

Accessory Pollen Adhesive from Glandular Trichomes on the Anthers of *Leonurus sibiricus* L. (Lamiaceae)

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Abstract: Glandular trichomes (ca. 16 per anther) on the anthers of *Leonurus sibiricus* produce a secretion that, when touched, is liberated at once and becomes sticky when in contact with the air. With successive visitations of the pollinators (species of *Bombus* in naturalized populations) the number of secretion-containing glands on each anther diminishes by mechanical rupture. On the pollinators, the secretion mixed with pollen was found adhered to the integument on the parts making contact with the anthers and stigma, mostly on the scape of the antennae. These trichomes are anatomically identical to the glandular scales common in the entire family and are formed by a multicellular cuticle-bounded structure, with a foot and head. The secretion is accumulated as a milky emulsion under the cuticle, outside the primary cell wall, and is liberated by rupture of the cuticle. The composition possibly differs from what generally distinguishes these glandular trichomes, i.e. volatile oils that give these plants their particular smell. Such volatile compounds are generally assumed to have defensive or attractive functions, different from those observed in this study, which would be strictly mechanical.

Key words: Glandular trichomes, pollen adhesive, pollenkitt, Lamiaceae, pollination, bumblebees.

Introduction

In animal pollination, mechanisms are generally needed for pollen grains to adhere to each other and to pollinators so as to optimize or ensure their transport from one flower to another with minimum loss. The aggregation of the pollen grains can be achieved by many strategies, of which the most frequent is the production of a lipid covering derived from the tapetum of the anthers, called pollenkitt (Stanley and Linskens, 1974).

Under some circumstances, pollenkitt is not sufficient to fulfil the adhesive function. Such is the case when pollen has to adhere to smooth surfaces, when it is unusually large, when it bears large sculpturings, or when it is subjected to extraordi-

nary forces. In these cases, adhesive substances that have originated in flower tissues other than the tapetum become important (Vogel, 2002). It is possible to provide such adhesives by means of glands on the anthers or other flower parts close to them. There are few reports where such glands have been shown to provide an accessory adhesive. It has only been mentioned for *Cylanthra* (Cucurbitaceae) (Vogel, 1981), *Hedychium* (Zingiberaceae) (Vogel, 1984) and *Drymonia* (Gesneriaceae) (Steiner, 1985), but the presence of anther glands in numerous species of different families (Acanthaceae, Bignoniaceae, Gesneriaceae, Lamiaceae and Verbenaceae) suggests that this phenomenon may be more common than the scarcity of published reports would suggest.

In this study, we analyze the anther glands of *Leonurus sibiricus*, with regard to the anatomy, nature of the secretion, and their possible role in providing an accessory pollen adhesive. *Leonurus sibiricus* is native to Siberia and China and now naturalized in Argentina. The anthers of the 4 fertile stamens bear small glandular trichomes, easily recognizable under the magnifying glass, that rupture at the slightest touch and release a sticky substance. Their location and behavior strongly suggest a role in the production of accessory pollenkitt, in which case we would expect the secretion to be transferred with pollen to the pollinators and from these to the stigma. We would also expect to find reasons for the presence of this extra adhesive in relation to the pollen itself or the surfaces where it must adhere.

Nothing is known about the pollination biology of any species of the genus *Leonurus* in native populations. In Europe, pollinators of species of this genus are reported to be primarily bumblebees, in addition to honeybees and leaf-cutter bees (Knuth, 1899). *Leonurus sibiricus* is pollinated in Brazil by several medium-sized bees (Knuth, 1899). Presumably, medium-sized bees are their natural pollinators in Asia.

Materials and Methods

Study site

Observations and material collection were done in a population located in Sierras Chicas de Córdoba, Argentina, 31°6.523'S; 64°20.616'W. AAC# 1365 (CORD).

Glandular trichome anatomy

Anatomical details of the trichomes were studied with a light microscope. Samples of anthers from 3 different stages were taken: early buds (ca. 7 mm long), late buds just prior to anthesis (ca. 10 mm long), and open flowers with dehiscent anthers. The anthers were dehydrated in an ethanol series and embedded in synthetic resin (Kulzer Technovit 7100). Sections 4 µm thick were made with a Leitz 1512 rotary microtome. These were stained with toluidine blue. The observations were carried out using a Leica DMLB microscope with transmitted and epifluorescent light provided with filter sets N2.1 and A. Samples of fresh material were also observed under a light microscope. The aspect, disposition, and number of glandular trichomes on the anthers were observed by means of a Leica M420 photostereomicroscope. The diameter of the intact glands and the sizes of the trichome cells were also measured in fresh material and thin sections, respectively.

