

FOLIAR ANATOMY OF THE SPECIES *Lantana camara* AND *L. radula* (VERBENACEAE)¹

Anatomia Foliar das Espécies Lantana camara e L. radula (Verbenaceae)

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ABSTRACT - The species *Lantana camara*, commonly used as ornamental, has spread worldwide becoming one of the world's most important weeds. To develop new methods of control of this plant, it is essential to distinguish it from other species of the same genus, and this is usually accomplished through taxonomic studies of fertile samples. Considering the similarity between *L. camara* and *L. radula*, and the consequent difficulty in distinguishing one from the other when only sterile samples are available, this work aimed to investigate the use of the anatomical characteristics of the leaves of both species as tools for supporting correct classification. The leaves of *L. camara* and *L. radula* were anatomically examined by light microscopy and scanning electron microscopy. The major differences were observed in the petiole, which presented secretory idioblasts in *L. camara*. Secretory idioblasts were observed in the leaf blades of *L. camara* and Crystalliferous idioblasts were found in *L. radula*. Glandular and nonglandular trichomes as well as the abaxial surface are different in each species. Such results can support the strategies aiming at the control of *L. camara* without interfering with *L. radula*.

Keywords: idioblasts, *L. camara*, *L. radula*, glandular trichomes, weed plant.

RESUMO - A espécie ***L. camara*** tem sido usada há séculos como ornamental e, conseqüentemente, espalhou-se pelo mundo, tornando-se uma das mais importantes plantas daninhas. Na busca de novos métodos de controle para essa planta, é essencial distinguir espécies do mesmo gênero, o que usualmente é feito com estudos taxonômicos de amostras férteis. Considerando a similaridade entre ***L. camara*** e ***L. radula***, e a conseqüente dificuldade em distingui-las quando somente amostras estéreis estão disponíveis, entendeu-se como necessário investigar o uso de características anatômicas das folhas como fonte de informação adicional para a distinção dessas duas espécies. As folhas de ***L. camara*** e ***L. radula*** foram examinadas sob microscopia de luz e microscopia eletrônica de varredura. A diferença mais marcante observada foi a presença de idioblastos nos pecíolos de ***L. camara*** e ***L. radula***. Na lâmina foliar de ***L. camara*** foram observados idioblastos secretores e em ***L. radula*** foram encontrados idioblastos cristalíferos. Os tricomas glandulares e não glandulares, bem como a superfície abaxial, apresentam diferenças morfológicas evidentes em cada espécie.

Palavras-chave: idioblastos, *L. camara*, *L. radula*, tricomas glandulares, planta daninha.

INTRODUCTION

The genus *Lantana* is native from tropical and subtropical America, with some species occurring in Asia and tropical Africa. The

species *Lantana camara* has spread across the world, causing problems in several countries where it was introduced as ornamental. In these countries it has adapted very well to the local climatic conditions, invading forests,

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pastures, and other areas where entropic interventions have occurred. Besides being toxic for many domestic animals (Barreto et al., 1995), *L. camara* has an allelopathic effect on the surrounding vegetation (Sharma et al., 1988) interfering in natural communities, and reducing the local diversity. So, countless attempts have been made aiming to control this weed, but with limited success (Sharma et al., 1988; Day et al., 2003).

There are several morphological varieties in the plants from the genus *Lantana* (Silva, 1999) and this hinders their identification in the field. Countless taxonomic problems have been reported and these plants are frequently classified incorrectly (Silva, 1999; Salimena, 2002). The separation between some species of *Lantana* is normally made by the analysis of fertile samples, which is difficult when the plants are sterile.

In Minas Gerais, *Lantana radula* SW appears together with *L. camara*. These two species are morphologically similar in many aspects, in the absence of fertile branches. Differently from *L. camara*, *L. radula* has a more limited occurrence, being found from Central America to Brazil, with the southern limit being in the state of Minas Gerais.

The continuous attempt to control *L. camara* can affect other species such as *L. radula*, due to incorrect taxonomic identification. For a long time, anatomic studies have shown to be an important tool associated with taxonomic studies, mainly when there is no reproductive organ in the investigated sample (Solereeder, 1908; Metcalfe & Chalk, 1950). In some cases, leaf anatomy allows the identification of hierarchically inferior levels (Alves et al., 2002; Sartori & Tozzi, 2002). The objective of the present study was to characterize the anatomy of the leaves of *L. camara* and *L. radula*, aiming to find characteristics that could contribute for the identification of sterile samples of these species.

MATERIAL AND METHODS

The botanical material was obtained from plants cultivated in pots and maintained in a greenhouse on the campus of the

Universidade Federal de Viçosa (20°45'24"S and 42°52'22"WO, 680 m of altitude).

The plants were identified by a specialist and herborized, with a voucher specimen of each plant being deposited at the VIC Herbarium (under the numbers 30159 - *L. camara* and 30160 - *L. radula*) in the Department of Plant Biology of the Universidade Federal de Viçosa (UFV).

Mature leaves from the 3rd to the 5th nodes were collected from three plants of each species. Fresh petiole and leaf blade samples were cut transversally using a table microtome (model LPC, Rolemberg and Bhering Commercial and Importation LTDA, Belo Horizonte, Brazil), with the cuts being stained for 5 minutes with Safrablau (Kraus & Arduim, 1997) and the blades mounted with glycerolized water.

