Ultrastructure of the venom gland of the Andean Red-tailed Coral Snake
Micrurus mipartitus decussatus (Duméril, Bibron & Duméril 1854) (Squamata Serpentes Elapidae)

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Venom glands (VG) in the Colombian coral snake Micrurus mipartitus decussatus (Duméril, Bibron & Duméril 1854) are described by light and transmission electron microscopy. Resting glands are compared with glands that restored their secretory activity after manual venom extraction, i.e. “milking”. Both accessory (AG) and main gland (MG) portions are considered. AG secretory units are ordinary mucous acini, which form the distal part of the VG. The MG is the proper venom-producing gland; it is proximal and consists of tubules with lumina ranging from narrow to dilated. Typically, the narrow-lumen tubules are elongated, and their secretory walls consist of tall pyramidal cells with basal nuclei. Tubules with large lumina are relatively short, and their component cells are cuboidal, with central nuclei. In both cases, secretory cell organelles include rough endoplasmic reticulum and Golgi stacks. Intracytoplasmic venom consists of granules with varying densities, whereas venom stored in the lumen of the tubules is structureless. Venom release into the tubule lumen involves both merocrine and apocrine processes, the latter leading to disintegration of the apical cytoplasm containing secretory granules. Although discharge amounts differed in stimulated specimens, ultrastructural analysis demonstrated that manual extraction is an effective procedure to activate biosynthesis in snake venom glands.

KEY WORDS: snake venom gland; ultrastructure; Micrurus mipartitus.

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INTRODUCTION

Typical venom glands (VGs) have been described in three families of snakes: Elapidae, Viperidae and Atractaspididae. Several colubrid species also possess venom-producing glands, but these organs are usually referred to as Duvernoy's glands and they vary considerably in both size and composition of secretory products (Kochva 1978a, 1987). Indeed, Duvernoy's gland is anatomically and functionally distinct from VG, although both are homologous organs (Kardong 2002).

As demonstrated by isotope labelling and ultrastructural analysis (Kochva et al. 1982), and later confirmed by molecular biology methods (Lachumanan et al. 1999), VG activity in Elapidae includes both biosynthesis and storage phases, the former commencing after the gland has been emptied of its content. A light microscope (LM) comparison between the Elapidae and Viperidae revealed substantial differences in VG functional cycles (Kochva 1978a, 1987). In elapids, the VG stores venom within the secretory cell (adenocyte) cytoplasm as well as in the gland lumen, as discrete granules and an amorphous mass, respectively (Kochva 1987, Kochva et al. 1982, Lachumanan et al. 1999). This contrast with the situation in viperids, in which the lumen stores venom but the adenocyte cytoplasm only contains immature secretory product along with a few mature granules (Warshawsky et al. 1973, Kochva 1987, Carneiro et al. 1991, Mackessy 1991). Intracytoplasmic storage of venom granules throughout the entire functional cycle in elapid snakes hinders recognition of secretory activity patterns under the LM. On the other hand, the secretory cycle of the viperid VG is marked by impressive morphological changes involving cell height and cytoplasm content (Oron & Bdolah 1973, 1978; De Lucca et al. 1974; Kochva 1978b, 1987; Carneiro et al. 1991; Mackessy 1991). Analysis by transmission electron microscopy (TEM) can disclose the sequential activity of the organelles engaged in venom production as well as features of secretory products undergoing maturational changes during the storage phase. Furthermore, ultrastructural studies allow detailed comparison between secretory units from different gland regions or between the gland component parts, i.e. main (proper) venom gland (MG) and accessory gland (AG). According to Rosenberg (1967), Kochva (1978a, 1987), Gopalkrishnakone & Kochva (1990) and Lachumanan et al. (1999), the AG should be regarded as an ordinary mucous gland, although it exhibits various mucocyte types (Mackessy 1991) that may contribute to the ultimate secretory product composition. Finally, a TEM study on coral snakes may bridge a wide information gap, because ultrastructural research in New World elapid species has been much neglected despite their relevance in ecology, taxonomy and health care (Roze 1996, Russell et al. 1997, Da Silva et al. 2003).