Chemical analysis

Extraction

The secretion was extracted from about 50 flowers by breaking the glandular heads and by gathering the substance on the point of a needle. The same physical and chemical tests were carried out on the substance removed with the tip of a needle from the body of the pollinators. The collected substance was placed on a glass slide and observed under the microscope.

Physical and chemical tests

Solubility tests were performed with small samples, left to dry for 5 min at room temperature, under the light microscope with the following solvents: acetone, acetic acid, water, ammonia, benzene, chloroform, *d*₆-dimethyl sulfoxide (*d*₆-DMSO), ethanol, ether, butane and methanol. The substance was heated to 100°C in sealed capillary tubes to observe eventual changes in solubility. The following tests were also performed: ruthenium red staining for mucilage, Molisch for aldehydes, Lugol for starch, Sudan IV staining for lipids and hydrolysis with 10% HCl for polymers.

Glandular function

A number of experiments were performed to verify whether the secretion of the glandular trichomes on the anthers effectively intervenes in the adhesion of pollen on the visiting insects and its transfer to the stigma.

To test if visitors effectively rupture the glands and remove secretions from the anthers, a number of plants, from which all open flowers were removed, were covered with a mosquito net to exclude visitors. After a day, the cover was removed and the newly-opened flowers were identified with coloured strings. A total of 83 flowers were observed continuously throughout periods of 3 to 8 h and the number of visits to each one were counted. At the end of the observation periods, all of the marked flowers were collected, along with 16 additional unvisited flowers that had been kept bagged. The number of intact trichomes remaining on each anther was counted on all flowers collected. A correlation analysis was carried out between the number of visits and the number of remnant trichomes. A Kruskal–Wallis non-parametric analysis was per-

formed taking the number of remnant trichomes by classes of 0, 1–10, 11–20, 21–30, 31–40, 41–50, 51–60 visits.

Another experiment was performed to test the transfer of pollen to the stigma with and without the presence of glandular secretions. A clean bumblebee antenna was used to gather pollen from the anthers, in one case avoiding the glands to obtain only pollen, and in a second case breaking them and obtaining secretions mixed with pollen. In each case the antenna was then carefully brushed with a small paintbrush. This was done considering that the bee wipes its antennae when grooming. Later, clean stigmas were rubbed against the antenna and placed on a slide under translucent adhesive tape. Finally, the pollen remaining on the stigma was counted under the epifluorescent microscope. Twenty repetitions were done for each case (with and without secretion), and a Kruskal–Wallis non-parametric analysis was performed to compare the number of grains on the stigmas.

Eighteen insects visiting the flowers (bumblebees of three different species: *B. bellicosus* Smith, 1879, *B. morio* Swederus, 1787, and *B. opifex* Smith, 1879) were collected to test for the presence of gland secretion on the body parts that could make contact with the anthers. In order to quantify the amount of secretion found on the different parts of the insect heads (clypeus, labrum, paraocular areas, supra-clypeal areas, supra-antennal areas, vertex, scape and distal parts of the antenna) the presence of secretions was scored only when in large amounts, and counted on each head part of the 18 bumblebees captured. With this data, independence between area frequencies was tested with the chi-square statistic.

Observations were also carried out on insect behavior while visiting the flowers.

Estimation of the relative amount of pollenkitt

The amount of pollenkitt in *L. sibiricus* was compared to that of other plant species, selected for having sticky pollen (*Ipomoea* sp., *Bidens pilosa* L. var. *pilosa*, *Hibiscus rosa-cinensis* L.), dry pollen (*Cyclamen persicum* Mill.), or because they also belong to the Lamiaceae (*Plectranthus australis* R. Brown and *Lavandula officinalis* Chaix). A Sudan IV lipid-staining test was performed with fresh pollen samples of these species and their pollenkitt amount assessed by means of a relative scale in which it was distinguished between none, scarce and abundant. With this comparison we expected to determine whether or not *L. sibiricus* could be considered a plant that produces low amounts of pollenkitt.

