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Structures involved in production, secretion and injection of the venom produced by the caterpillar *Lonomia obliqua* (Lepidoptera, Saturniidae)

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Abstract

The number of accidents caused by injection of the venom of *Lonomia obliqua* caterpillars in Southern Brazil has increased in the last years. Even though this kind of envenomation has an important social and medical impact, nothing is known about the cellular structures responsible for the production and secretion of this venom. Here we identify and analyse morphological structures possibly responsible for the production and secretion of the active principles of the venom, as well as the histological relationship of these structures with the urticating spines of *L. obliqua*. Detailed microscopic observations showed that: (a) *L. obliqua* has a complex tegument, with several cuticular specializations, (b) there are no pores along the tegument neither in the spines and (c) the spines bear a hollow canal—where the venom is deposited—and an area that can be easily broken when touched, releasing the venom. Histological and histochemical techniques revealed that: (a) there is no single gland cell that produces the venom, (b) a secretory epithelium, composed of cells containing vesicles that increase in size and number as they reach the apical region, underlies the tegument and the spines and is responsible for secretion of the venomous substances and (c) the venom is deposited in the subcuticular space and at the tips of the spines.

Keywords: *Lonomia obliqua*; Caterpillar; Urticating spines; Venoms; Morphology

1. Introduction

Cutaneous reactions caused by accidental contact with the hairs and spines of many lepidopterous larvae are well known. The first relevant publications on the subject date from 1848 (for references see Picarelli and do Valle, 1971). Also, the structure of these urticating hairs and spines of some species have been studied and reported (von Ihering, 1914; Gilmer, 1925; Bücherl and Buckley, 1971; Eaton, 1988; Matos and Azevedo, 1991; Scoble, 1992). The clinical profile resulting from these accidents vary depending on the species involved and on the victim's physical condition: some might cause simple burning sensations, while others—as in the families Megalopygidae, Saturniidae and Lasiocampidae – can cause severe haemorrhagia and even lead to death (Pesce and Delgado, 1971; Rotberg, 1971; Scoble, 1992). The severity of symptoms can be influenced by the extension of the skin area affected, by the deepness of the injury, by the amount of venom injected and by the number of smashed larvae—the latter being the case of species that live in aggregation, when in the larval stage, as a protection against predation (Vulinec, 1990).

The moth *Lonomia obliqua* (Lepidoptera, Saturniidae) is very venomous when in the larval stages, which occur during spring and summer in Southern Brazil. The caterpillar is responsible for severe and even fatal accidents caused by skin contact with the bristles that cover the animal's body. Victims of the envenomation caused by *L. obliqua*

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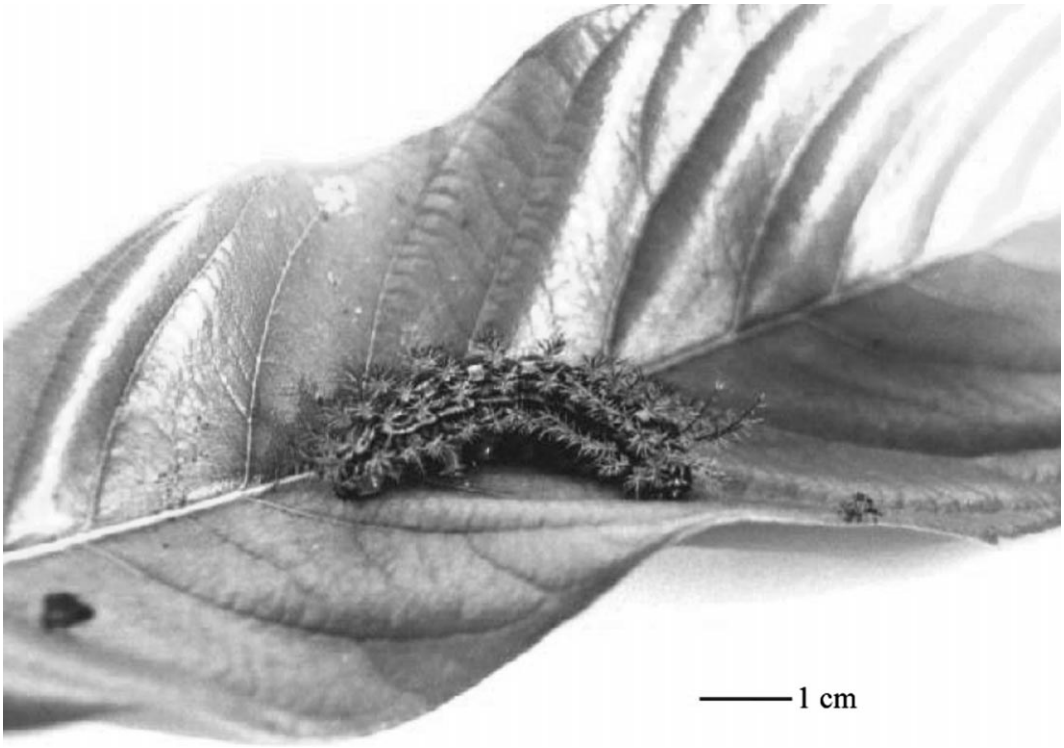