Three leaf fragments were affixed for 48 hours in FAA₇₀ (formaldehyde, acetic acid, ethanol 50%, 5:5:90, v/v) (Johansen, 1940) and preserved in 70% ethanol. Samples with approximately 5 mm² of leaf blade and petiole were dehydrated in an ethylic series (70% to 95%) and embedded in a histological resin (Historesin Leica). To make the penetration of the solutions easier, the samples were maintained in a dehydrator under constant vacuum. The samples were sectioned in transversal and longitudinal planes, with an automatic advancement rotary microtome (RM 2155, Leica), using a glass razor. Cuts 5 to 7 µm thick were distended on glass plates, stained with Blue Toluidine in pH 4.4 (O'Brien & Maccully, 1981) during 10 minutes and mounted with a synthetic resin (Permount-Fisher).

For diaphanization, three leaves from the 3rd to the 5th node were individually selected from each species, with leaves being collected from three specimens. The leaves were subdivided into apical, median and base regions, and for each region two samples per leaf were used to analyze the abaxial and adaxial surfaces. These samples were treated with aqueous sodium hydroxide at 10%, washed with running water and stained with aqueous safranin at 1% (Johansen, 1940). The plates were mounted with jelly glycerinate. The number of glandular and nonglandular



trichomes was quantified for the abaxial and adaxial surfaces in each region under a light microscope (magnification of 40 and total area of 29.7 mm²). In this experiment, 45 areas of approximately 0.22 mm² each were examined for each surface and region (apical, median and base). The number of trichomes was calculated independently for each surface and evaluated portions. The results were analyzed by the Tukey's average test.

Observations and photographic documentation were made with a light microscope (model AX70TRF, Olympus Optical) equipped with U-Photo system.

For the description of the micro-morphology of the glandular and non-glandular trichomes, the samples were dehydrated in an ethanol series, submitted to critical point drying with liquid CO₂ and covered with metal gold to 20 nm of thickness (SCA 010, Balzers, Liechtenstein). Such samples were analyzed and the images obtained in a scanning electron microscope (SEM) Zeiss model LEO 1430VP (Cambridge, England).

RESULTS

L. camara and *L. radula* presented some common morphological leaf characteristics, such as simple leaf, complete with petiole and pubescent; opposite-decussate phyllotax, sharp acuminate top and serrated edge.

The petioles of the two species (Figures 1A-D) are flat and convex on the adaxial and abaxial surfaces, respectively. They are covered with a thin cuticle and the epidermis is uniseriate with regular size cells and several types of glandular and non-glandular trichomes throughout its extension. In the subepidermic portion there are nearly three layers of collenchyma. The vascular system is collateral for both evaluated species. In *L. camara*, the vascular system is open, forming a flattened arch in the "V" form with two accessory bundles located dorsally (Figure 1A). In *L. radula*, the vascular system is open with curved edges, in a horseshoe form, by two accessory bundles arranged laterally (Figure 1C). Groups of idioblasts located laterally in the cortical parenchyma were observed in *L. camara* (Figure 1B) but not visualized in *L. radula* (Figure 1D).

In both species, the venation pattern is of pinnate type, with simple lateral craspedodromous venation, where all side veins and their branches end in the edge (not documented). The areoles had a quadrangular format with single venation (Figures 1E, F).

On the surfaces of the leaf blade of *L. camara* (Figures 2A, D) and *L. radula* (Figures 2E, I), the epidermic cells presented a winding outline with recesses in the form of "U". In *L. radula*, the abaxial surface is not flat, presenting depressed regions, where glandular trichome incidences are common (Figure 2H).

The stomata occur in both surfaces (amphistomatic), though they were rare in the adaxial surface. They were located at the same level as the other epidermic cells, in the form of complex diacytic and anomocytic stomata (Figures 2A, C, E, H).

Glandular and non-glandular trichomes were found scattered through the entire petiole and leaf blades, with types varying according to the species (Figures 3, 4 and 5).

Nonglandular trichomes found in both *Lantana* species (Figures 3A, F) are of the conical type, presenting a large base and a thin extremity, and ornamentations on the wall. These trichomes are uni or bi-cellular and presented a set of bulky epidermis cells arranged radially at the base (Figures 3C, F). In *L. camara* (Figures 3A, C, E) the trichomes were visually larger (Figures 3B, D, F) and more numerous (Table 1), compared to those found in *L. radula*. As the frequency of nonglandular trichomes in *L. radula* was very low for the two leaf surfaces (inferior to 1, Table 1) no statistical difference was observed. For *L. camara*, trichome frequency in the adaxial surface was double the value of the abaxial surface (Table 1). Regarding the evaluated regions, no differences were observed in terms of trichome frequencies for the two species investigated (Table 2).