Results

Glandular trichomes

Distribution and number

The anthers and the stigma are positioned on the upper side of the flower, the anthers in two pairs of different length and the stigma almost reaching the first pair of anthers (Fig. 1A). The pollen is released before the stigma becomes receptive. The glandular trichomes are found on both dorsal and ventral faces of the anthers, being restricted to the connective dorsally (Fig. 1D) and to the thecae ventrally (Fig. 1C). In unvisited flowers the number of glands ranged from 7 to 21 per anther,

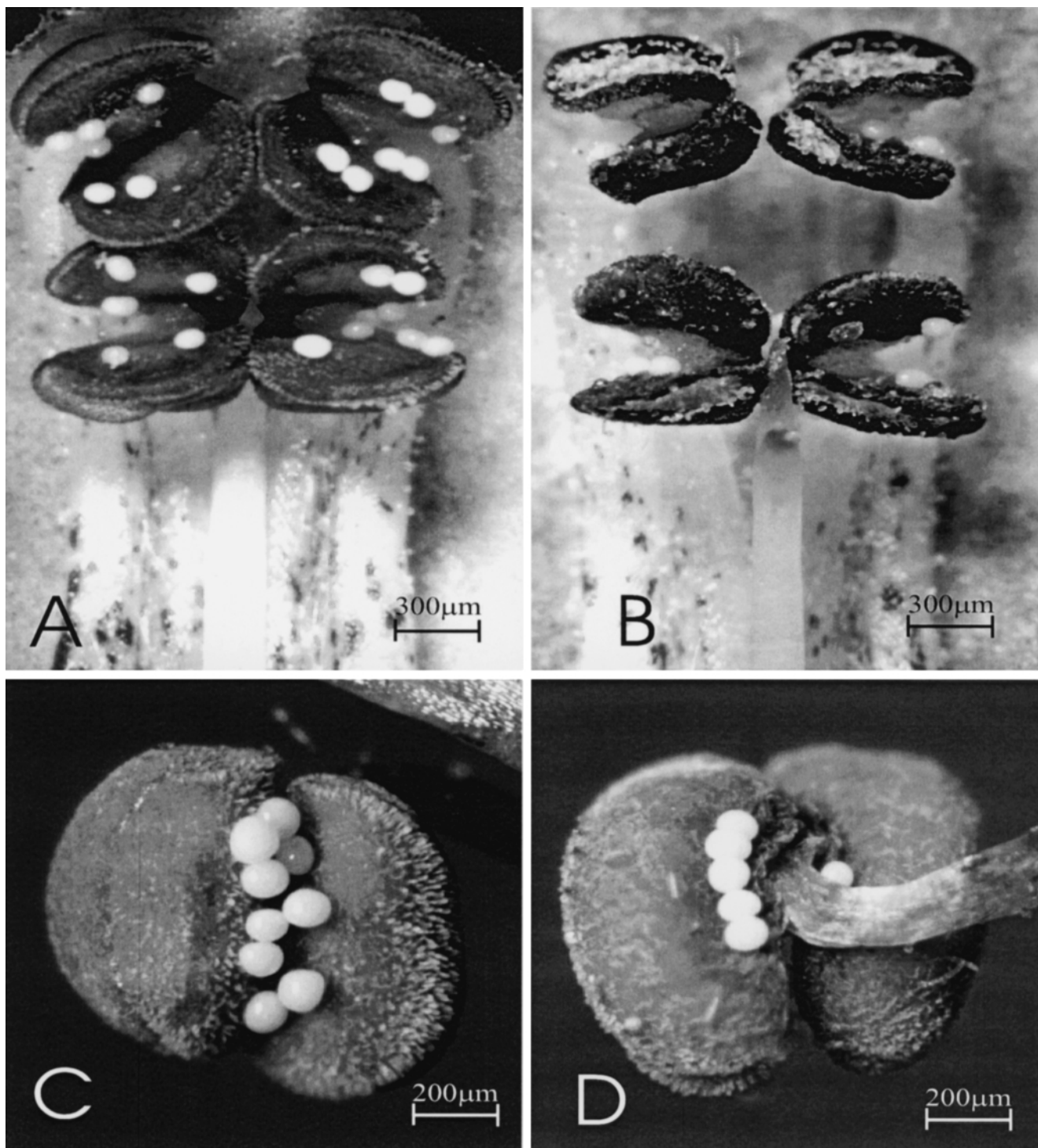


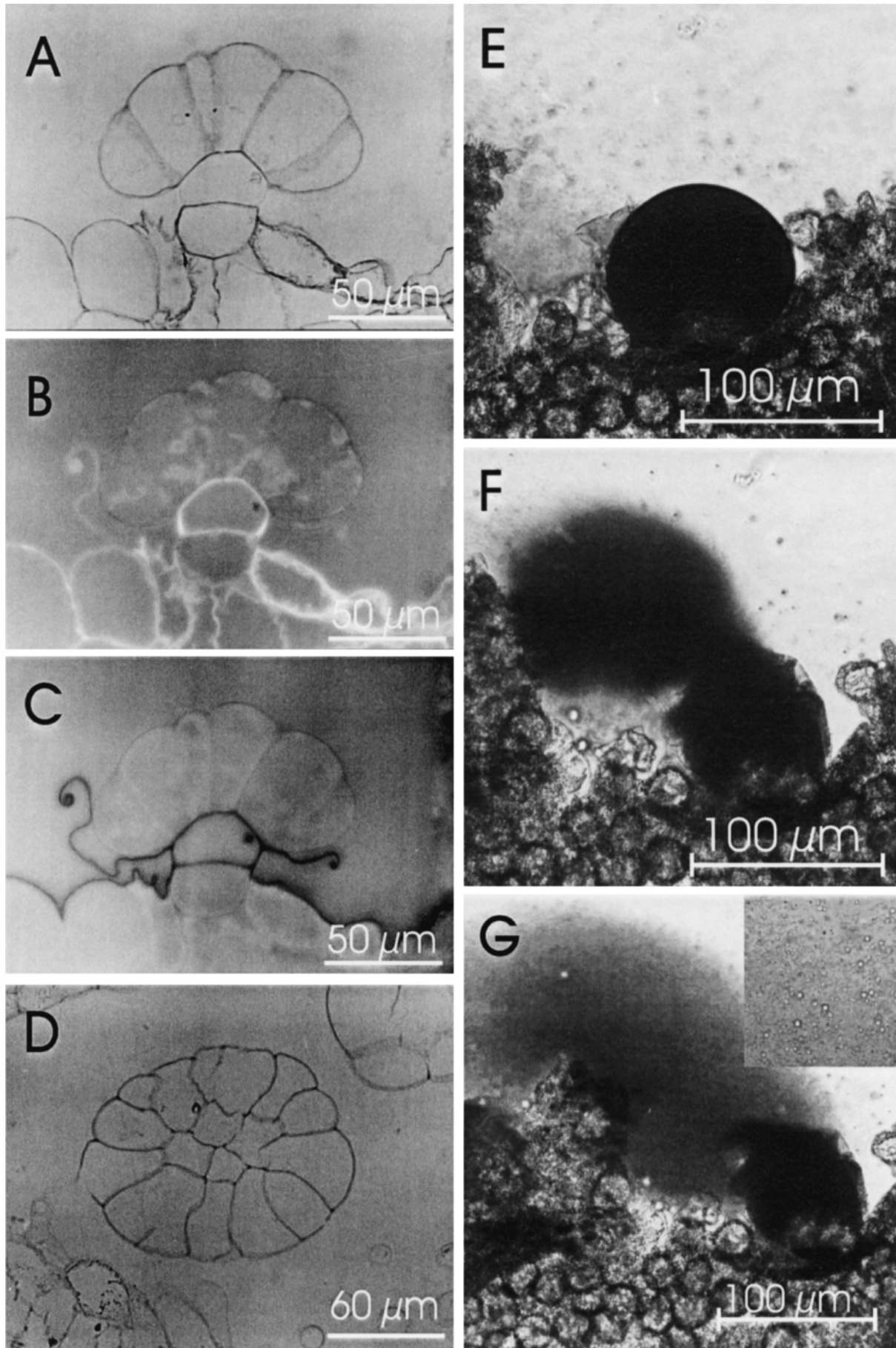
Fig. 1 Stamens of a young (A) and an old (B) flower showing a decreasing number of remnant trichomes. Localization of glandular trichomes on the ventral (C) and the dorsal (D) side of the anthers.

with an average of nearly 13. On the dorsal side, the glands are lined up in two rows, one along each theca, with an average of 4 glands per row. On the ventral side, these trichomes are found in a less orderly manner, also with around 4 per theca. These glandular trichomes reach maturity before the flower opens (Figs. 1A, B).

Anatomical features

The trichomes correspond to the so-called peduncle scale type (Metcalf and Chalk, 1979). Seen from above in fresh material (Figs. 1A–D), the intact glands are white in colour and approximately spherical in shape, with a mean diameter of 91 μm. This corresponds to a volume of $4.73 \times 10^{-4} \text{ mm}^3 \pm 1.13 \times 10^{-4} \text{ mm}^3$ (n = 15).

Fig. 2



◀ **Fig. 2** Longitudinal (A) and cross (D) sections of a trichome seen with transmitted light. (B, C) The same trichome as A seen with epifluorescent light through filter N2.1 and A, respectively. Note the thickness of the neck cell wall and the detached cuticle. (E–G) Glandular trichomes in fresh material seen with a light microscope. E Intact trichome with secretion accumulated under the cuticula. F, G Two stages of secretion release after a slight pressure was exerted on a damaged trichome; detail of the emulsion in G.