Fig. 1. *Lonomia obliqua*. Sixth instar larvae.

present a typical profile of an acquired haemorrhagic disorder (Duarte et al., 1990; Kelen et al., 1995; Abella et al., 1998; Ministério da Saúde, 1998). Initial symptoms include pain and burning sensation at the site of contact, generally followed by more severe clinical manifestations, such as bleeding from skin and mucous membranes, epistaxis, hematuria, acute renal failure and melena. If the victim is not quickly treated, intracerebral bleeding may occur leading to death. Furthermore, since *L. obliqua* caterpillars have gregarious habit (Ministério da Saúde, 1998), the accident frequently involves many larvae, leading to the worst consequences.

Symptoms such as hematuria and bloody saliva were reported after an accident with a caterpillar around the year 1912 (von Ihering, 1914). The first reported haemorrhagic disorders caused by *Lonomia achelous* occurred in Venezuela (Arocha-Piñango, 1967; Arocha-Piñango and Layrisse, 1969). In these cases the envenomation effects indicate interferences with the haemostatic system, including: strong involvement in the fibrino(geno)lytic system; enzymatic plasmin-like activity and urokinase activity upon specific chromogenic substrates (Arocha-Piñango and Pepper, 1981); and fibrinolytic activity over human blood clots (Coll-Sangrona and Arocha-Piñango, 1998). With *L. obliqua*, besides all these symptoms, a consumption coagulopathy with fibrinolysis was recently reported (Reis et al., 1999).

All reports describing accidents with caterpillars show that the venom enters the human skin through the urticating spines of the animal. Actually, it is believed that the envenomation can involve not only the injection of secretion, but also other caterpillar's fluids, such as haemolymph. Usually, the bristles are homogenized and the resulting extract is used in biochemical studies, as well as in production of the antivenom (Silva et al., 1996). In this study we analyse and describe the structures involved in production and injection of *Lonomia obliqua* venom because even though the spine structure and the cellular morphology of glands and other components underlining the epiderm of this kind of bristles are characterized as the poison apparatus able to cause the envenomation (Gilmer, 1925), there are no detailed studies of this kind for *L. obliqua*.

2. Materials and methods

Lonomia obliqua larvae are usually found in groups feeding on leaves of guava tree, yellow plum tree, fig tree and other trees in country areas of Southern Brazil (states of Rio Grande do Sul, Santa Catarina and Paraná). The colonies,

