ab) = abaxial surface, (ad) = adaxial surface, (pt) = protuberances, (arrow head) = glandular trichomes. Bars = 50 µm (C), 100 µm (A,B,D)

The stigma epidermis was papillate (Fig. 5A). The style presented epidermis, parenchyma, two vascular bundles and spongy transmitting tissue (Fig. 5B); in the base the style contained a single canal lined entirely by glandular transmitting tissue (Fig.5C).

The ovary was composed of glabrous and uniseriate epidermis both on the internal and external surface, and the parenchymatous mesophyll is made up of mainly of isodiametric cells, interspersed with crystal (druse) cells (Fig. 6A). Each carpel was supplied by dorsal, lateral and marginal vascular bundles, all collateral; the marginal bundle was more strongly developed than the others. Ovarian septum presented epidermis with cells of rectangular shape, the placentary cells were papillate, and the parenchyma had druse cells. The placenta was strongly developed, occupying almost half of the locule. There was a split in the top of the septum and between the loculi, which may play as a connection ("compitum") among the carpels (Fig. 6B).

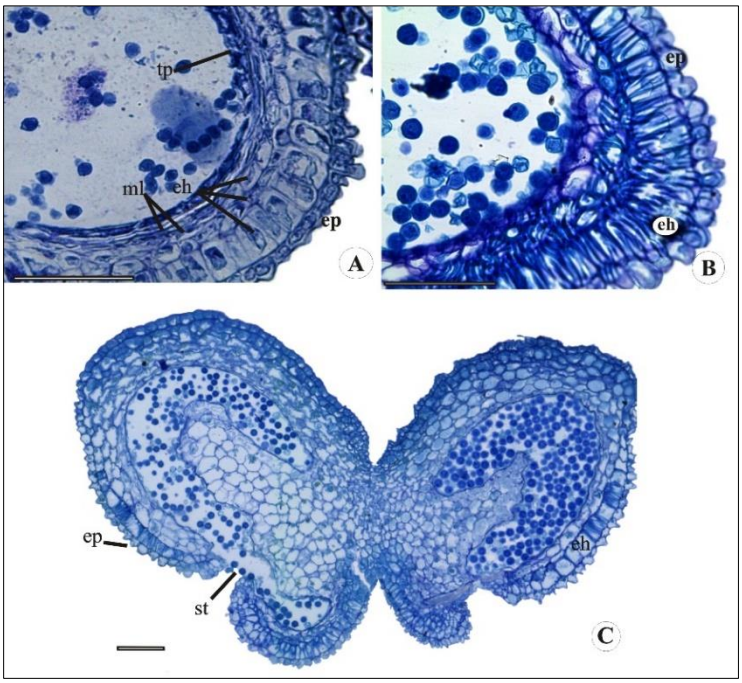

Figure 4 Anther structure of *S. caavurana* Vell., in longitudinal section (A,B) and cross-section (C). A) Young anther wall. B) Mature anther wall. C) Mature anther section in the pore region. (eh) endothecium, (ep) = epidermis, (ml) = middle layer, (st) = stomium, (tp) = tapetum. Scale bars = 100 µm

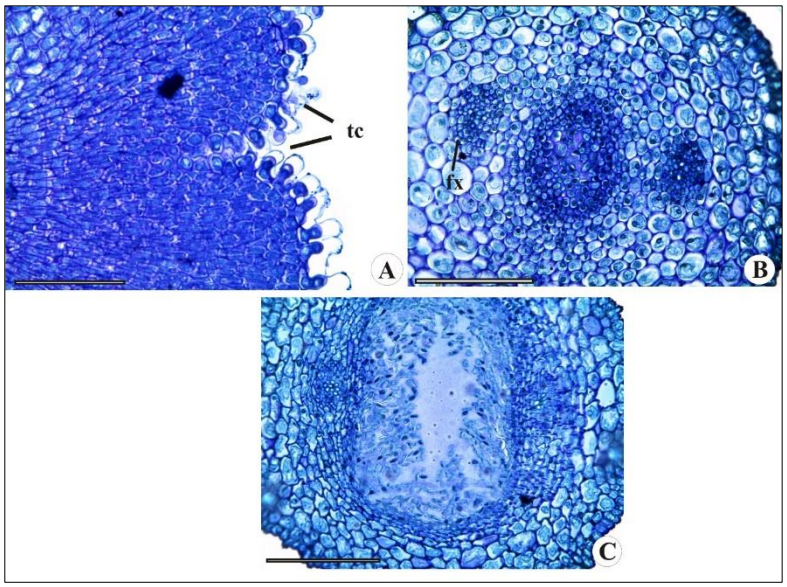

Figure 5 Stigma and style structure of *S. caavurana* Vell., in longitudinal section (A), and cross-section (B,C). A) Stigma detail. B) Style detail in the middle region. C) Style detail in the apical region. (ep) = epidermis, (tc) = trichomes, (arrow head) = transmitting tissue. Bars = 100 µm