A longitudinal section through the trichome shows a short foot and a broad head (Figs. 2A–C). One or two more-or-less isodiametric cells form the foot: a neck cell and a base cell. Staining and the appearance under epifluorescent light revealed that the walls of the neck cell, particularly the anticlinal ones, are lignified (Fig. 2B). It is also evident that the cuticle is thick and continuous between the trichome and the epidermal cell (Fig. 2C). Many long radial cells, of which a maximum of 16 was counted, form the head (Fig. 2D). All the cells in the head are rich in vacuoles even at the bud stage, suggesting that secretory activity ceased early in development.

The epidermal cuticle of the trichomes detaches from the base of the neck cell (Fig. 2C) and forms a covering that surrounds the head and contains the secretion in a subcuticular space (Fig. 2E).

Secretion process

The substance is produced and secreted by the head cells into the subcuticular space. The latter becomes expanded with the accumulated secretion so that the trichomes appear as small pearls on the anther (Fig. 1). When the cuticle that covers the glandular head is slightly pressed, it ruptures and releases the secretion (Figs. 2E–G). In contact with air, the latter dries rapidly, becoming a solid, sticky and amorphous mass (Fig. 3A). The cuticle, once broken and the secretion released, remains loosely attached to the trichome base (Fig. 2C). Considering the small extension of the broken cuticle, which would barely cover the head, it is evident that it must be stretched when containing the secretion.

The occurrence of these trichomes even in small buds suggests that the secretion is stored under the cuticle at an early stage of development while the cell stores are consumed.

Other glandular scales, with similar features to those just described, can be found on external parts of the corolla and calyx. These, which also produce an emulsion that solidifies when released, are slightly smaller and with more translucent content.