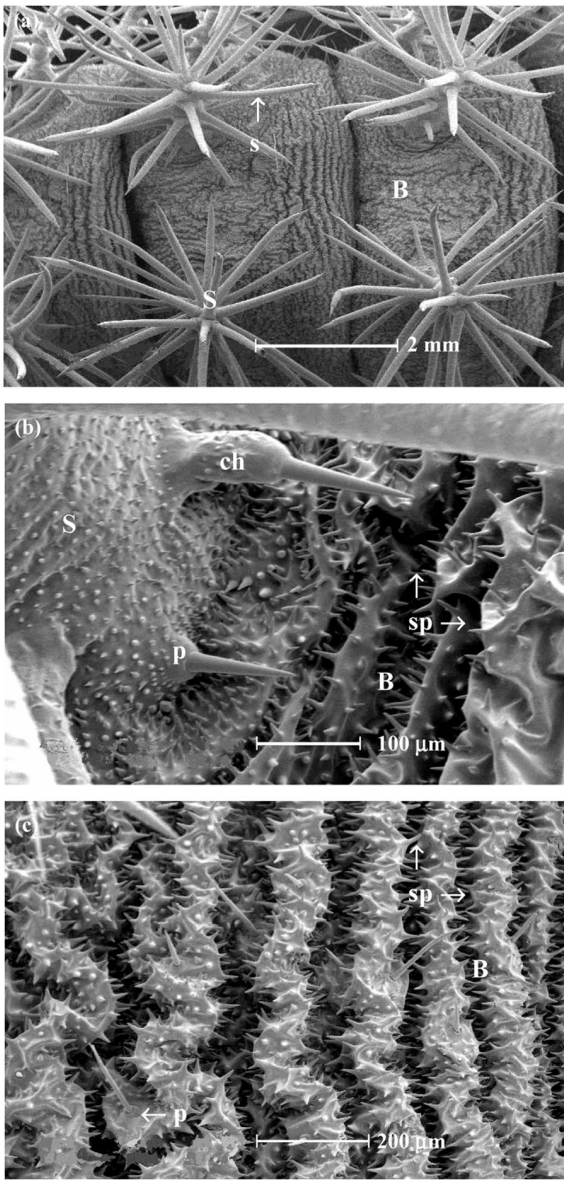

Fig. 2. Dorsal views of the tegument under SEM (Philips XL 30 scanning electron microscope). The tissues were prepared as described (see Material and methods section). In 2(a), *scolus* (S) bearing lots of setae (s); in 2(b), detail of the base of a *scolus* showing the presence of both a *pinaculum* (p) and a *chalaza* (ch) and also the spinules (sp) at the base of the tegument (B); in 2(c), a close view of the base of the tegument (same region as B in 2(a)) (Nomenclature based on Scoble, 1992).

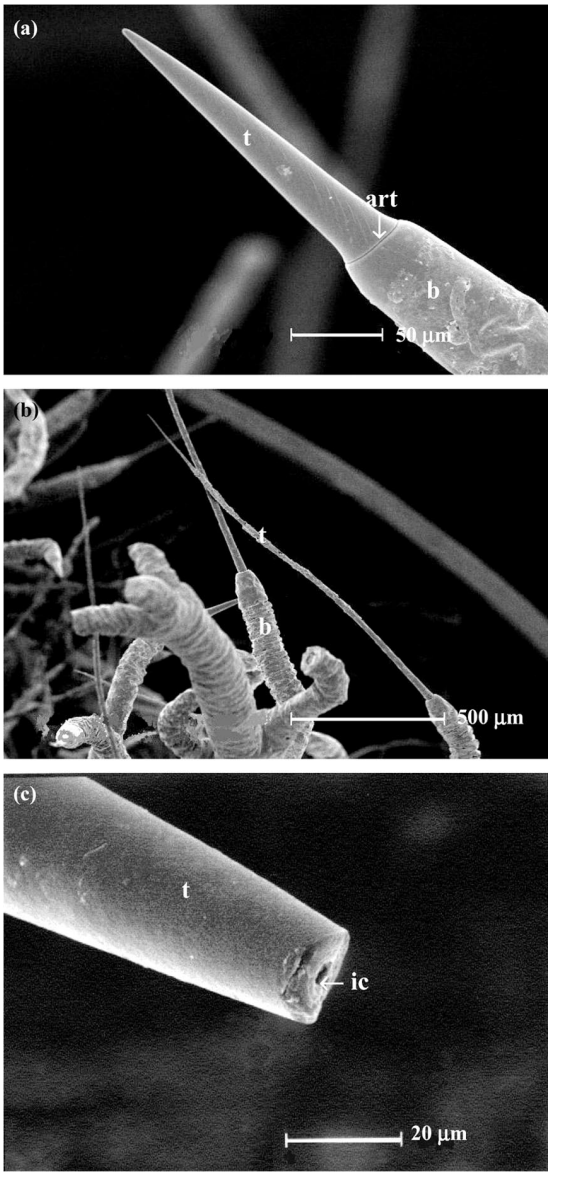

Fig. 3. Tips at the distal end of the seta. 3(a): in a seta of a dorsal *scolus* the tip is short (about 100 μm in length); the weak articulation (art) is easily seen between the tip (t) and the base of the seta (b). See Discussion for more details. 3(b): setae of a lateral *scolus* bearing long tips (about 1 mm in length). 3(c): opening at a broken tip showing the internal canal.

when collected by local people, are sent to study centers or health assistance centers. Specimens used for this study were part of different colonies kindly provided by Centro de Informação Toxicológica (CIT) in Chapecó (state of Santa Catarina), CIT in Porto Alegre and EMBRAPA in Passo Fundo (both in state of Rio Grande do Sul).

Effective elucidation of the internal structures involved in production and injection of venom require the utilization of light microscopy (LM) and scanning electron microscopy (SEM), as well as histological and histochemical analysis, each with its own sample preparation. For fixation, ten specimens of fifth and sixth instar larvae (Fig. 1) were placed in paraformaldehyde 4% buffered with a phosphate solution, pH 7.2, at 4°C, for 24 h.