Three types of capitate glandular trichomes were identified (Figures 4 and 5). Type I: multicellular, with a cell at the base, two lengthened cells of variable length on the stalk, a short cell on the neck and the head multiseriate with two to eight cells. Type II: multi-cellular with a base cell, a short cell on the neck and with one, two or four apical cells



in the secretory head. Type III: bi-cellular, with a base short cell and an apical dilated cell composing the secretory head, with its cuticle expanded during the secretory phase. In *L. camara*, trichomes of types I (Figures 4A, H), II (Figures 4I, J) and III (Figures 4L, M) were visualized. In *L. radula*, trichomes of types I (Figures 5A, B), II (Figures 5C, D, E, F) and III (Figures 5G, I) were also observed. However, the difference between the two species consists in the number of cells in the head of the capitate trichomes of types I and II. Trichome frequency was found to be higher in the abaxial surface for both species (Table 1). Regarding the evaluated regions (base, median and top) no statistical differences were observed for the middle frequency of the trichomes, the exception being *L. radula* in the abaxial surface (Table 2).

For the two species, the leaf blades presented uniseriate epidermis cells with thin periclinal walls and a relatively thick cuticle. The mesophyll is dorsiventral, with two layers of palisade parenchyma (Figures 6A, B) and three to four layers of spongy parenchyma, which is more compact in *L. camara* (Figure 6A) than in *L. radula* (Figure 6B). In *L. camara*, secretory idioblasts found in the mesophyll were similar to those in the petiole. (Figure 6C). The idioblast cytoplasm was stained purple with Blue Toluidine (Figures 6A, C, E). In *L. radula*, only idioblasts containing styloid crystals in the chlorophyllian parenchyma were visualized (Figure 6D). The vascular system of the central vein (Figures 6E, F, G, H) is of collateral type, in the form of an open arch in both species. However, in *L. radula*, it is more curved, having the remotest extremities of the arch.

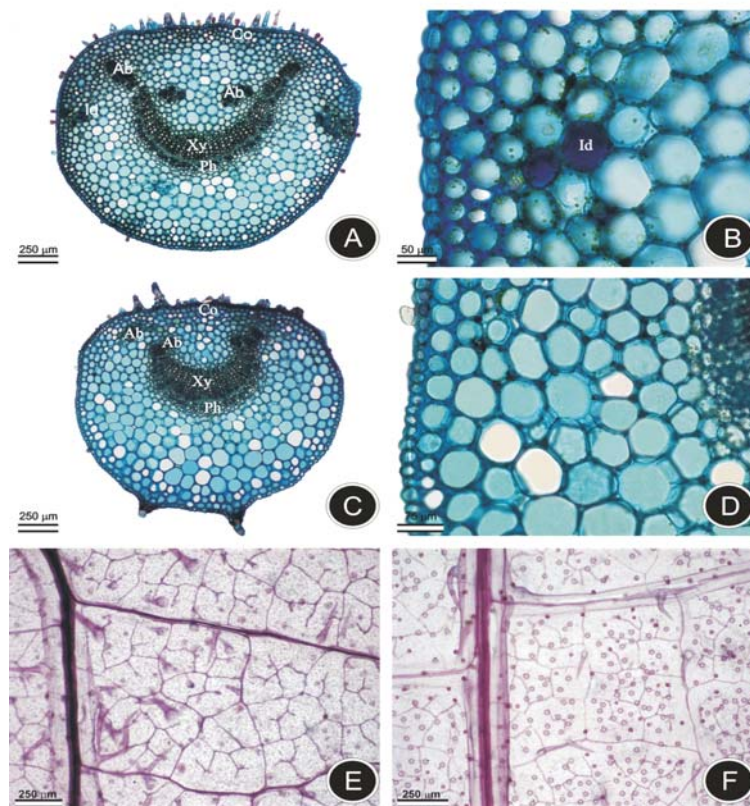


Figure 1 - Leaves of *Lantana camara* (A, B and E) and *Lantana radula* (C, D and F). A to D-Cross section of the distal region of the stained petioles. E and F- Leaf clearing of the leaf blades showing venation. A and C-General view. B – Detail of the cortex showing the secretory idioblasts. D – Cortex. E and F-Areoles. Id = idioblasts, Co = collenchyma, Xy = xylem, Ph = phloem, Ab = accessory bundles.