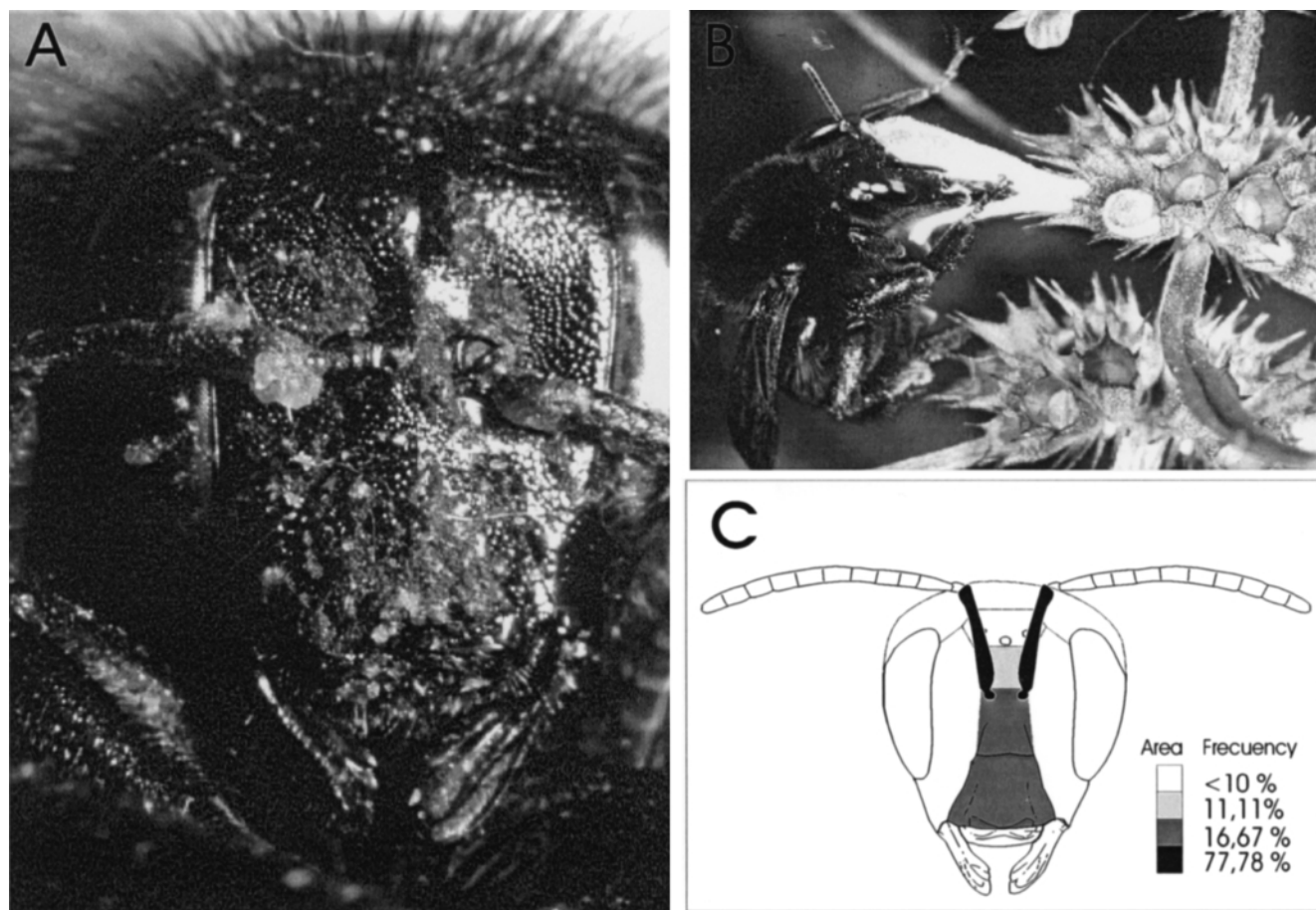


Fig. 3 (A) Head of a pollinator showing clumps of the adhesive–pollen mixture. (B) *Bombus morio* visiting the flowers of *Leonurus sibiricus*. (C) Distribution of the adhesive–pollen mixture in the tegument areas of the front of the head of bumblebees caught on the flowers (n = 18).

The highest frequency of bees (78%) presented a large amount of the mixture on the scape of the antennae. The next highest frequencies were much lower: 17% for the clypeal and supra-clypeal areas, 11% for the frons, and all other areas with less than 10%.

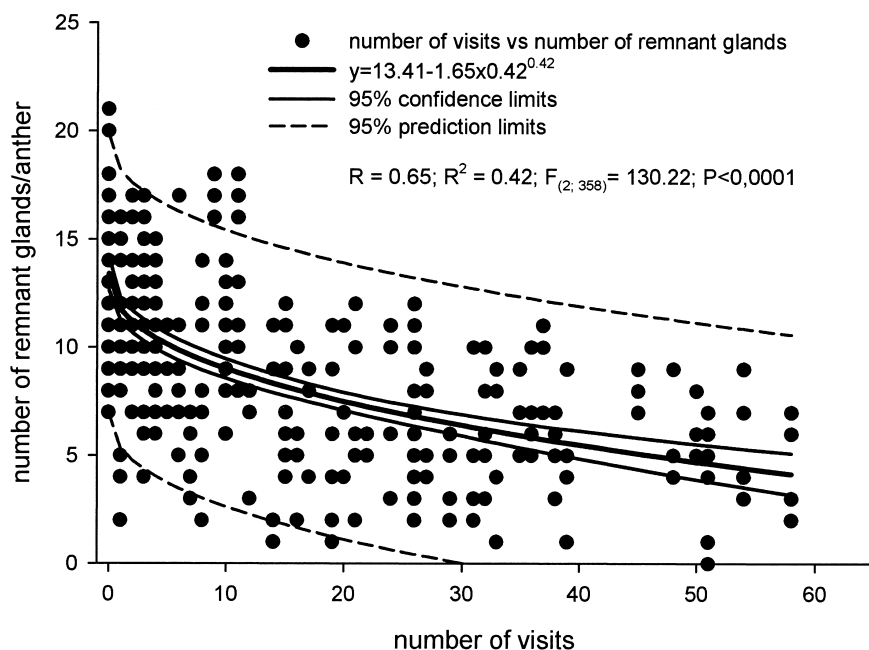


Fig. 4 Correlation between the number of remnant trichomes/anther and the number of visits/flower.

Secretion: physical and chemical features

The secretion has a milky white colour in fresh material. Under the microscope and mounted in water it reveals itself as an emulsion of tiny droplets (Fig. 2G). When released, the aqueous phase evaporates and the non-soluble droplets condense.

The solid secretion was only soluble in d_6 -DMSO. It became an emulsion in water and in concentrated ammonia, and was insoluble in all other solvents used. The emulsion could not be dissolved in water even when heated to 100°C. The aldehyde test was very weak, while the lipid, starch, mucilage and HCl hydrolysis tests were negative.

The same solubility and emulsion tests were carried out on the dry material obtained from the insect bodies, giving identical results as those from the secretions from the anther trichomes.

Function of glandular trichomes

Pollinator behaviour

The population of *L. sibiricus* observed was visited almost exclusively by three different species of bumblebees (*B. bellicosus*, *B. opifex* and *B. morio*), which gather nectar. These three species exhibit similar behaviours. After an exploratory low flight, they land near the base of the inflorescence and visit the flowers by climbing upwards or with short upward spiralling flights. To obtain the nectar, they seize the lower lip of the corolla with their front and middle legs and then introduce their head into the flower in such a way that the anthers rub against the upper part of the head (Fig. 3B).

Location of the secretion on the insect body

The secretion mixed with pollen was found on most parts of the face of the bee; all of which normally make contact with the anthers and stigma.