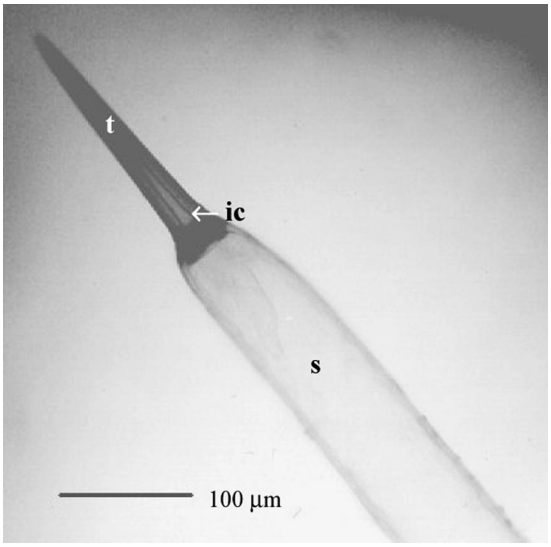

Fig. 4. Seta (s) seen under a light microscope (LM). The internal hollow canal (ic) can be seen at the tip (t). The cuticle is darker in regions with more chitin, such as the tip.

2.1. Scanning electron microscopy (SEM)

For SEM analysis we used one entire specimen, the anterior and posterior segments of other specimen, as well as lateral and dorsal urticating spines of another specimen. Fixed samples went through an ethanol series for dehydration: 12 h in ethanol 70%, 30 min in ethanol 80%, 30 min in ethanol 90%, and twice in ethanol 100% for 30 min. Samples were washed with acetone for 1 h, and then submitted twice to ultrasound for 15 min to remove undesired residues from the cuticle. Finally they were critical-point dried with CO_2 and coated with either 25 or 50 nm of gold.

Samples were viewed and analysed in a Philips XL 30 Scanning Electron Microscope at the Centro de Microscopia e Microanálise da Pontifícia Universidade Católica do Rio Grande do Sul.

2.2. Light microscopy (LM)

Two fixed larvae were used for observations in an Axioskop Zeiss light microscope. A sagital cut was made in each specimen and internal organs were removed. The tegument and adjacent tissues were stained with basic fucsin and methylene blue. Urticating spines (*scoli*) and areas around it were analysed, and photographs were taken.

2.3. Histology and histochemistry

Five fixed larvae were used for histological and histochemical investigations. Body segments were excised with a blade; some segments were then divided into six *scoli* regions, so that each section beared a *scolus*: two with a dorsal *scolus*, two with a lateral *scolus* and two with a subspiracular *scolus* (Scoble, 1992).

Samples were washed with phosphate buffer, pH 7.2 and then kept in ethanol 70% for 12 h. After dehydration in ethanol series (up to ethanol 95%, 10 min in each solution),

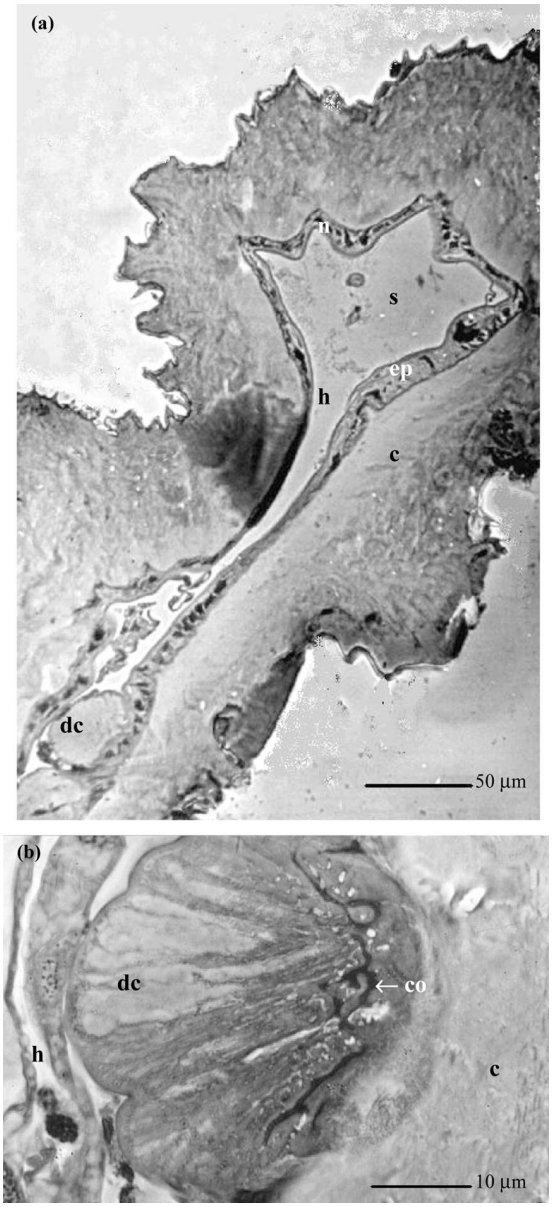

Fig. 5. Longitudinal sections of a seta (s) without the tip, visualized in a LM; 5(a) was stained with Basic Fucsin—Methylene Blue, while 5(b) with Periodic Acid Schiff (PAS). 5(a): the epithelium (ep) goes on along the seta, between the haemolymph (h) and the cuticle (c). The nuclei (n) of the epithelial cells are clearly seen. A group of differentiated cells (dc) is seen near the base of the seta. 5(b): detail of the region with differentiated cells (dc) seen in 5(a). Granules of secretion form a coalescence (co) at the apical region.

