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COMPARATIVE HISTOLOGY OF THE VENOM GLANDS IN A LYCOSID AND SEVERAL OXYOPID SPIDERS (ARANEAE)

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Abstract

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The structure and histochemistry of the poison glands are described in *Lycosa tarentula* (Lycosidae), four *Peucetia* species and *Oxyopes lineatus* (Oxyopidae). All these species show two voluminous poison gland sacs which extend dorsally in the prosoma, over the central nervous system, their base reaching up to the central body of the brain. A muscle layer surrounds the gland sac; it is thicker in *Lycosa* than in the oxyopids and stops at the beginning of the excretory duct. The latter, rather narrow in *Lycosa*, starts at the base of the chelicera. It forms a secretory ampulla in the last third of the chelicera, then continues its way for about 400 µm to the entrance of the fang. In oxiopids, the gland sac itself enters the chelicera. An elongated ampulla appears at a quarter (*Peucetia*) or half (*Oxyopes)* the length of the cheliceral basal article) and reaches almost the extremity of the chelicera: the excretory duct proper runs only 40 µm before entering the fang. In all cases, the body of the glands presents two distinct regions secreting different substances. In *L. tarentula*, the main part of the poison gland secretes a complex protein product, with a fine granular appearance; a small accessory lobe, located ventrally in the proximal region of the gland sac, produces a glycoprotein. In oxyopids, the accessory portion of the gland is much more extensive; both regions produce protein; in the ventral proximal pouch, two substances are detected, one of which appears as flat square crystals, isolated inside the cells but stacked up in the gland lumen. The histological characteristics of the poison glands are examined from a phylogenetic point of view, as well as in relation to the behaviour of these species of hunting spiders.

Introduction

The contents of venom glands are better known than their structure and secretory process, especially in some species, such as *Atrax robustus*, *Latrodectus mactans*, *Loxosceles laeta* or *Phoneutria nigriventer*, the bites of which are dangerous to man. However,

Reese (1944), Smith, Russell (1967) and Smith et al. (1969) have published precise histological data on the venom glands of *Latrodectus mactans*. The microscopical anatomy of cheliceral glands in species belonging to 29 families of spiders, including two mygalomorphs living in France, was briefly described by Millot (1931). From this general work, the histophysiology of the venom glands of particular species could be studied. Legendre (1953), in an article treating the prosomal glands of *Tegenaria*, showed that the venom of the cheliceral glands was composed of two different secretory products. Much later, Wasowska (1969) followed the variation of the epithelium of these glands during the secretory cycle in *Tegenaria atrica.* The histochemical characteristics of agelenid venoms were furthermore reported by several authors (Gabe, 1959; Suomalainen, 1964; De Luca, 1965; Arvy, 1966).

Some cheliceral glands of spiders exhibit two or more regions secreting different products. This complexity has been demonstrated in *Latrodectus* (Barth, 1962; Smith, Russell, 1957), *Pholcus* (Kovoor, Zylberberg, 1971), *Scytodes* (Millot, 1930, 1931; Kovoor, Zylberberg, 1972), *Argyroneta*, *Gallieniella* (Lopez, Llinares, 1973; Lopez, 1977), *Desidiopsis* (Lopez, 1976) and also in several Salticidae and Thomisidae (Lopez, 1977).

In the present paper, we analyse and comment on the structure and histochemistry of venom glands that were never previously studied, in adult specimens of a lycosid and 5 oxyopid species. Developmental aspects of venom-, silk-gland and visual systems in two *Peucetia* species have been published earlier (Kovoor, Muñoz-Cuevas, 1995). Meanwhile, visual and behavioural activity rhythms of the same lycosid and oxyopid spiders have been under investigation for several years (Kovoor, Muñoz-Cuevas, 1998; Kovoor et al., 1992, 1995, 1999).