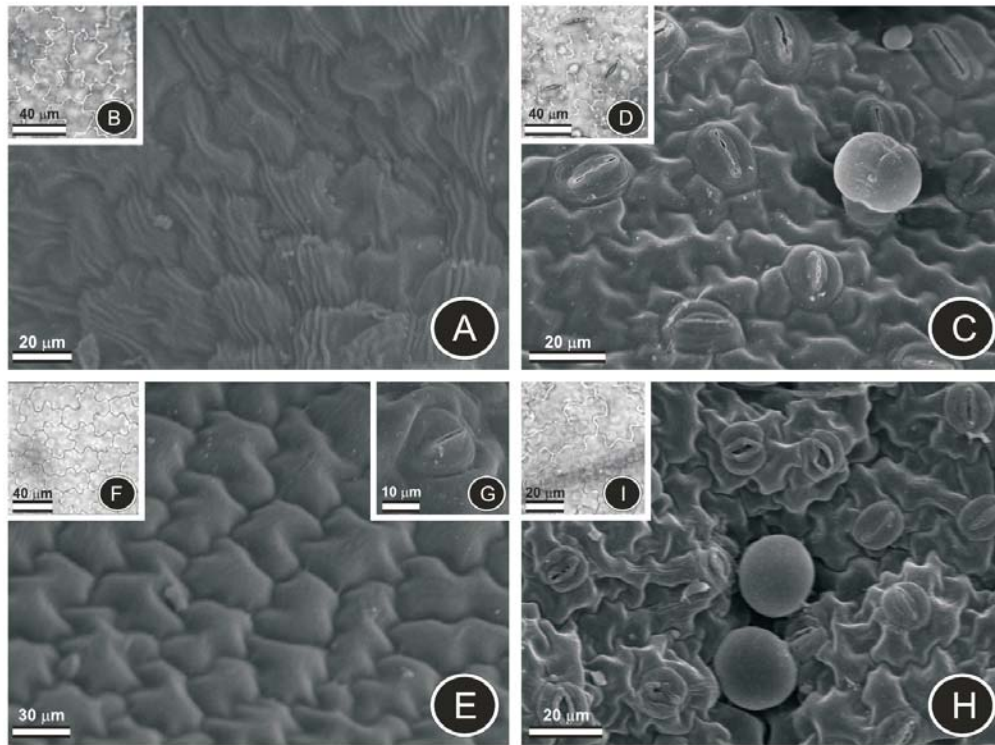


Figure 2 - Front view of the epidermis of the adaxial and abaxial surfaces of the *Lantana camara* and *Lantana radula* leaves showing anticlinal walls with winding outlines. A to D – *L. camara*. E to I – *L. radula*. C - Stomata at the same level of the epidermic cells. H – Irregular epidermis due to the presence of depressions. A, C, E, G and H – Scanning electron microscopy (SEM). B, D, F and I = Leaf clearing. A, B, E, F and G – Adaxial surfaces C, D, H and I – Abaxial surfaces.

DISCUSSION

Some of the anatomical characteristics of *L. camara* and *L. radula* were similar, such as simple leaf craspedodromous venation. The use of leaf venation for taxonomic studies (Moraes & Paoli, 1999; Cardoso & Sajo, 2006) should be considered with care (Dilcher, 1974). However, it was possible to identify diagnostic characteristics that allowed distinguishing one species of *Lantana* from the other.

In the petiole of the two *Lantana* species, the vascular system pattern organization and the secretory idioblasts (visualized only in the cortex of *L. camara*) are good distinctive characteristics. The anatomy of the petiole frequently supports the identification of some taxa, with the distal portion of the petiole being the most significant in terms of taxonomy (Howard, 1979). The petiole has been confirmed as a good taxonomic characteristic helping to distinguish species from the

Melastomataceae family (Reis et al., 2004) as well as in the separation of species of *Erythroxylum* P. Browne (Erythroxylaceae) (Bieras & Sajo, 2004).

The thick cuticle on the adaxial surface of the two *Lantana* species can be interpreted as an adaptive strategy (Dickison, 2000; Larcher, 2000; Machado et al., 2008). The cuticle recovers the epidermis of the plant and acts as an interface between the inside and outside of the organism (Bukovac et al., 1990) and must be considered in the interventions aiming at the chemical control of plants (Procópio et al., 2003; Ferreira et al., 2007).

The sinuosity of the epidermis cells appears to be fixed genetically (Arruda, 1994) or could also be considered as a response to environmental conditions (Alquini et al., 2003), once they increase the contact surface between adjacent cells (Wylie, 1943) and rigidity (Haberlandt, 1928). In the present investigation the results showed that this was not a good distinctive characteristic.