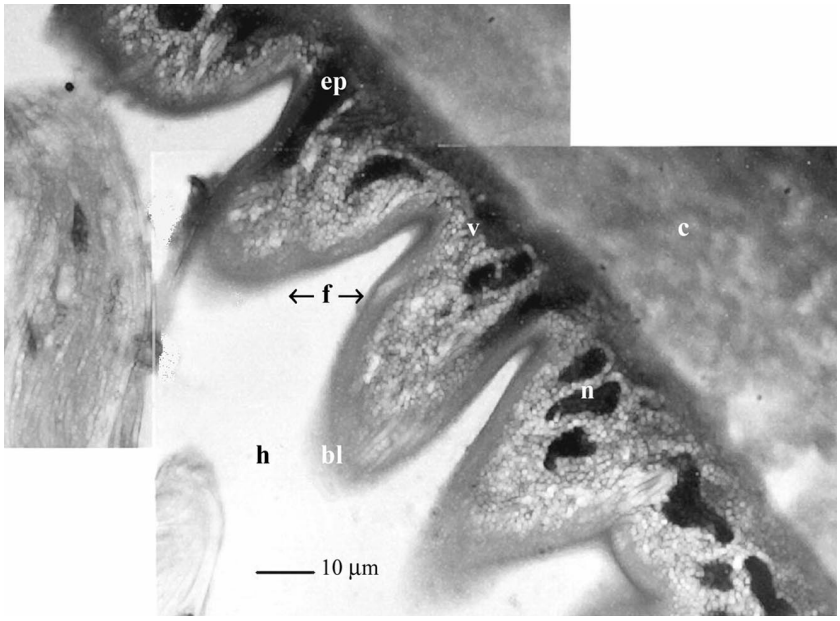

Fig. 6. Longitudinal section of the tegument at the base of a *scolus*, stained with Basic Fucsin—Methylene Blue and visualized in a LM. In this region the epithelium (ep) is thicker than in others, and folds (f) of the basal lamina (bl) are clearly evidenced. Cells have large nuclei (n), besides many vesicles (v) that increase in number and size from the basal to the apical region. (c): cuticle; h: haemolymph.

samples were washed with intermediate infiltration solution containing 1:1 of ethanol 95% and historesin infiltration solution (Technovit Kulzer Histo-Technik) and kept in vacuum for 2 h. Then the solution was replaced by pure historesin solution; after 2 h in vacuum, samples were finally embedded in a solution containing historesin and polymerizer. Historesin blocks were kept at 37°C.

Serial sections were cut at 3–4 μm with tungsten blades in a Leica microtome, and then placed over histological slides for staining. Staining of the material was either with Basic Fucsin – Methylene Blue or with Periodic Acid Schiff (PAS) according to Böck (1984).

The material was analysed and photographed using an Axioskop Zeiss light microscope.

3. Results

As shown by scanning electron microscopy (SEM), the caterpillar presents a complex tegument. This well organized structure consists of lots of setae (spines) and other specializations. These 'sculptural elements' are integumental outgrowths of the larval cuticle (Scoble, 1992). Fig. 2 shows the different types of specializations and their distribution throughout the caterpillar's body. According to the nomenclature proposed by Stehr (1987), several integumental outgrowths could be found in *L. obliqua*, such as *pinacula*, *chalazae*, spinules and *scoli*. The latter is the most prominent structure, bearing lots of setae containing the toxic substances.

Varied setae patterns are seen under SEM. As indicated in Fig. 3, the *scoli* found in *L. obliqua* exhibit setae bearing tips of different sizes: either short tips (about 100 μm on dorsal *scoli*) or long ones (about 1 mm on subdorsal and subspiracular *scoli*). Some setae seem to have a pore at its distal end (Fig. 3(c)); however, this opening is part of an internal canal of the tip that is observed when the setae gets broken or under the light microscope (see below). Indeed, no pores were found neither along the setae nor at the base of tegument (Figs. 2 and 3).