Material and methods

The burrowing lycosid spider, *Lycosa tarentula* (Linneus), was collected in Spain, in the vicinity of Canto Blanco (Madrid) University campus. Five oxyopid species were studied: *Peucetia cauca* Lourenço, 1990 (8 animals) from Colombia (Valle del Cauca); *P. gerhardi* van Niekerk et Dippenaar-Schoeman, 1994 (12 animals) from Nigeria (100 km from Port-Harcourt); *P. graminea* Pocock, 1900 (2 specimens) from Thailand (20 km from Bangkok); *P. viridis* (6 specimens) from Southern Spain (Altea); and *Oxyopes lineatus* Latreille, 1806 (12 specimens), found in the Réserve naturelle of Nohčdes (Pyrénées orientales, France). The prosoma of adult males and females was cut off and fixed in Bouin's fluid, dehydrated in 95% ethanol and preserved for three months in n-butanol before embedding in paraffin. Transverse and longitudinal sections (6 µm thick) were stained by classical general methods. Histochemical reactions and specific staining methods were used to visualize a) *anionic groups* and *polysaccharidic substances*: P.A.S. reaction, alcian blue, aldehyde fuchsin and toluidine blue staining; b) *proteins*: Danielli's coupled tetrazonium reaction, Morel and Sisley's reaction for tyrosin, aldehyde fuchsin, lead and phosphotungstic hematoxylin staining, and Adams's ferricyanide reaction for sulfhydryl and other reducing groups. Technical procedures are detailed in the handbooks of Gabe (1968) and Lillie, Fullmer (1976).

T a b l e 1. Main staining affinities and histochemical characteristics of the venom gland in *L. tarentula*, *Peucetia* species and *O. lineatus.* Technical references : (1) Danielli's coupled tetrazonium reaction (PEARSE, 1960); (2) Morel and Sisley 's reaction (LILLIE, 1965); (3) ferric ferricyanide reaction (ADAMS, 1956); (4) plumbic haematoxylin (SOLCIA et al., 1969); (5) P.A.S.- reaction (MAC MANUS, 1946); (6) aldehyde fuchsine (GABE, 1953).

	Acidophily Basophily	**Basic aminoacids Proline Tyrosine Tryptophan** (1)	**Tyrosine** (2)	**Reducing groups** (3)	**Carboxyl groups** (4)	**Polysaccharides Mucosubstances anionic groups** (5, 6)
L tarentula						
Part A	complex	++	/	±, +	±	0, +
Part B	cyanophilic, basophilic	+++, ++++	/	++	++, +, ±	+++, ++++
Peucetia sp.						
Part A	complex	+	0	±, +, ++	+	0, +
Part B :						
Background	complex	+	0	+	0	0
"crystalls"	basophilic	++	+	±	++	++
O. lineatus						
Part A	complex	+	0	+	0	0
Part B	basophilic	++	0	±	++	+++

Results

Microanatomical data

Cheliceral glands of the lycosid *Lycosa tarentula*, as well as those of the oxyopids *Peucetia* and *Oxyopes* comprise two voluminous sacs applied to the dorsal surface of the central nervous system; they frequently extend behind the central body of the brain, especially in adult females. The excretory duct of the gland begins at the base of the chelicera in *L. tarentula* (Fig. 1). In oxyopids, the gland sac penetrates into the chelicera and the excretory duct is therefore much shorter. It finally opens onto the upper surface of the fang, a little before the tip.

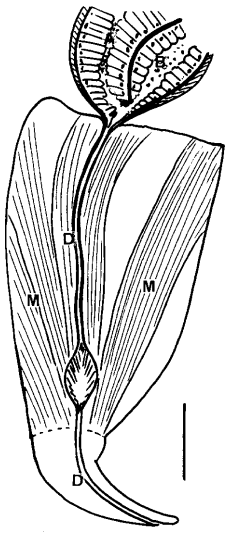

Fig. 1. Diagrammatic representation of a longitudinal section of a chelicera of *Lycosa tarentula* adult female. A, B: main and accessory pouches of the venom gland; D: excretory duct; M: cheliceral muscles. Scale line: 1 mm.