This paper describes structural and ultrastructural traits of the VG in Micruurus mipurititus decussatus to provide a functional characterization of the secretory tubules in the main gland, as well as mucous acini in the accessory gland. For this purpose we observed both resting and extracted glands, adopting the fundamental criterion for ultrastructural analysis of exocrine glands, namely the basal-apical functional polarization of secretory cells. Due to the small number of specimens available, the research design was purely descriptive; indeed the extraction treatment served to trigger inducible secretory processes for a comparison with constitutive activity in the resting gland.
Venom gland of *Micrurus mipartitus*

**MATERIALS AND METHODS**

*Micrurus* Wagler 1824 is one of three genera of coral snakes and includes about 20 species distributed in Colombia (Campbell & Lamar 1989, Roze 1996, Páez et al. 2002). *M. mipartitus* (commonly named *rabo de aji*, *cabeza de chocho*, *mata perro*) lives in the Central and Western Cordilleras, from sea level to 1900 m altitude (Roze 1996). Despite its toxic venom, this animal is placid and rarely bites (although the consequences of bites are sometimes serious).

Three adult specimens of the coral snake *Micrurus mipartitus decussatus* (Duméril, Bibron & Duméril 1854) were collected from Carolina del Príncipe (Antioquia, Colombia) and transferred to the laboratories of the Instituto Colombiano de Medicina Tropical in Sabaneta, near Medellin. During captivity (1 month) the snakes received only water, as their natural prey, caecilian amphibians and limbless lizards, were not available. However, these ectothermic animals usually undergo long-term fasting under natural conditions, and lack of predatory activity guarantees a fairly homogeneous level of activity in the VG.

Venom was extracted by gentle manual pressure on VG while the snake was actively biting a wax film (parafilm) on the top of a glass test tube.

The first snake (specimen no. 1, male 70 cm length) discharged about 12 mg of venom; it was sacrificed six days after milking and the VG was surgically removed. This time lag falls within the average interval adopted in similar investigations of VG secretory cycles (Kochva et al. 1982).

The second snake (specimen no. 2, male 65 cm length) discharged only a small amount of venom (about 4 mg). In this case, the VG was removed two days after venom collection, since the gland was affected to a lesser extent by stimulation, and a larger time lapse might have hindered patterns of mild restoring activity.

The third snake (specimen no. 3, resting, female 68 cm length) was sacrificed without milking.

The snakes were killed by decapitation after they had been kept at 4°C (30 min). The paired venom gland was surgically removed from each side of the head, reduced into three fragments and pre-fixed (2 hr, 4°C) in Karnovsky (1965) fluid. The samples were then rinsed in the same buffer as the pre-fixation fluid (cacodylate buffer, 0.1 M, pH 7.0) and transferred in this solution to the Dipartimento di Biologia Animale e Genetica, Università di Firenze, Italy. The gland samples were then rinsed once more, reduced to smaller fragments (8-27 mm³), and post-fixed in 1% OsO₄ (90 min) again in cacodylate buffer. After rinsing in the same buffer, the samples were dehydrated in an ethanol series followed by propylene oxide, and samples were infiltrated with and then embedded in Epon 812 blocks. These blocks were cut into semithin (1.5 µm) and ultrathin sections (silver-grey to gold-yellow interference colours) with a NOVA LKB ultramicrotome. The former were stained with buffered toluidine blue and used for the structural analysis; the latter were collected on 300 mesh uncoated copper grids and stained using a saturated solution of uranyl acetate in 50% aqueous ethanol, followed by alkaline lead citrate (2 mg/ml in water). The ultrathin sections were observed under a 101 Siemens electron microscope (80 kV).

**RESULTS**

Investigation followed the basic anatomy of the elapid VG: first we considered the distal accessory portion (AG) and then the proximal main gland (MG). Because LM findings collected from the resting specimen (not shown) confirmed that the accessory portion closely resembles an ordinary mucous gland, the type found in all vertebrates, only AGs from extracted VGs (specimens no. 1 and no. 2) are shown and discussed in this paper. However, since MGs are exclusive, samples of this
gland type were analysed in the resting specimen (no. 3) as well as in the extracted snakes.

**Light microscopy findings**

The AG secretory units in specimen no. 1 (which released a larger amount of venom) resemble acini in the resting specimen and exhibit homogeneous structural traits with little differences between mucocytes. These are polyhedral cells and show a remarkable morpho-functional polarization, with basal nuclei and apical secretory product (Fig. 1A). As observed at the boundary between the two VG portions, AG consists of acini with tall mucocytes encircling a virtual lumen, whereas MG has secretory tubules with obvious lumina (Fig. 1A). AG in specimen no. 2 shows greater morphological variability of its structural traits: the mucocytes in the acini are characterized by different stain affinities of their products, ranging from faint to intense, in the same as well as in contiguous secretory units (Fig. 1B).