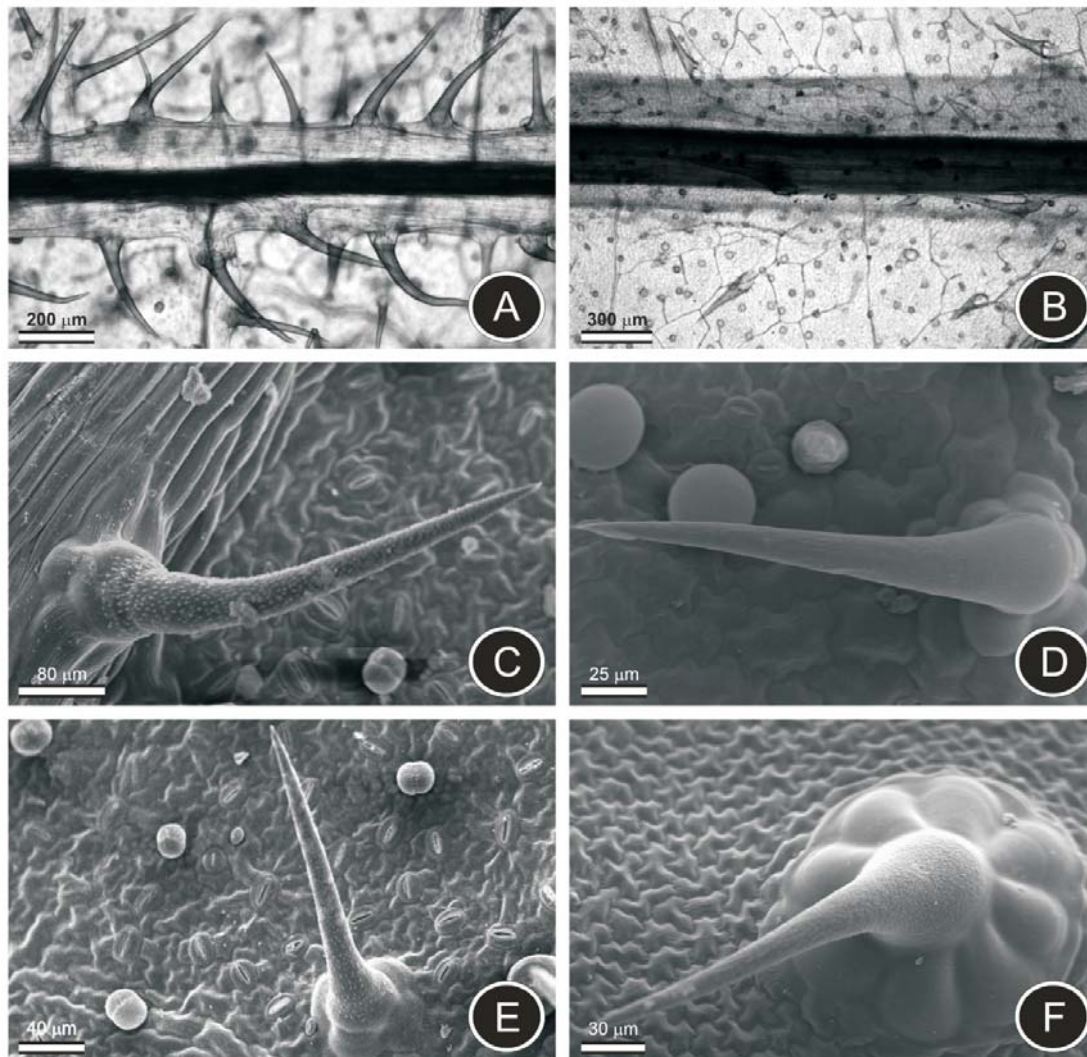


Figure 3 - Nonglandular trichomes of *Lantana camara* and *Lantana radula*. A, C and E – *L. camara*. B, D and F – *L. radula*. A and B – Leaf clearing. C, D, E, F – Scanning electron microscopy (SEM).

Stomata distribution did not differ in the two species studied, being both amphistomatic, with a greater number of stomata in the abaxial surface. Stomata in two leaf surfaces characterize some species of the Verbenaceae family (Metcalf & Chalk, 1950; Inamdar, 1969) and are ecologically less variable characters (Dilcher, 1974). The amphistomatic leaves generally present larger quantities of stomata in the epidermis of the abaxial surface (Greulach, 1973), to which it seems to be a preventive mechanism against photo-inhibition, since the adaxial surface is more exposed to solar radiation, as most of the leaves are in the horizontal position (Smith et al., 1998).

The glandular and nonglandular trichomes, observed for both *Lantana* species (Figure 5 and 6), are distributed widely in the Verbenaceae family (Solereeder, 1908; Metcalfe & Chalk, 1950) including some *Lantana* species (Solereeder, 1908; Metcalfe & Chalk, 1950; Inamdar, 1969; Moura et al., 2005). Trichomes, particularly the secretory ones, are considered important tools for taxonomy (Solereeder, 1908; Metcalfe & Chalk, 1950; Fahn, 1979; Theobald et al., 1979).

The unicellular nonglandular trichomes observed in the two species of *Lantana* have been described for plants of this genus (Solereeder, 1908; Metcalfe & Chalk, 1950)