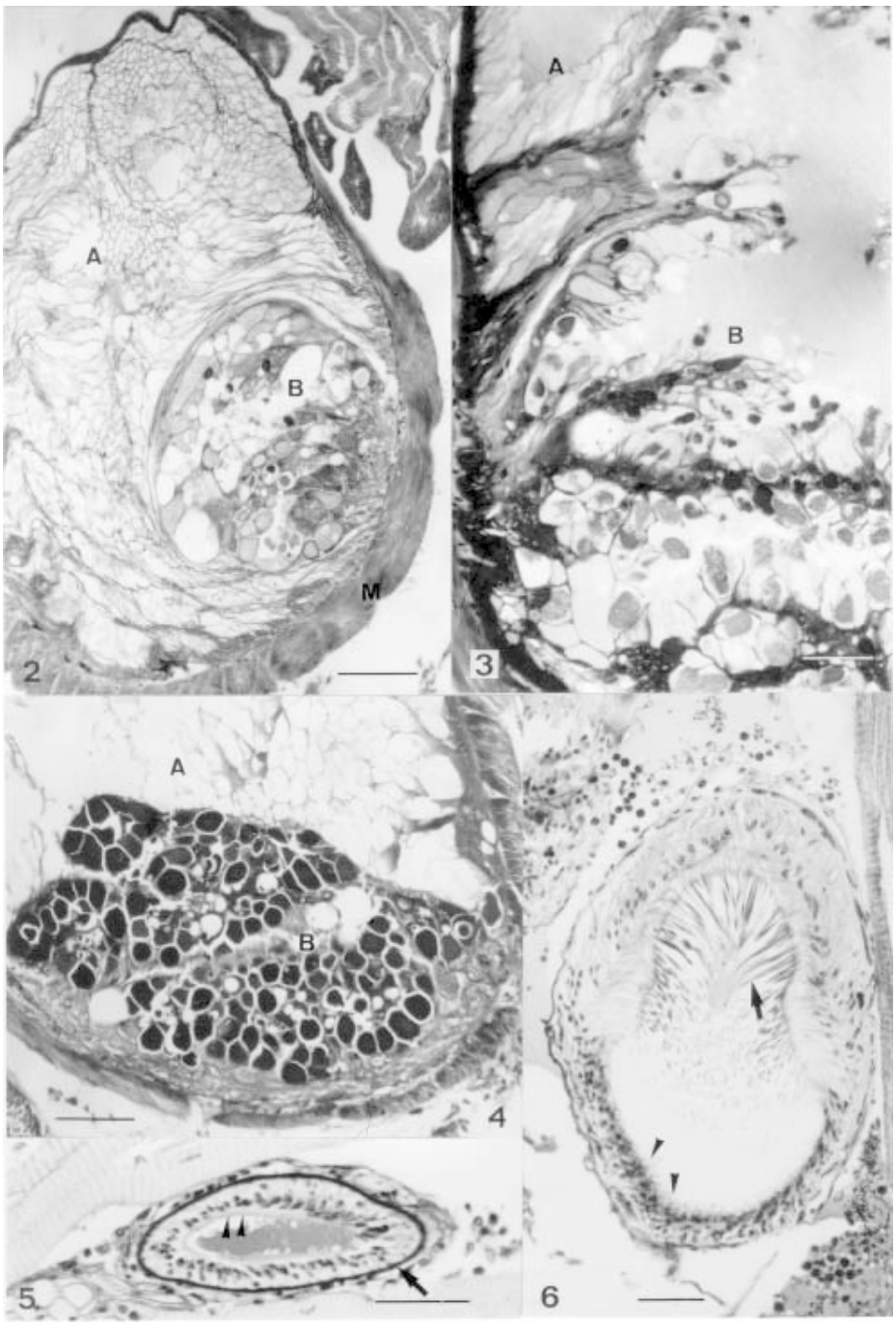
A
B
M
2
A
B
3
A
B
4
5
6

Fig. 2. Oblique section of the anterior part of the venom gland sac in *L. tarentula*. The ventral accessory pouch (B) shows a heterogeneous content: small granules and large vesicles are mixed in the gland lumen. Reducing groups (from *light grey* to *black*) are present in both products. In the main pouch (A), the secretory product, rather homogeneous, reacts weakly (*light grey*). Ferric ferricyanide reaction, orange filter. M: muscle. Scale line: 100 µm.