Ovules were hemicampylotropous, unitegmic and tenuinucellate with short funiculus (Fig. 6C). A single massive integument consisted of cuboid and elongated cells, whose inner epidermis showed endothelium aspect. The chalazal region presented hypostase with thicker walled cells and more intense coloration (Fig. 6C).

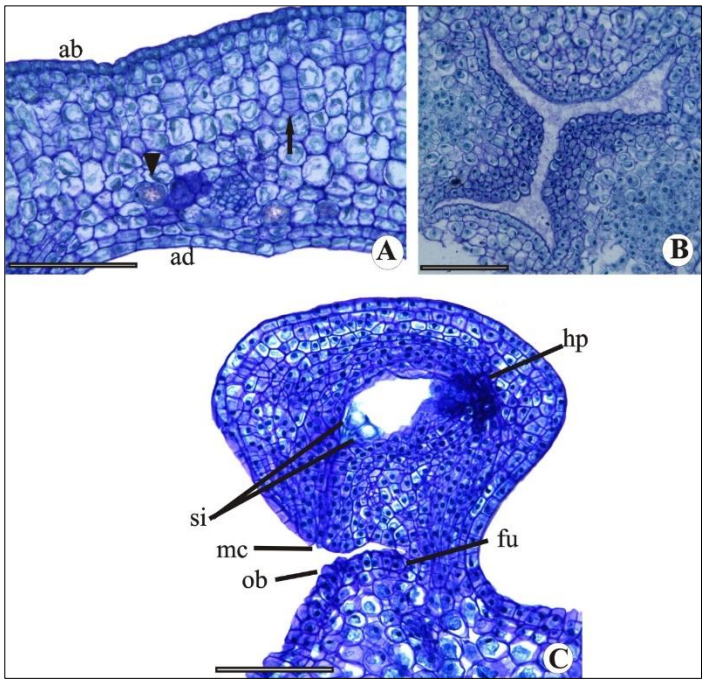

Figure 6 Ovary and ovule structure of *S. caavurana* Vell., in cross-section (A,B) and longitudinal section (C). A) Anther wall detail. B) Compitum detail. C) Ovule. (ab) = abaxial surface, (ad) = adaxial surface (ei) = inner epidermis, (fu) = funiculus, (hp) = hypostase, (mc) = micropyle, (ob) = obturator, (si) = synergids. Scale bars = 100 µm

4 Discussion

Solanum caavurana had a flower common to the entire genus, which was characterized by Vogel [37], Endress [1] and D'Arcy and Keating [38] as olygandrous androecia, often in widely open flowers facing downwards or sideways with the petals often reflexed, with powdery pollen often in poricidal, large, optically attractive anthers and short filaments. The pollen liberation by the pores of the *S. caavurana* anthers is made by the vibrations of the bees. Endress [1] considered the most fascinating evolutionary response of flowers to pollen collection by vibration is the reduction of anther dehiscence to apical pores. Buzz-pollination (pollen collection by vibration) is considered as an interaction between plants with characteristic floral morphologies and a particular type of behavior exhibited by some bees [39]. Plants with flowers typical of the buzz pollination syndrome are found in at least 64 plant families, many of which may contain plants from which humans derive useful products, materials, or foods [40].

It is likely that the flowers of *S. caavurana* displayed yellow colour of the anthers, the scent –producing parts of the perianth and pollen production for their pollinators. Osmophores were identified in the margins of the calyx and corolla of *S. caavurana*, where occurred glandular trichomes. The osmophores of *S. caavurana* seemed to be of the epidermis histological type described by Endress [1], where the volatiles were secreted by the epidermis. Osmophores were reported in other species of *Solanum*, as *S. sessiliflorum* Dun. [17], *S. paniculatum* L. [18] and *S. stramonifolium* Jacq. [20]. It is important to emphasize that there are *Solanum* species in which bees collect floral scents produced by the anther connective, which is developed and differentiated in osmophore [26].