Ordinary LM investigation failed to disclose any significant differences in secretory activity between resting and extracted MG tubules. Therefore, the structural analysis only considered their roughly cylindrical shape, which ranges from elongated, with relatively narrow lumina (Fig. 1C, E), to short with wide lumina (Fig. 1F-G). In some instances, the tubule profiles are irregular in section (Fig. 1D), possibly indicating ramifying points, as suggested by the occurrence of luminal branches diverging from common trunks (Fig. 1C, F). The secretory wall consists of a single layer of secretory cells, tall prismatic to cuboidal in shape, typical of elongated and short tubules, respectively. In both cases, large amounts of secretory granules occur in the cytoplasm (Fig. 1D-E, G). The secretory product within the lumen consists of structureless material (vacuolised, Fig. 1C, E or finely grained, Fig. 1F-G) as well as discrete clusters of granules (Fig. 1D). These clusters seem to result from apocrine release, although the effect of sections involving pedunculate cell apices cannot be excluded. The connective tissue (stromal) septa emanating from the VG capsule separate gland tubules and allow small blood vessels to reach their secretory walls (Fig. 1F-G).

**Transmission electron microscopy findings**

As stated above, AG in specimen no. 1 showed homogeneous patterns under LM, closely resembling features in the untreated specimen and conforming to the usual features of tonic secretory activity described in ordinary mucous glands. Therefore, ultrastructural analysis of the mucous portion was only performed on specimen no. 2; this analysis disclosed a wide range of morphological traits. AG mucocytes exhibit the usual shape of truncate pyramids with a basal nucleus and secretory organelles, while the supranuclear cytoplasm is filled with secretory product (Fig. 2A). Smaller cells are located at the AG periphery and display a high nucleo-plasmatic ratio (Fig. 2A): these may be stem cells involved in gland regeneration by replacing exhausted mucocytes. This hypothesis is confirmed by the occurrence of peripheral cells involved in secretory cytodifferentiation, with dilated rough endoplasmic reticulum (rer) cisterns containing an opaque product (Fig. 2B). Most ultrastructural differences between contiguous mucocytes involve the density of their respective products (mucous granules, Fig. 2C). The mucocyte apical surface
Venom gland of *Micrurus mipartitus*

Fig. 1. — LM features of accessory (A, B) and main glands (C-G) in *Micrurus mipartitus*. A: Specimen no. 1: close contiguous elongated tubules (mg) and mucous acini (ag). Notice that only weak staining differences characterize mucocytes in the accessory gland; arrows point to basal nuclei. B: Specimen no. 2: mucous acini in this accessory gland lobe show highly variable stain affinities (black and white arrows). These features are also obvious between cells in the same acinus. C: Specimen no. 3, elongated tubules: a gland tract in this resting specimen branches to give rise to two tubules (diverging arrows). Notice secretory product (*) in the common trunk. D: Specimen no. 1: small secretory masses (arrows) in the lumen of an elongated tubule, resembling products of apocrine processes. E: Specimen no. 1: contiguous elongated tubules; the upper one contains structureless venom (*). F: Specimen no. 2: short, dilated tubules; notice different venom densities, ranging from light, finely granular to moderately opaque. Diverging arrows point to offshoots from a branching tubule; v = blood vessels. G: The same specimen as above: detail of previous section, showing connective tissue septum with blood vessels (v).
possesses a thick platform of short, slender cytoplasmic processes, resembling minute microvilli (Fig. 2A). Once released, the mucous granules merge to form a foamy product (Fig. 2A), although granules may also merge within the cells (Fig. 2B-C).

In the MG of the resting specimen, elongated (Fig. 3A-D) and short (Fig. 4A-D) tubules share common subcellular traits in their adenocytes. Secretory products vary considerably in density even in the same cell, and consist of light vesicles to

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**Fig. 2.** — Ultrastructural features of AG in specimen no. 2; arrows point to merging processes. A: Closely contiguous mucocytes exhibit two maturational phases of secretory products (m and m'); ab = mucous adenoblast (immature mucous cell), mv = thin apical outgrowths (microvilli). B: The paranuclear cytoplasm in the lower cell possesses remarkable amounts of rough endoplasmic reticulum (rer); notice mucous vesicles with light content in the upper cell. C: Details of mucous products in contiguous mucocytes; in the one to the right, cytoplasm areas are still noticeable between opaque granules (arrowheads); the one to the left contains light vesicles that occupy the whole cytoplasm.
opaque granules (Fig. 3A). The apical surface of adenocytes exhibits thin cytoplasm
outgrowths (Figs 3A, C and 4A-C), resembling those described in AG.