In addition, the chitin thickness varies along the tegument. In the spinules (not shown) and at the tip of a setae that forms a *scolus* the cuticle appears to be very thick, with more chitin (Fig. 4). In those setae, the chitin appears to be thin at the base; at the tip, where it is thicker, a narrow hollow canal is clearly observed (Fig. 4).

Histological and histochemical observations showed that the whole seta is formed by a secretory epithelium. The epithelium underlying the tegument goes on along the spine (Fig. 5(a)), as a continuous evagination of the body. In some regions along this epithelium, cells expand and become higher, more cylindrical than cubic. Some even form a differentiated group (detail in Fig. 5(b)); at the apical region of these cells products of secretion accumulate and form a deposit instead of granules, as a result of their coalescence.

At the base of tegument the epithelium thickness is not regular: at the base of a *scolus* the epithelium is swelled, and the basal lamina forms large folds (Fig. 6); in this region, the epithelium is over five times thicker than in other regions (as

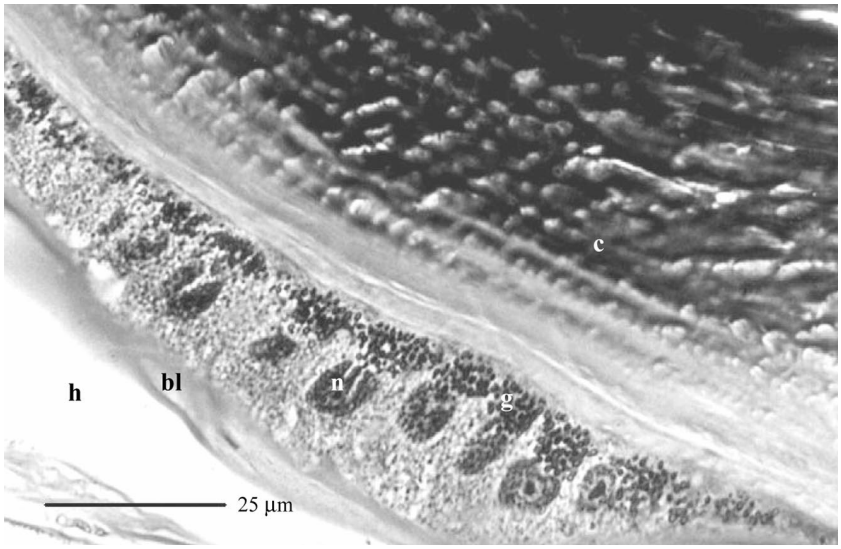

Fig. 7. Cross section of the secretory epithelium stained with Basic Fucsin—Methylene Blue and visualized in a LM. The basal lamina (bl) does not fold in this region, but the cells still show large nuclei (n) and accumulation of vesicles in the apical region, which is even more evident than in Fig. 6(b). Further, the granules (g) concentrate in the apical region, near the cuticle (c). h: haemolymph.

in Fig. 7). Besides clearly evidenced nuclei and nucleoli, vesicles in the cytoplasma increase in size and number as they reach the apical region of the cell; in other words, at the apical region the vesicle concentration is higher and a deposit is formed (Figs. 6 and 7). As in regions of the seta, granules accumulate in an extracellular space between the epithelial layer and the cuticule.

The vesicles in epithelial cells stained pink in the PAS staining, which means that they consist of glycoconjugates, differing from nuclei.

The cuticle of *L. obliqua* is not regular, showing a network of thin channels perpendicular to the chitin layers (Fig. 8).

No other specialized gland or glandular structure connected to the spines was found.

4. Discussion

Several accidents with *Lonomia obliqua* leading to haemorrhagic syndrome have been reported in Southern Brazil (Abella et al., 1998; Ministério da Saúde, 1998). Physiological effects of the venom over the blood system are under study by many groups (Duarte et al., 1990; Kelen et al., 1995; Reis et al., 1999), as well as the life cycle and external morphology of the species (Lorini, 1999). In this paper we show, for the first time, the internal morphology and ultrastructure of the components possibly involved in production and injection of this venom.