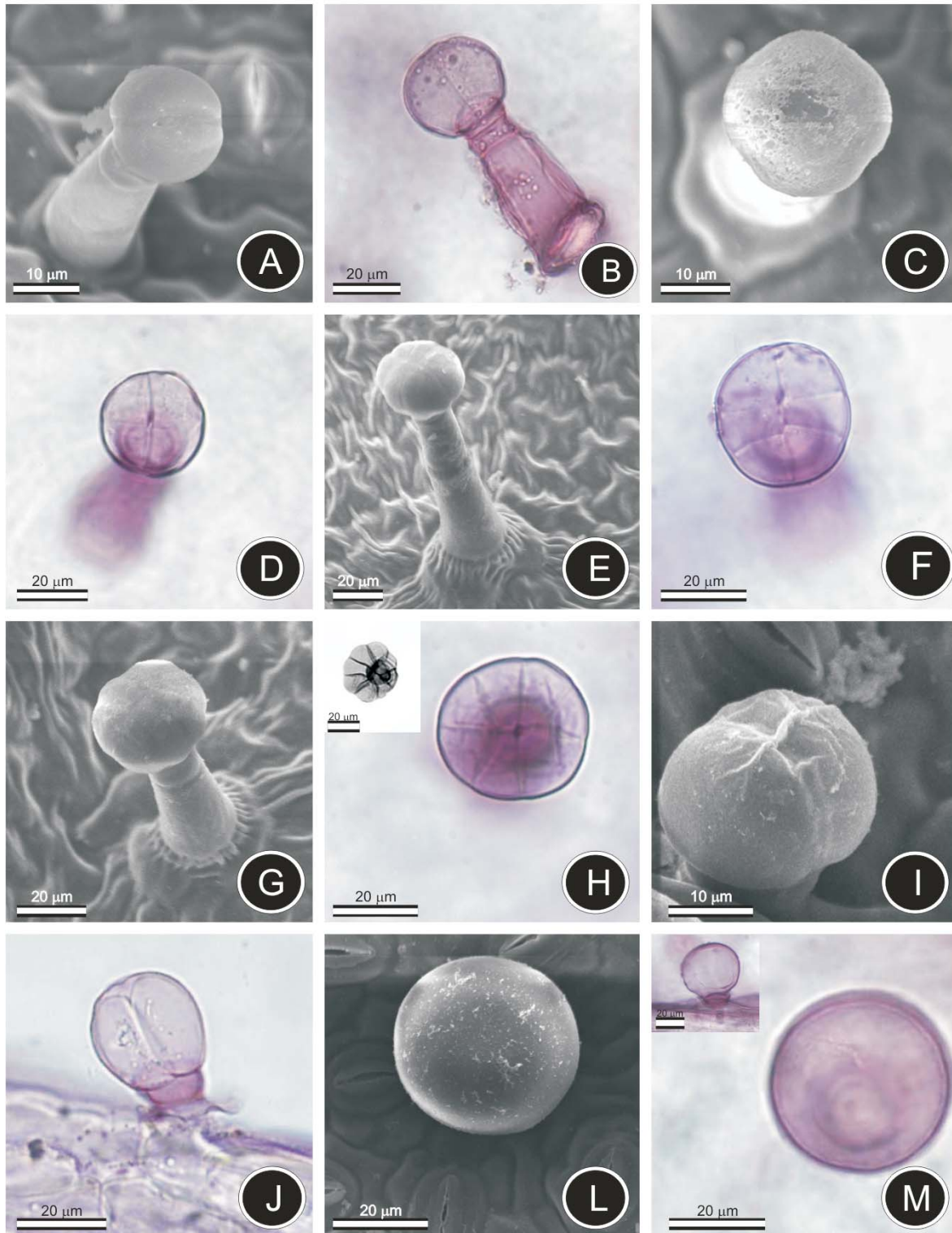


Figure 4 - Types of glandular trichomes in *Lantana camara*. A, C, E, G, I, L-Scanning electron microscopy (SEM) B, D, F, H, J, M-Leaf clearing. A and B-Capitate trichomes of type I with two cells in the secretory head. C and D-Capitate trichomes of type I with four cells in the secretory head. E and F-Capitate trichomes of type I, with six cells in the secretory head. G and H-Capitate trichomes of type I with eight cells in the secretory head. Detail: Secretory head. I and J-Capitate trichomes of type II with two cells in the secretory head. L and M-Capitate trichomes of type III, unicellular. Detail: side view.

including *L. camara* (Inamdar, 1969; Moura et al., 2005). The largest frequency of these trichomes in the adaxial surface of *L. camara* can be related to several factors such as protection against excessive radiation and high temperatures, as reported in the literature (Francino et al., 2006; Hallahan & Gray, 2000; Valkama et al., 2003). However, in most cases, the true ecological function of the trichomes has not been supported by experimental data (Werker, 2000). The penetration of herbicides in the plant tissues is essential for the effective chemical control of weed (Procópio et al., 2003). The anatomical characteristics practically determine the ease with which these products can be absorbed (Hess & Falk, 1990). Trichomes in the leaf

surface can intercept pulverized drops, preventing these from reaching the epidermis. The efficiency of herbicide absorption by the trichomes and their translocation to the epidermic cells are still partially unknown (Hess & Falk, 1990). However, the absorption of these substances can in part take place through the trichomes (Hull, 1970). Some authors consider that trichomes, especially the nonglandular types, are an efficient point for the penetration of herbicides in the plant tissue. Hess & Falk (1990), observed the negative relation between herbicide adherence in trichomes and the efficiency of these products. Thus, the high frequency of non-glandular trichomes in the adaxial surface of *L. camara* would be advantageous for the