Fig. 3. Both regions of *L. tarentula* venom gland. In the main region (A), one substance appears homogeneous and cyanophilic; in the accessory pouch (B), one basophilic substance is granular, a second one looks like that of the main region. Masson-Goldner's trichrome, green filter. Scale line: 50 µm.

Fig. 4. B portion of *L. tarentula* venom gland. Strong positive PAS-reaction of the granular secretory product. PAS-reaction, green filter. Scale line: 100 µm.

Fig. 5. Oblique section of the venom gland duct in the frontal part of the basal article of the chelicera. Note the thick basal lamina (*arrow*) surrounding the epithelium of the duct lined by a cuticular intima (*arrow heads*). PAS-reaction, green filter. Scale line: 50 µm.

Fig. 6. Junction of the ampulla to the duct proper, and the end part of it, shortly before it enters into the fang. Note groups of very long microvilli at the apex of high ampulla cells (*arrow*), and short ones in the next portion (*arrow heads*). Phosphotungstic haematoxylin staining, green filter. Scale line: 50 µm.

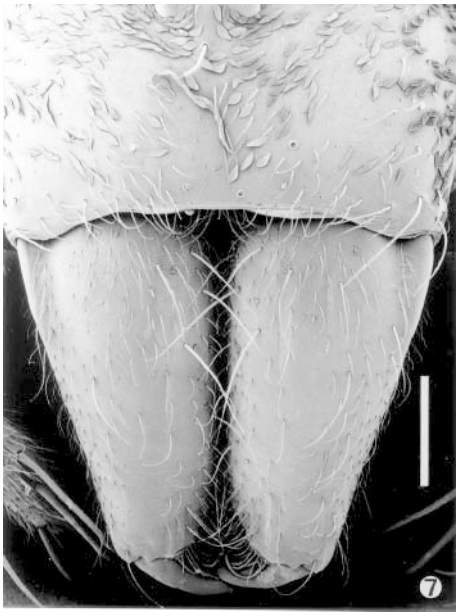

Fig. 7. Frontal view of the clypeus and chelicerae of *Oxyopes lineatus*. Scale line: 0.2 mm.

Gland sac

Venom components are produced in the large pouches of the poison glands. Each gland comprises two distinct regions secreting different substances. In *L. tarentula*, the distal pouch (A) is, by far, the widest. An accessory lobe (B) is appended to the main part in its proximal region, just before the collar of the gland (Figs 1, 2). A single festooned epithelial layer produces the venom which accumulates in the inflated apical part of the cells before being released into the lumen. A dense basal lamina ensures a link between the epithelium and a muscle fibre layer which surrounds the gland sac spirally (Fig. 3). Replacement cells (= substitution cells or qualified "auxillary" cells (Barth, 1962)) are present here and there at the base of the epithelium. The excretory duct is not provided with a muscle cover (Fig. 5), neither is the contact zone between the two pouches (Fig.