In elongated tubules the apical surface invaginates deeply towards the nuclear
level to form narrow channels. These are secretory canaliculi, lined with numerous
microvilli that partially occlude their lumina, containing a thin product (Fig. 3A),
possibly venom released through exocytosis. During release the granule-limiting
membrane fuses with the plasmalemma and the secretory product flows into the
lumen (Fig. 3B). This is a typical merocrine process occurring in undamaged cells.
In this region, discrete cytoplasm portions can also be seen, which lie close to the
cell apices and contain secretory cell organelles as well as granules of varying den-
sity (Fig. 3C, contrast with 4D). These discrete profiles correspond to apical cyto-
plasms detached from cells undergoing what appear to be early steps of apocrine
processes. Venom manufacture involves both rer and the Golgi apparatus, easily

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Fig. 3. — TEM features of MG in the resting specimen (no. 3): elongated tubules; mv = microvilli.
A: Apical cytoplasm contains secretory granules with various degrees of density. Notice secretory
canaliculi in the left cell (arrows). B: Secretory granule involved in merocrine release; during exo-
cytosis, its dense product seems to disappear (arrow, compare with 6F). C: This cytoplasm appar-
ently becomes detached from an apocrine cell (compare with 4D). D: Early secretory product result-
ing from Golgian activity; G = Golgi stack, rer = rough endoplasmic reticulum. E: Neurite bundles
(arrows) within the stromal spaces (intertubular septa).
detectable in elongated tubules. The former consists of scanty, short cisterns containing an opaque product, whose density is similar to the background cytoplasm.

Fig. 4. — TEM features of MG in the resting specimen (no. 3); tubules with dilated lumina; mv = microvilli. A: Notice relatively flat, secretory epithelia in contiguous tubules, with no apparent functional polarization; s = stroma. B: This relatively tall secretory cell exhibits obvious polarization, with peri-nuclear early product (black arrows) and apical dense granules (white arrows). C: Cell apices of adjacent cells are joined together by a tight junction (encircled); arrow points to labyrinthine patterns of contiguous plasma membranes. D: The lumen of this gland tubule contains dispersed material along with a cluster of secretory granules, which are held together by a vanishing cytoplasm (arrow) lacking any plasma membrane. This looks like an advanced apocrine release pattern (compare with 3B).
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(Fig. 3C-D). The latter includes contiguous stacks of sacculi that release early secretory products (Fig. 3D). This material is contained in small vesicles, which merge together to give rise to larger structures containing a denser product. TEM investigation provides details of stromal structures related to MG tubule activity, such as small nerve bundles consisting of parallel neurites (Fig. 3E). The low prismatic (cuboidal) adenocytes in the secretory wall of tubules with dilated lumina contain scanty biosynthesis organelles; this contributes to the lack of a clear functional polarisation in their cytoplasms (Fig. 4A). The nuclei lie at an intermediate level and both the supra- and infra-nuclear cytoplasm contain large numbers of secretory granules. However, the immature venom deposits (secretory vesicles and granules with low-density products) largely prevail in the basal cytoplasm (Fig. 4B). Dense secretory granules crowd against the apical surface provided with short, scanty microvilli (Fig. 4A, C). Plasma membranes of contiguous cells are involved in labyrinthine relationships, but at the very distal level their paths become straight and they exhibit typical junctional complexes (Fig. 4C). The intraluminal secretory product has a finely granular appearance, which strongly contrasts with the dense intracytoplasmic granules (Fig. 4A, C-D). The lumen also contains discrete clusters of dense granules, held together by a moderately opaque cytoplasm. These are fragments of cell apices, which will lose their plasma membranes and disappear until secretory granules are released (Fig. 4D, contrast with 3C), in what appear to be advanced stages of an apocrine process. A comparison with cytoplasms of integral contiguous cells (Fig. 4D) demonstrates that the above pattern is not due to damage during specimen preparation.