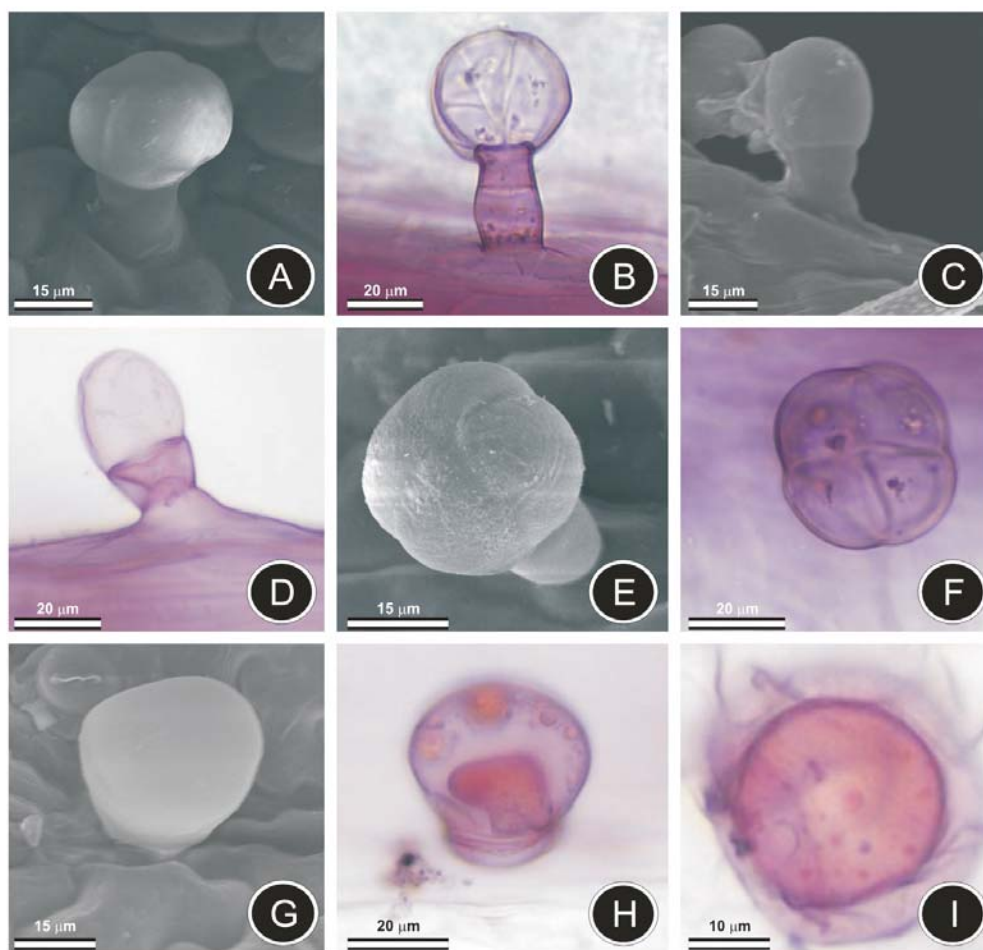


Figure 5 - Types of glandular trichomes in *Lantana radula*. A, C, E and G - Scanning electron microscopy (SEM). B, D, F, H and I - Leaf clearing. A and B - Capitate trichomes of type I with four cells in the secretory head. C, D, E and F - Capitate trichomes of type II with one or four cells in the secretory head. G, H, I - Capitate trichome of type III, unicellular.

species when undergoing chemical control strategies. Unsuitable chemical control would be prone to negatively affect *L. radula* since this plant has a low frequency of non-glandular trichomes in the adaxial surface (Table 1), rendering the epidermic cells more exposed to the agrochemical action.

The different types of capitate glandular trichomes described for the two species are important distinctive characteristics. The Verbenaceae family stands out for presenting different types of glandular trichomes. Considering the large number of *Lantana* species, few studies describing such structures are available. Furthermore, the lack of standardization in the classification of these trichomes limits the use of this characteristic for taxonomic studies (Inamdar, 1969; Cantino, 1990; Moura et al., 2005). Lamiaceae, a family phylogenetically related to the Verbenaceae family, presents a different type of capitate trichomes, with the various classifications of the trichomes resulting in confusion and rendering difficult the comparison between the reported studies in the literature (Werker, 1993; Corsi & Bottega, 1999; Ascensão et al., 1999).

Table 1 - Middle values of the frequency of the non-glandular and glandular trichomes for mm² in the abaxial and adaxial surfaces of *Lantana camara* and *Lantana radula* leaves

Surface	Nonglandular trichomes		Glandular trichomes	
	<i>L. camara</i>	<i>L. radula</i>	<i>L. camara</i>	<i>L. radula</i>
AB	2.8 B	0.3 A	21.2 A	23.0 A
AD	5.2 A	0.9 A	1.7 B	0.6 B

Means followed by the same letter do not differ at 5% probability by the Tukey test. AD = adaxial, AB = abaxial.

The glandular trichomes in the two species, are more abundant in the abaxial surface than in the adaxial. Aromatic plants grow in sunny environments and the trichomes, being protected in the abaxial surface, allow the secretions to remain for an extended time in the plant. *L. camara* is rich in essential oils (Misra & Laatsch, 2000; Alitonou et al., 2004; Randrianalijaona et al., 2005) and these compounds normally evaporate and are released under high temperatures and low humidity. In *L. radula*, the trichomes (mainly those of type III) occur in depressions, which reinforce the hypothesis of protection. The glandular trichomes present ecological significance, being associated with the plant interaction with the environment, interfering efficiently against the attack of herbivores and pathogens (Werker, 1993). Based on the results obtained, it can be suggested that the occurrence of glandular trichomes can be considered an important distinctive characteristic for *L. camara* and *L. radula*.

L. radula presents an irregular abaxial surface resulting in depressions, while in *L. camara* a flat surface is observed. This characteristic represents an additional distinction between the two species. The dorsiventral arrangement observed in the two studied *Lantana* species is characteristic of the Verbenaceae family (Metcalf & Chalk, 1950).

Secretory idioblasts were observed only in *L. camara* and the crystalliferous idioblasts containing styloid crystals were found only in *L. radula*. These two characters are useful in distinguishing the species. Biosynthesis or storage of pentacyclic triterpenoids from this plant could occur in the idioblasts (Sharma et al., 1988; Moura et al., 2005). The

Table 2 - Middle values of the frequency of the nonglandular and glandular trichomes for mm² in the base, median and apical regions of *Lantana camara* and *Lantana radula* leaves

Region	Non-glandular trichomes				Glandular trichomes			
	<i>L. camara</i>		<i>L. radula</i>		<i>L. camara</i>		<i>L. radula</i>	
	AD	AB	AD	AB	AD	AB	AD	AB
BA	5.3 A	2.7 A	0.9 A	0.4 A	2.1 A	23.5 A	0.6 A	22.5 B
RM	4.2 A	3.27 A	0.8 A	0.3 A	1.7 A	19.3 A	0.5 A	26.2 A
AP	6.1 A	2.53 A	1.0 A	0.2 A	1.4 A	20.7 A	0.6 A	20.6 B

Means followed by the same letter do not differ at 5% probability by the Tukey test. AD = adaxial, AB = abaxial, BA = base, RM = median region and AP = apex.