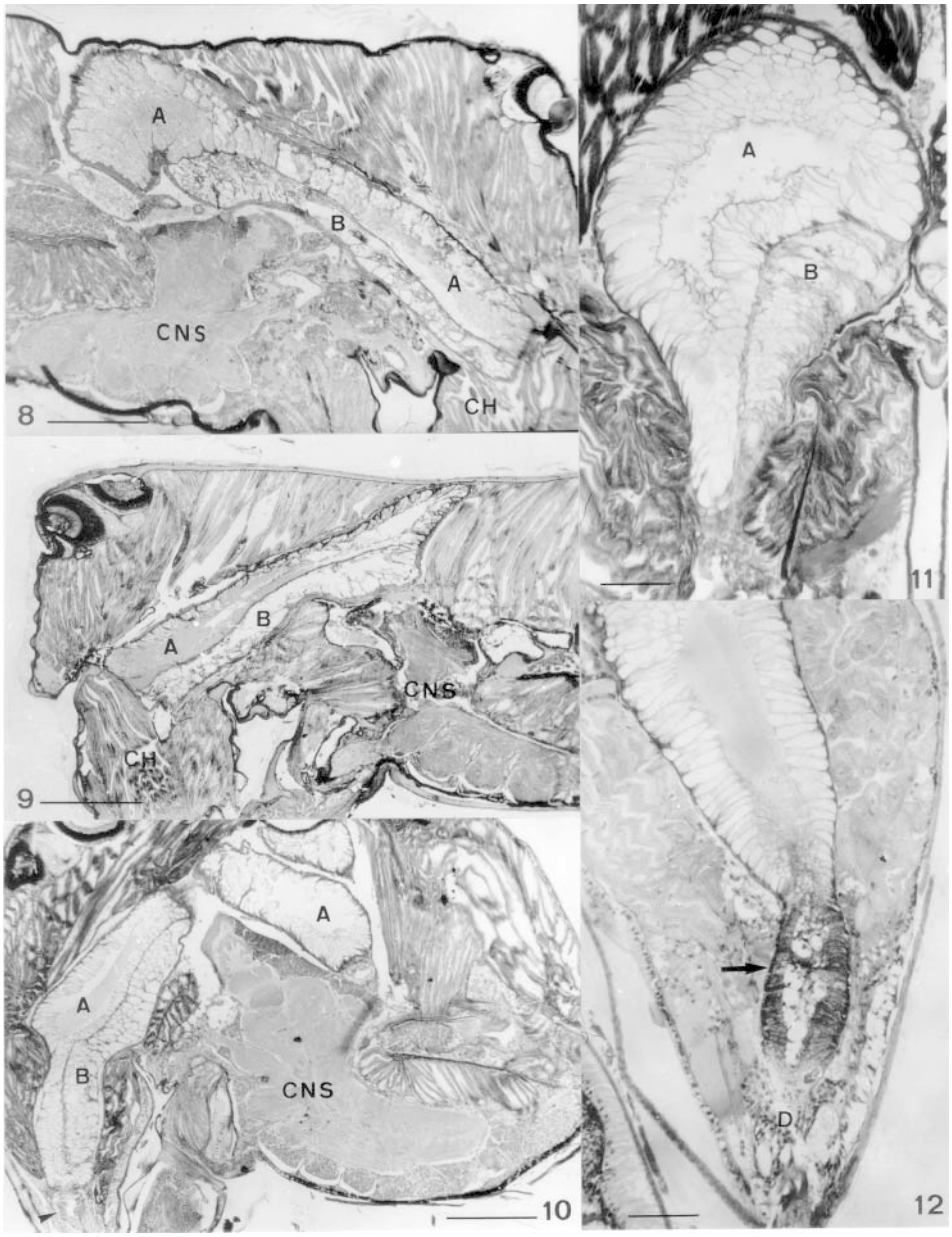

Fig. 8. Parasagittal section of the prosoma of *Peucetia gerhardi* adult female showing the extension of the poison gland sac, dorsally, above the central nervous system (CNS). A: main pouch, B: ventral accessory pouch of the poison gland. CH: chelicera. Ferric ferricyanide, orange filter. Scale line: 0.5 mm.

2). The basic histological structure of the venom glands in oxyopid species studied is the same as that in *L. tarentula*. The muscle layer surrounding the glands is half as thick as in *L. tarentula.* The general shape of the glands is quite irregular and the "accessory" lobe, much elongated, extends to the level of the optic lobes of the brain (Figs 8-10). The double gland sacs are prolonged inside the chelicerae (Fig. 11). Both pouches open into the excretory duct at the same level.