Specimen no. 2 shows morpho-functional traits that closely resemble the ultra-structural patterns in the resting snake. These similar aspects involve both elongated and short MG tubules, and are mostly related to the biosynthesis machinery; rer complements are scanty and somewhat dilated, with a product as dense as the cytoplasm, so that only rough membranes serve to distinguish these opaque materials from each other (Fig. 5A). The Golgi apparatus is contiguous to relatively large vesicles, containing sparse material (Fig. 5B-C) corresponding to early venom. Secretory granules are of homogeneous density (Fig. 5A-F) and sharply contrast with the lighter vesicles, released by the Golgi apparatus (Fig. 5B-C). In both elongated (Fig. 5C) and short tubules (Fig. 5D) the relationships between contiguous secretory cells consist of interwoven, labyrinthine plasma membranes. At the cell apices, flat surface areas are involved in junctional devices that seal off the slender intercellular interstices from the lumen (Fig. 5D). Following a consistent pattern, the stromal space between tubules contains capillaries that provide a rich blood supply to the secretory cells (Fig. 5E). As described in the previous specimens, the stromal space also contains thin neurites (Fig. 5F), which derive from axonal bundles enclosed in Schwann cells observable near the tubule periphery. On the peripheral side, the tubule wall includes cells with a high nucleo-plasmic ratio, provided with rod-like mitochondria and a remarkable apparatus of free ribosomes (Fig. 5F). Due to their undifferentiated features and position, these cells could form the regenerative component part in the MG secretory units.

Specimen no. 1 exhibits conspicuous features in the biosynthesis apparatus of MG cells, in both elongated (Fig. 6A, C, E-G) and short (Fig. 6B, D) tubules. As a consistent trait, rer are numerous and dilated (Fig. 6A-D), and contain a finely granular product (Fig. 6B-C), so their wide compartments show a homogeneous, relatively transparent background (Fig. 6A, D). Contiguous, dilated rer cisterns exhibit several interconnections, forming a complex net. Adjacent cisterns press against the inter-
posed cytoplasms and reduce them to thin, dense partitions (Fig. 6B), which emphasize their lighter content (Fig. 6A, D). These patterns of dilated rer cisterns are not
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Fig. 6. — TEM features of MG in extracted specimen (no. 1). A: Elongated tubule: typical patterns of secretory cell in transverse section; notice dense granules as well as dilated profiles of the rough endoplasmic reticulum (rer). B: Short tubule: details of granular cisterns (rer) with wide compartments containing thin products. C: Elongated tubule: stacked sacculi of the Golgi apparatus (G) and dilated rough cisterns (rer); arrow points to merging processes affecting post-Golgian secretory product. D: Contiguous short tubules; note the clear functional polarisation with basal cytoplasms rich in profiles of the rough endoplasmic reticulum (rer) and apices containing dense granules; fb = fibroblast; nf = nerve fiber bundles. E: Elongated tubule: Schwann cell (Sc) inserted between basal portions of secretory cells; its cytoplasm contains unmyelinated axons (arrows). F: The same as above: merocrine release (arrow) of thin product from a secretory granule (compare with 3B). G: Elongated tubule: detail of a cytoplasm bleb (arrows), possibly an apocrine process involving a scanty amount of cytoplasm; mv = microvilli. H: The dilated lumen of this short tubule contains structureless, vacuolized products.
artifacts, since they occur in adenocytes with no damage features and contiguous to integral Schwann cell-nerve fiber associations (Fig. 6D, E). Golgi apparatus activity is expressed by marginal saccule dilatations and secretory vesicles, which contribute to granulogenesis (Fig. 6C). Closely opposite gland tubules, with secretory cells sectioned along to their functional axis, reveal remarkable amounts of secretory products and their location in the supra-nuclear (apical) cytoplasm, whereas infra-nuclear granules are scanty (Fig. 6D, H). This functional polarization (not obvious in transverse sections of secretory cells, (Fig. 6A), is emphasized by the occurrence of large rer cis-

Fig. 7. — Semi-schematic representation of the venom gland in Micrurus mipuritus, details in the text, not at scale; m = muscles; A = accessory gland; A = accessory gland acini; AII = mucous cell; B = main gland; B = main gland tubules; BIII = high prismatic serous cell in specimen no. 1; BIV = high prismatic serous cell in specimens no. 2 or 3; BIV = low prismatic serous cell in specimens no. 2 or 3.
terns around and below the basal nuclei (Fig. 6D-E, H), as well as release patterns from the cell apices. These consist of typical merocrine activities (Fig. 6F) as well as development of cytoplasm blebs, with a thin peduncle, which seem to separate from the apical cytoplasm in the fashion of micro-apocrine release, although they do not contain any secretory product (Fig. 6G). As a result of these processes, a structureless, vacuolized product accumulates in the tubule lumen, as already detected under the LM (Fig. 6H, compare with Fig. 1C, E). Thin stromal partitions derive from the connective tissue septa inside the MG, and separate contiguous tubules (Fig. 6D). Along with flat fibrocytes (Fig. 6D), the peri-tubular stroma contains Schwann cells, characterized by nuclei with dispersed chromatin and light cytoplasm, that envelope thin neurites with no myelin sheaths (Fig. 6E).