Usually the hairs and spines of caterpillars contain substances that cause irritation. According to Gilmer (1925) a hair is a single seta derived from a single hypodermal cell; a

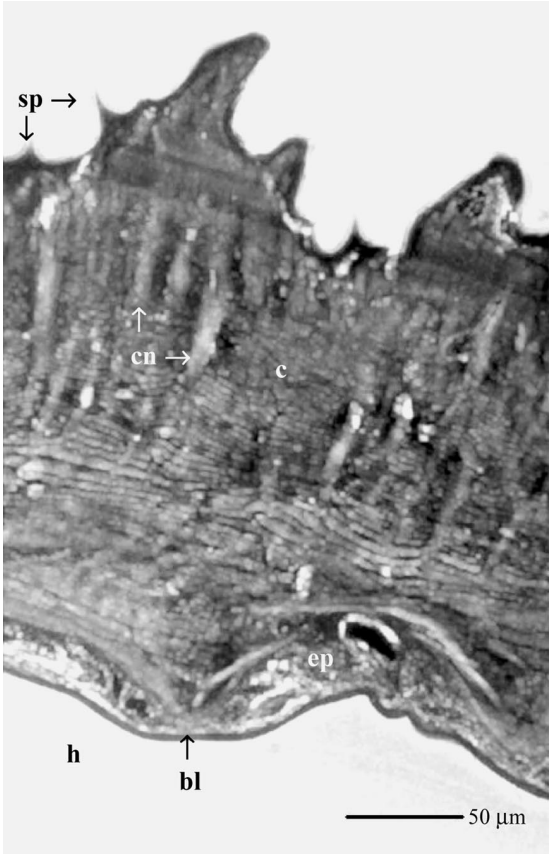

Fig. 8. Cross section of the tegument stained with PAS and seen in a LM, showing the channel network (cn) inside the cuticle (c). h: haemolymph; ep: epithelium; sp: spinules.

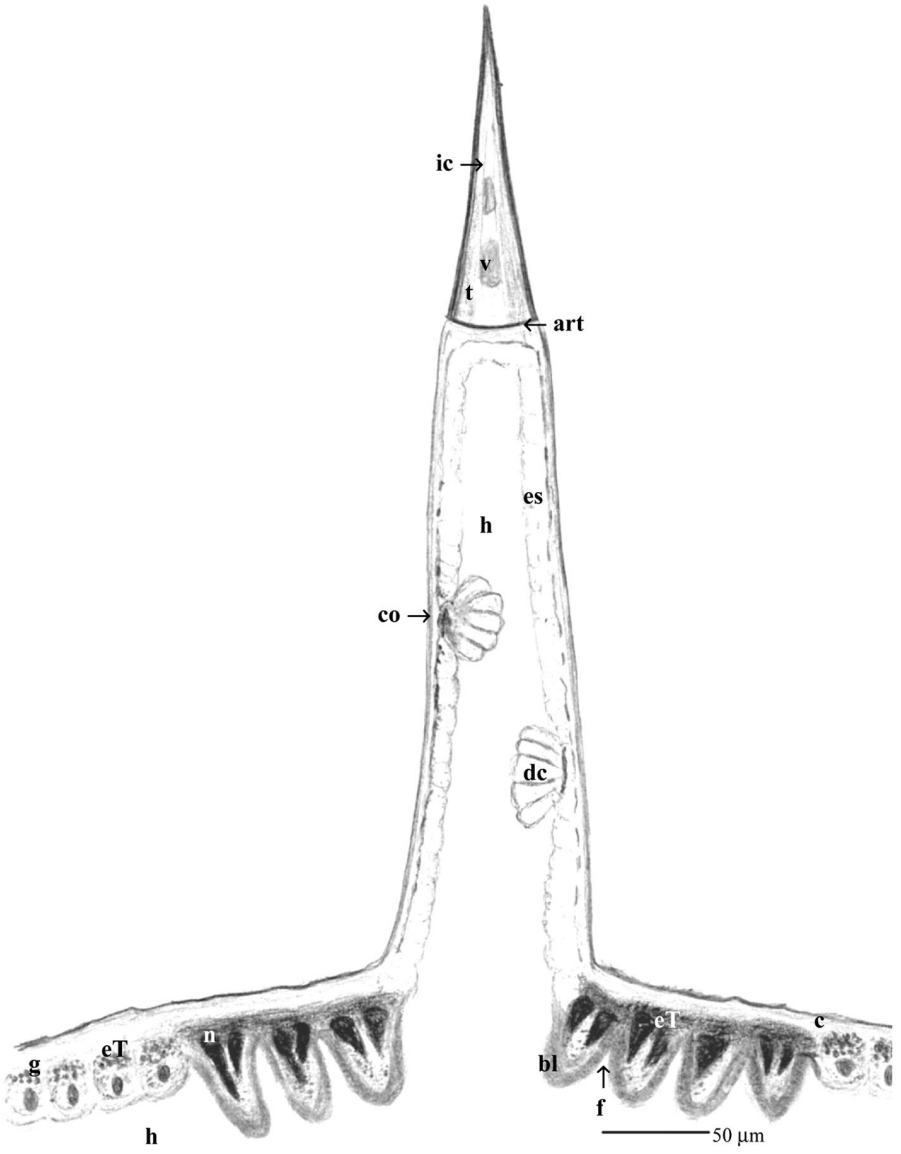

Fig. 9. Schematic model for the system involved in production and injection of the venom of *Lonomia obliqua*. h: haemolymph; bl: basal lamina; f: folds in the epithelium; eT: epithelium at the base of tegument; c: cuticle; n: nuclei of epithelial cells; g: granules of secretion in epithelial cells; dc: group of differentiated secretory cells in the seta; co: coalescence of granules; es: epithelium of seta; art: weak articulation easily broken during physical contact; ic: internal canal of the tip (t) containing the venom (v).