Three different substances have been distinguished from their staining affinities and histochemical characteristics in the venom of all species studied. The largest part of the glands (A) produces a single complex protein product, the staining affinities of which are double, i.e. acidophilic and basophilic. It is generally PAS-negative (Fig. 4), slightly reducing and does not contain histochemically detectable tyrosine. Histochemical differences in the above characters are noticeable in *Oxyopes lineatus*: in the main component of the venom, acidophily and reducing groups are more obvious (Table 1). The accessory pouches (B) secrete two different products in the six species studied, no matter what family they belong to. In *L. tarentula*, the B pouch is very small, but generally full of vesicles of different diameters bathed in a fine granular substance. Both products are proteinaceous with reducing groups and associated with a polysaccharidic fraction (Fig. 4). They are distinguished by their appearance, but also by their eosinophily or cyanophily (Table 1). The four *Peucetia* species obviously differ from *L. tarentula* in the appearance of the secretory products of the B pouch.. The epithelial cells of this pouch synthesise glycoprotein "crystals" and a granular protein substance accumulating in vacuoles (Figs 14-16). Crystals appear at first as short isolated sticks inside the cells (Fig. 15); they progressively enlarge up to a length of 20 µm, and are finally extruded into the lumen where they stack up, forming low piles (4µm) of three or four elements (Fig. 16). The corresponding region of the venom gland of *O. lineatus* secretes two substances showing the same histochemical characters as in *Peucetia* (Fig. 13); few differences appear in their general staining affinities (Table 1).

Fig. 9. Parasagittal section of the prosoma of *Peucetia gerhardi* adult male. Same labels and details as in fig. 7. PAS-reaction, green filter.

Fig. 10. The venom gland of an *Oxyopes lineatus* female entering the chelicera vertically; both regions of the gland run side by side until both open at the junction of the ampulla. One-step trichrome, green filter. Scale line: 100 µm.

Fig. 11. Poison gland sac of *Oxyopes lineatus* adult female, above the CNS, and penetrating the two third of the length of the chelicera where the duct starts as an ampulla (*arrow*). Danielli's coupled tetrazonium reaction, green filter. A: main pouch; B: accessory pouch; CNS: central nervous system. Scale line: 0.3 mm.

Fig. 12. *Oxyopes lineatus*. Proximal end of the poison gland sac, inside the chelicera; the ampulla (*arrow)* is followed by the terminal excretory duct (D) which reaches the fang. PAS-reaction, green filter. Scale line: 100 µm.