**DISCUSSION**

Our study confirms that VG in *Micrurus mipartitus* includes two specific component glands (AG and MG, Fig. 7) according to the main structural pattern shared by elapine snakes.

Studies of AG (Rosenberg 1967, Kochva 1978a) suggested that its mucous product could play a role in protecting mouth tissues from venom-induced damage or, alternatively, in activating the venom chemically. AG mucocytes may release their products following electrophysiological stimulation of the VG (Hatttingh et al. 1984, on *Bitis arietans* (Merrem 1820)). This suggests that the secretory product of AG (the distal component part of VG) is discharged independently, representing the first material collected during milking. Indeed, 2 days after stimulation, AG in specimen no. 2 (which released only small amounts of venom) exhibited obvious patterns of secretory activity, resembling a mucous gland engaged in restoring. In contrast, the venom-producing cells, which contributed little to secretory release, resembled cells in resting MG.

In the following discussion on the MG, we will compare: (a) resting with fully extracted glands; (b) resting with partly extracted glands and (c) both extracted glands. This cross-comparison reveals close similarities between MG in specimens no. 3 and no. 2, possibly related to the weak discharge response from the latter snake. Despite the different conditions, MG in specimens no. 3 and no. 2 had secretory organelles in a phase of moderate activity. In contrast, the secretory epithelium of MG in specimen no. 1, which released large amounts of secretory product, was involved in obvious biosynthesis activity.

The most remarkable trait of venom biosynthesis in specimen no. 1 was the impressive enhancement of rer activity, as demonstrated by the enlarged granular profiles of the endoplasmic reticulum. These patterns of rer activity, previously reported in viperid species (Oron & Bdolah 1973, 1978; Carneiro et al. 1991; Mackessy 1991), indicate that high levels of protein synthesis occur after manual venom extraction.

Secretory cells are filled by granules of various densities, which probably represent different stages of venom maturation. In *Naja haje annulifera* Peters 1854 (Kochva et al. 1982) different patterns of granule maturation are present in extracted and unextracted glands, although low-density granules are seen more frequently in extracted (4 days after milking) glands. In specimen no. 1 the secretory granules produced by renewed activity appeared more homogeneous (with prevalent elec-
tron-dense granules) than in specimens no. 3 and no. 2, where intermediate stages of condensation were observed in the product stored in the cytoplasm.

A common trait in all specimens was the clear contrast between the features of intraluminal and intracytoplasmic products, consisting of structureless dispersed material and discrete granules, respectively. The intracytoplasmic accumulation of secretory products (or at least their precursors) involves some adaptations in gland epithelia, such as labyrinthine patterns between contiguous plasma membranes, which may become extended to allow cell enlargement during storage. Alternatively, these wide plasmalemma systems may represent a membrane reserve which compensates for loss through apocrine secretion. The intraluminal material includes both secretory product and cytoplasm debris: the former derives from the intracellular granules released through merocrine and apocrine processes and the latter is formed by disintegration of the apical cytoplasmic material detached from secretory cells through apocrine mechanisms. Both types of release processes allow intraluminal venom accumulation; nevertheless, apocrine activity provides large amounts of granules. Patterns of apical release also include protrusion of small blebs of cytoplasm. Although this “micro-apocrine” activity does not involve secretory granules, it demonstrates the basic ability of MG cells to perform release processes through loss of apical cytoplasm.

The results of the present study agree with morphological data available on VGs of elapine snakes (ROSENBERG 1967, GOPALAKRISHNAKONE & KOCHVA 1990), including TEM features (KOCHVA 1978a, 1987; KOCHVA et al. 1982; GOPALAKRISHNAKONE 1986; GOPALAKRISHNAKONE & KOCHVA 1993) and, to some extent, of viperid snakes (WARSHAWSKY et al. 1973; ORON & BDOLAH 1973, 1978; CARNEIRO et al. 1991; MACKESSY 1991). Furthermore, our findings confirm that the discharge of the venom stored in the gland tubules triggers secretory cell activity. Therefore, ultrastructural investigation of extracted glands is a suitable approach to the morpho-functional analysis of these organs.

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