Many of the flowers that have the pollen as reward exhibit poricidal anthers; in pollen collected by Hymenoptera and Diptera there is selection of oil-containing pollen [1]. *S. caavurana* flowers had anthers with pores, oily pollen, and collector and consuming insects (bees and flies) were found visiting flowers. The *S. caavurana* anthesis was diurnal and there was a higher frequency of visits by bees, principally by the bee *Augochloropsis* which may be the more effective pollinator in the forest fragment of Maringá, Paraná, Brazil. It is stood out that *Solanum* does not produce nectar and is pollinated by pollen-gathering bees and flies [6].

The white and pulpy calyx of *S. caavurana* protected the flower bud and was persistent in the mature fruit, probably acting in the photosynthetic process during fruit growth. In the flower buds of this species the margins of the petals overlapped, and this was enough to keep the buds tightly closed. Weberling [41] called this process of interlocking of perianth segment margins by adhesion. Sigmond [42] refereed to the two basic types of these special attachment organs,

and we adopted the petal adhesion of *S. caavurana* as belonging to the type dentonection, which comes about by the engaging and interlocking of pointed papilliform epidermal cells on the marginal surfaces.

The anther wall formation of *S. caavurana* seemed to be of the basic type presented by Davis [43], resulting in four cell layers which differentiate into endothecium, two middle layers and tapetum. The probable indication of this type was based in Garcia [12], who recorded the basic type for other three *Solanum* species Dahlgren' [44] observations are also interesting from this point of view; for this author in all the sympetalous groups with unitegmic ovules (including Solanaceae) exhibit the dicotyledonous anther type. Therefore, the confirmation of this anther classification for *S. caavurana* needs ontogenetic study.

The opened stomium of *S. caavurana* was formed by an apical pore and a longitudinal slit, but the pollen liberation only occurred by pores. Structurally, the *S. caavurana* endothecium of the pore region was strikingly different from the slit region, in which the former region showed thick-walled cells and the later one thin-walled cells. García et al. [15] analyzed the anther opening of *S. caavurana* and they classified it as poricido-longitudinal stomium. According to Weberling [41] the poricidal mode of anther dehiscence is derived in general from the longicidal mode by shortening the slit and moving it either towards the base or the tip. García et al. [15] reported three types of anther opening in *Solanum* (poricidal, poricido-longitudinal and longitudinal stomia), but the authors believe that the study may possibly provide information about the relationship between species, or may only represent minor adjustments in relation to the pollination mechanism of each species.

Carr and Carr [45] made an extensive study about the functional significance of syncarpy, and they have classified the gynoecia of flowering plants as apocarpous, pseudo-syncarpous and eu-syncarpous. It is possible the gynoecium of *S. caavurana* be identified as eu-syncarpous by its possession of a compitum which consisted of splits in the septa between loculi. Carr and Carr [45] have considered the compitum as a connection between the carpels and stigma, which allows the pollen tubes to fertilize ovules belonging to more than one carpel. However, the eu-syncarpy of the *S. caavurana* may only be confirmed by the study of the development of pollen tubes in fertilized gynoecia.

Corner [46] mentioned the anatropous to campylotropous ovules for Solanaceae species. The description of hemicampylotropous ovule of *S. palinacanthum* Dunal [47] and *S. chenopodioides* Lam. [48] applies to *S. caavurana*, whose chalaza and the embryo sac were not arranged in a horizontal position, nor the micropyle was close to the funiculus as it is verified in the campylotropous ovule.

The hypostase seems to occur throughout the whole system and is thereby presumably of no particular phylogenetic importance at higher taxonomic level; however, it can be noted, as far as it can be seen, the hypostase is lacking in some superorders, e.g., Solananae [44]. Cabrera et al. [48] give the description of *S. chenopodioides* ovules, but do not mention the hypostase. On the other hand, the ovules of *S. caavurana* resembled the *S. palinacanthum* [47] one, which presented hypostase.

5 Conclusion

Solanum caavurana had the *Solanum*-type flower with diurnal anthesis and pollination by bees. Anthers were poricidal and there was no functional longitudinal stomium. Gynoecium presented style with intermediate structure between the hollow and solid patterns, and ovary with compitum consisting of splits. Ovules were hemicampylotropous and presented markedly hypostase.

Compliance with ethical standards

Acknowledgments

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Disclosure of conflict of interest

The authors declare no conflict of interest.

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