The percentage of bee individuals presenting secretions on the scape of the antennae (78%) was significantly higher than those of other head areas ($n = 18$, $\chi^2 = 63.28$, $p = 0.0001$), the latter being noticeably lower: clypeal 18%, supra-clypeal 17%, frons 11%, and all remaining areas with less than 10%. Fig. 3C shows, for each area, the percentage of individuals presenting secretions.

Correlation between the number of the remnant anther trichomes and the number of visits

There is an inverse correlation between the amount of visits and the number of glands. The curve that best fitted the obtained values reflects the equation $y = 13.41 - 1.65(x)^{0.42}$, with an $R^2 = 41.86\%$, $r = -0.65$ (Fig. 4). The non-parametric Kruskal–Wallis analysis showed a significant difference between the numbers of glands in each class of visit frequency, with a 95% significance level.

Transfer of pollen to the stigma

This test resulted in more pollen being transferred to the stigma with the presence of adhesive than without. The Kruskal–Wallis analysis showed a significant difference between the number of pollen grains transferred with and without adhesive (Table 1).

Table 1 Kruskal–Wallis analysis for pollen transfer to the stigma, with and without adhesive

Adhesive	N	Means	Medians	H	<i>p</i>
with	20	2.00	2.00	7.24	0.0034
without	20	0.50	0.00	–	–

Pollenkitt

Based on the amount of pollenkitt detected by staining pollen with Sudan IV, plant species tested can be separated into three groups: with no pollenkitt (*Cyclamen*, *Lavandula*, *Bidens*), with scarce pollenkitt (*Leonurus*, *Plectranthus*), and with abundant pollenkitt (*Ipomoea*, *Hibiscus*).

Discussion

Presence of glandular trichomes in L. sibiricus and in other members of the family

The trichomes described here are characteristic of the Lamiaceae and have been categorized anatomically as glandular scales (Lamiaceen – Drüsenschuppen according to Uphof and Hummel, 1962; Napp-Zinn, 1973). The glandular trichomes observed in this study are anatomically similar to those described by Fahn (1988), in which the walls of the neck cell are completely cutinized. This characteristic would avoid the flow of substances accumulated in the trichome into other plant tissues. In this study, we also saw that these walls are reinforced with lignin, its function being unknown but possibly having a similar function of preventing the flow of liquids out of the trichome, and/or a mechanical function, holding the trichome in position.

In a screening of 142 species of the Lamiaceae, Mattern and Vogel (1994a) found that 95% had these glandular trichomes on the leaves and/or the calyx and 80% had them on the corolla. Their presence on stamens was not studied. The same authors studied the development of these trichomes (scales) from small buds to post-floral stages on calyces of *Satureja montana*. The cuticle rises and the subcuticular space is filled with secretion days before and after the flower opens. They never observed rupture of the trichome. Only Bruni and Modenesi (1983) indicate, for *Thymus*, that the glandular scales release their secretion by rupture of the cuticle, as occurs with those studied here.

Although these widely distributed vegetative glandular trichomes are anatomically identical to those of the anthers, an adhesive function has seldom been attributed to them. Mattern and Vogel (1994a, b and authors mentioned therein) admit that on the leaves and on the calyx the trichomes produce essential oils that are associated with defence against herbivores and attraction of pollinators, respectively. Delpino (1869, 1873) seems to be the only one to have attributed the function of providing an adhesive for pollen to these glands, which he called “globuli” or “perline de viscina”. He observed them in lamiaceous species of *Sideritis*, *Marrubium*, *Stachys recta*, *Salvia glutinosa*, *Salvia officinalis* and *Vitex agnus-castus*. In spite of those preliminary observations, the subject since then has remained unexplored. This study provides the first evidence that these glandular scales release a secretion when the flowers are visited and that this secretion sticks to the visitors, taking along pollen, which it can effectively carry and deposit on the stigma. The secretion forms a solid covering on the pollinators, mainly on the antennae. This covering is readily dissolved on the stigma, presumably by the emulsifying action of the humid receptive surfaces.

Other cases of accessory pollen adhesives produced by stamen trichomes

As far as we are aware, trichomes secreting adhesive substances are reported for the Cucurbitaceous species of *Cyclanthera* and *Rhytidostylis trianaii*, for which detailed studies were made, and apparently for other members of the family such as melons, squashes and *Echinocystis*, according to older literature mentioned in Vogel (1981).