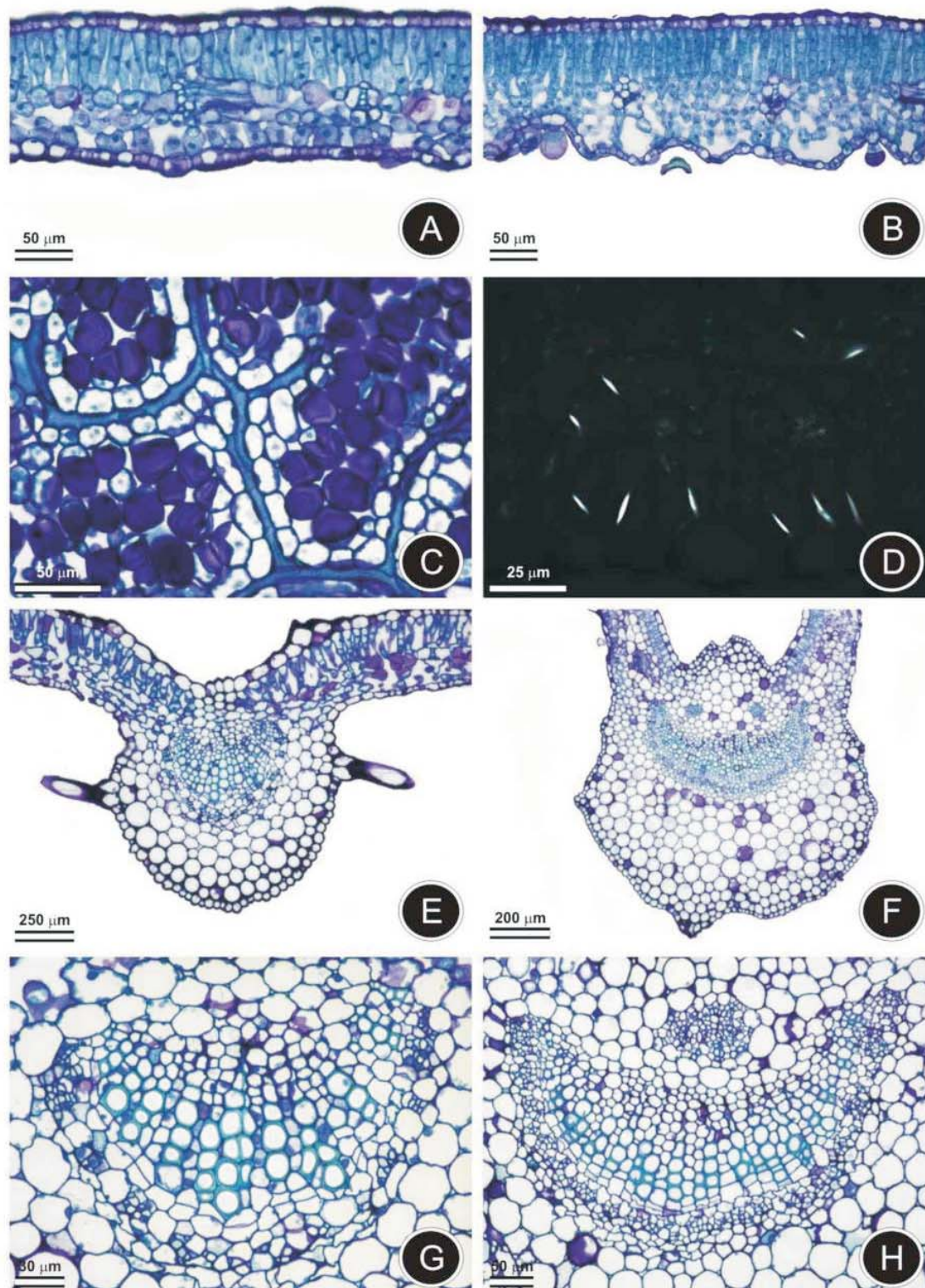


Figure 6 - Sections of *Lantana camara* and *Lantana radula* leaf blades stained with Blue Toluidine. A, C, E and G - *L. camara*. B, D, F and H - *L. radula*. A and B - Transversal section of the leaf blade showing mesophyll dorsiventral. C - Paradermal section of the leaf blade showing the secretory idioblasts. D - Detail of the cortex showing the crystalliferous idioblasts under polarized light. E to F - General aspect of the median vein of leaves. G and H - Detail of the vascular bundle showing xylem and phloem.

morphology and distribution of these crystals is a constant characteristic among the species (Franceschi, 2005), being important for taxonomic purposes (Lersten & Horner, 2000; Prychid, 2003), as its deposition is genetically controlled (Franceschi, 2005).

The results presented in this paper allowed the identification of leaf characteristics useful for the distinction of two morphologically similar species of *Lantana*. The anatomical description of *L. radula* is presented for the first time, which contributes to further knowledge of the Verbenaceae family.

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