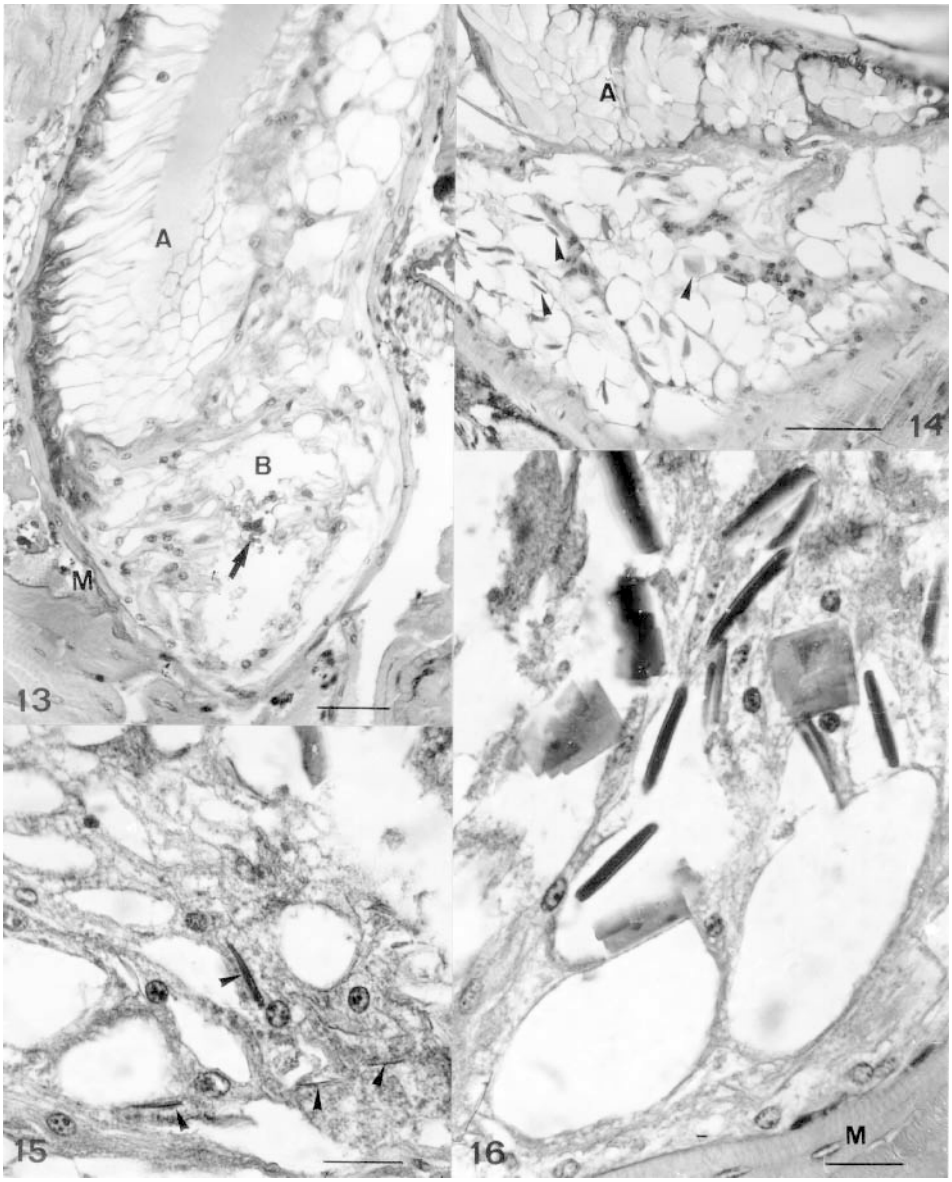

Fig. 13. Aspect of the anterior part of the venom gland of *Oxyopes lineatus*. Histological characteristics of the A and B regions of the gland are obviously different. One secretory product of the B region, granular or crystallised, is PAS-positive (*arrow*). M: muscle. PAS-reaction, green filter. Scale line: 50 µm.

Figs. 14. *Peucetia gerhardi*. A and B regions of the poison gland. One secretory product of B appears as PAS-positive crystals (*arrow heads*). Scale line: 50 µm.

Excretory duct

Lycosa tarentula. The excretory duct, lined by a cuticular intima, starts at the apex of the stout basal article of the chelicera, where the gland sac has narrowed in the shape of a funnel. Its total width varies from 50 to 70 µm, according to the age and size of the adult spiders (Fig. 1). *L . tarentula* adult females can live for more than one year. The duct runs laterally to the sagittal plane of the chelicera, along its frontal wall, for 3.4 mm. At this level, the duct diameter increases to 200 µm and an "ampulla" is formed. It is about 650 µm long and its epithelial cells, 50 µm high, bear long microvilli forming groups of several elements stuck together and almost completely filling the lumen (Fig. 6). Ampulla cells secrete a fine granular glycoprotein substance (PAS- and coupled tetrazonium reactions are positive). In the last third of the ampulla, microvilli progressively decrease in size and appear single (Fig. 6), fine granules still extrude from the cells but they do not react to PAS, and thus seem devoid of a polysaccharide component. From 380 µm to the fang, the last portion of the excretory duct, like its first part, is a narrow, thin-walled tube, internally covered by a cuticular intima.