In *Cyclanthera pedata*, the most thoroughly studied species in this respect (Vogel, 1981), a circle of glandular trichomes crowns the monotheal synandrium. Each trichome has a large basal cell and a small apical one. When a trichome is touched, the apical cell breaks off leaving an opening on the tip of the basal cell. The basal cell then automatically contracts and ejects the adhesive substance it contains. The latter is instantly expelled as a transparent mass onto the integument of the visitor. The adhesive mass makes it possible for pollinators, usually wasps, to carry clusters of pollen. In the flowers of *Cyclanthera*, the need for accessory adhesive substances can be explained by the large size of the pollen grains ($\approx 70 \mu\text{m}$ in diameter), their scarce number (ca. 500 grains) and the relatively low amount of pollenkitt.

In *Hedychium* (Zingiberaceae) two rows of trichomes secrete and push a mucilaginous covering over the single anther. When the walls of the theca contract, this covering adheres to the pollen. This enables it to be extracted as a whole by the flapping wings of the pollinating lepidoptera (Vogel, 1984).

In *Drymonia serrulata* (Gesneriaceae) glands are found on the interior upper part of the corolla. Before the flower opens, the anthers are pushed against the glands by the growing filaments so the secretion sticks onto them. When an insect of the right size visits the flower looking for nectar, its thorax makes contact with the secretion and the pollen grains fall over it. The pollen itself is not adhesive since it must pour from the anther when the insect pushes and turns it over (Steiner, 1985).

Why are the anther glands needed on Leonurus sibiricus?

Based on these known cases, we can attempt to understand the necessity for accessory glands with pollen adhesive in *L. sibiricus*. Conditions of the pollen itself can justify the existence of these structures: large pollen (*Cyclanthera*) or scarce pollenkitt (*Cyclanthera* and *Drymonia*). Other reasons can be the conditions of the surface to which it must adhere: smooth integuments (*Cyclanthera* and *Drymonia*) or surfaces otherwise unsuitable for pollen transport, such as the beating scaly wings of lepidopterans (*Hedychium*).

In the case of the *L. sibiricus*, the pollen, although not very large ($\approx 30 \mu\text{m}$), has scarce pollenkitt and must adhere to smooth parts of the bee's integument. The pollenkitt, alone, would be only sufficient to keep the pollen from falling out of the anthers when these open and expose it “hanging” horizontally. The characteristics of the surface where the pollen is transported are critical, since pollen mostly adheres to the scape of the antenna (Fig. 3C: black). This part of the antenna is particularly smooth and frequently cleaned by the bee. This location of the pollen is possibly related to the shape of the stigma and

its receptive parts: bifurcated, "Y" shaped, and receptive at the internal part of the branches.

To summarize, the following hypothesis on the importance of the adhesive secretions in *L. sibiricus* can be given:

1. It prevents the pollen from being easily wiped off, helping it remain adhered to the insect integument.
2. It makes it possible for pollen to stick to smooth parts of the integument and to be easily gathered by the stigma.

With the results obtained in this study, it is evident that insects visiting the flowers are permanently being contaminated with the secretion while gathering nectar. This shows the secretion is actively involved in the process of pollination, whether or not it represents an advantage for the plant. The test for pollen transfer to the stigma suggests that it is advantageous. The secretion is probably important when the bee grooms itself. It will not do this every time it visits a flower, but there are other situations – such as when the pollen is subjected to vibrations, wind or other physical forces – in which the secretion may also be acting as an adaptive adhesive, keeping the pollen safely stuck to the antenna until it touches the wet surface of a receptive stigma, where it can emulsify and release the pollen.

An examination of the pollinators and the environment of the native populations in Asia may provide further insight concerning the adaptive nature of this secretion.

Observations on the chemical properties

With the results obtained, we cannot determine with any certainty what substances make up the secretion, for which a more profound study at the chemical level is needed. Nonetheless, we can anticipate it as a mixture of various compounds. Aliphatic terpenes are possible components of the solid phase. Compounds of this chemical family are very common in glands of Lamiaceae, although normally they have been described based on their volatile phase with the collective name of essential oils.

Possible origin of accessory adhesive glands

Glandular scales are ubiquitous on vegetative and floral parts in the family Lamiaceae and they probably represent a symplesiomorphy for the group. Their location on the anthers could easily be derived from vegetative organs or from other flower organs, such as sepals and petals, where they play a role in defence or even in pollinator attraction (Mattern and Vogel, 1994a). At least in *L. sibiricus*, the scales from vegetative parts and from the calyx secrete an adhesive substance that might serve to immobilize small insects. The existence of glandular scales with an adhesive function on the anthers of *Vitex* (Delpino, 1869), which is now placed in a basal position with respect to Lamioideae and Nepetoideae (Cantino, 1992), suggests that this acquisition could have occurred very early in the evolution of the family and that it could be more common in Lamiaceae than we know.

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