spine (seta) is not derived from a single cell, but is an evagination of the body wall lined by hypodermis. *Lonomia obliqua*, as our results show, is covered only with spines, distributed as cuticular specializations. According to the nomenclature used by Stehr (1987), the large branched spines, believed to break off and release the venom, are classified as *scoli*. As previously reported (Scoble, 1992), an arrangement where three pairs of *scoli* exist on each body segment (one dorsal, one subdorsal and one subspiracular *scolus*), as seen in *L. obliqua*, frequently occurs in Saturniidae. These type of urticating setae are known to be a defence apparatus of lepidopteran larvae, particularly those living in trees (Scoble, 1992).

The fact that no pores were found excludes the hypothesis that the venom flows through the end of the tip or through the caterpillar's skin. Thus, the only way to release the venom is by dislodgement of the tips, which is believed to happen during physical contact when the caterpillar's hairs are brushed against the skin (von Ihering, 1914; Gilmer, 1925; Eaton, 1988; Whitman et al., 1990; Scoble, 1992).

Interestingly, the limiting area between the tip and the rest of the seta is believed to be a poorly defined articulation that can break off easily (Maschwitz and Kloft, 1971).

A gradient of vesicles is a characteristic of glandular cells, in which the basal pole with invaginations is the main entrance of substrates from the haemolymph, while the apical pole is the exit for the modified products (Barth, 1957); this situation is clearly observed in the epithelium of *L. obliqua*.

Two kinds of urticating setae in caterpillar – those with a poison gland at their base and those without – have been reported by Scoble (1992). Eaton (1988) establishes three kinds of urticating structures for caterpillars: a simple seta with a glandular cell at its base (Gilmer's urticating hair); a branched seta (*scolus*) with a glandular cell at its base; a more especialized seta, formed from epidermal cells as a result of cuticular evagination (Gilmer's urticating spine), with a poison cell in the lumen of the base of the spine. However, in the latter type, the author does not explain the connection of the poison gland with other tissues. As observed, the setae of *L. obliqua* are revested by the epithelium as an evagination of the tegument. This kind of structure has been reported for some other larvae (Gilmer, 1925; Eaton, 1988; Maschwitz and Kloft, 1971); however, different from Eaton's third type of seta, the ones found in *L. obliqua* do not bear a poison cell.

We also report, for the first time, the histology and ultrastructure of the tegument of *L. obliqua*. Furthermore, it was shown that the absence of a single venom gland or a single glandular structure in *L. obliqua*, together with the presence of a vesicle gradient in the epithelial cells, mean that this especialized secretory epithelium is the responsible structure for venom production in this species. Maschwitz and Kloft (1971) reported that in *Megalopyge opercularis* (Lepidoptera, Megalopygidae) there is no single glandular structure, but some epithelial cells have large nuclei and appear to be secretory. The folds of basal lamina appear to be a way to increase the absorption of the primary substances that will be processed in the cells, leading to the production of the venom. The secretion might be deposited in the extracellular space between the epithelial layer and the cuticle. In some moth caterpillars of the family Zygaenidae the toxic substances are stored in cavities within the cuticle, such as the thin channels seen in our observations; no specialized secretory structures can be found and the secretion is discharged through cuticular weak areas when the insect is squeezed (Whitman et al., 1990). Based on our observations we proposed a model for the system involved in production and injection of the venom in *L. obliqua* (Fig. 9).

The colour of the vesicles on the cytoplasma, after PAS staining, means that they consist of glycoconjugates. Previous reports show that the venom of *L. obliqua* is composed of a serine-protease, among other substances (Reis et al., 1999; Donato et al., 1998). Moreover, most substances transmitted by larval spines and setae are proteinaceous, and it is likely that these structures provide effective deterrents to vertebrates, such as insectivorous birds and mammals (Scoble, 1992). Thus, we propose that the venom of *L. obliqua* is composed of glycoproteins produced in the epithelium and stored in regions of the cuticle and in the spines. Further investigations are under way for better biochemical and molecular characterization of all these components.

Acknowledgements

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