Peucetia species and *Oxyopes lineatus*. Chelicerae of Oxyopidae are conical, long (*Peucetia*) or rather short (*Oxyopes*, Fig. 7) appendages, with a short but acute fang. The double sac of the poison gland enters the chelicera and fills its summit (Fig.11); it runs into one fifth or a third of the length of the basal article in *Peucetia*, and nearly two thirds in *Oxyopes lineatus* (Fig.12). The excretory duct starts with a secretory part, about 700 µm long and 120 µm wide in *Peucetia* species, shorter (from 260 to 300 µm long) and thicker walled (from 145 to 160 µm wide) in *Oxyopes* (Fig.12). This region corresponds to the "ampulla" present in *L. tarentula* and, similarly to the latter, secretes a glycoprotein substance (Fig.13). The narrow duct proper follows, it runs for 50 to 100 µm only before entering the fang.

Discussion and conclusion

Lycosa tarentula and the five oxyopid species of spider so far studied hunt their prey in the same way, whether at ground level (*L. tarentula*) or above, in foliage (Oxyopidae). When ambushing prey, at the opening of a burrow or on leaves of bushes, these spiders use visual cues along with chemical and mechanical signals to locate a possible prey.

Fig. 15. Aspect of the elaboration of both products in B cells of the venom gland in *P. cauca*. Native crystals are seen in the cytoplasm at different stages of their synthesis (*arrow heads*), together with light vesicles of different sizes. PAS-reaction, green filter. Scale line: 20 µm.

Fig. 16. Crystals, in profile and full face, and large vesicles representing both secretory products of the B pouch of the venom gland of *P. cauca*. M: muscle. PAS-reaction, green filter. Scale line: 20 µm.

They do not spin any web. The capture of prey is mainly dependent on eyesight, speed of movement and venom effectiveness. These three factors seem to be optimised in salticid spiders.

The cheliceral glands of the species studied are very large. The largest, in proportion to the size of the prosoma, are those of *Oxyopes lineatus*. As a whole, the visual performances of *L. tarentula* and *O. lineatus* are similar, but *O. lineatus* feeds on preys that are often larger than itself; and which may be subdued by a large quantity of venom or a very active venom. The shape of the venom glands in Oxyopidae, their thin muscle investment and their wide prolongation inside the chelicerae up to the secretory ampulla of the duct, indicate a massive flow of venom, which may be not only injected into the prey, but also sprayed over it. FINK (1984) observed that *Peucetia viridans* females expelled venom from their fangs straight at objects moving in front of them. This spitting behaviour "most likely serves a defensive function" which has not been described elsewhere.

Nothing of that sort was observed in *L. tarentula*. Anatomically, poison glands of *L. tarentula* resemble those of other Lycosidae, Agelenidae, Argyronetidae, Desidae (LOPEZ, 1977), and most probably of many other hunting or web building araneomorph spiders. The presence of a small anterior accessory pouch, although not indicated by MILLOT in his general work (1931), seems fairly common. It was found in the anterior part of the small cheliceral gland sac of even Salticidae (LOPEZ, 1977; KOVOOR, pers. obs.). In other evolutionary lines, such as in Theridiidae and Pholcidae, the whole anterior collar differs cytologically and histochemically from the rest of the gland. It was first described as the "lipocrine gland" by BARTH (1962) and then by SMITH, RUSSELL (1967) in *Latrodectus mactans*. Similarly, the venom gland of *Pholcus phalangioides* FUESSL. shows two secretory zones that differ both in the form of the cells and in the nature of the secretory products. The collar region secretes a glycoprotein instead of lipid substance (KOVOOR, ZYLBERBERG, 1971). Meanwhile, the extension of the accessory pouch up to a third of the gland length, and its crystallised secretory product, seems, at present, a characteristics of Oxyopidae. It should be noted that the venom filling the excretory duct always looks homogeneous: we could never detect any crystal in this last part of the gland. Crystals are likely to be solubilized in the mixture of the three substances present in the duct.

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