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On the Structure and Function of the Glue-Secreting Glands of *Henia vesuviana* (NEWPORT, 1845)

(Chilopoda: Geophilomorpha)

by

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A bstract: Each segment of the centipede Henia vesuviana contains a large gland that secrets glue as a defensive response to attack. The structure and function of these glands has been studied by light microscopy, and scanning and transmission electron microscopy of serial sections through whole segments. Each gland contains about 200 huge secretory cells. The cells supply glue to their 'own' ducts which open individually on the ventral surface via pores in the sternal cuticle. The walls of each duct are formed into a valve which, under normal circumstances, prevents the glue from escaping from the pores. During attack, muscles surrounding each gland contract, and glue is forced past the valves onto the ventral surface where it coalesces into a large sticky droplet. Potential predators of Henia vesuviana, such as the beetle Staphylinus olens (MÜLLER), are physically immobilised by the secretion when they attack, allowing the centipode to escape.

1. Introduction:

The centipede *Henia vesuviana* secretes copious amounts of proteinaceous glue in response to attack from potential predators (HOPKIN et al. 1990). The glue hardens within a few seconds of exposure to air and is able to physically immobilise large insects such as the Devil's Coach Horse beetle (*Staphylinus olens* MÜLLER) for more than 20 minutes (Figs 1, 2) (HOPKIN & GAYWOOD 1987).

In an earlier paper (HOPKIN et al. 1990), the glue was shown to be composed principally of low (12K) and high (130K) molecular weight proteins. In this paper, we describe the structure of the glue-secreting glands, paying special attention to the valves which control release of glue from the secretory cells.

2. Materials and Methods:

2.1. Transmission Electron Microscopy (TEM):

Specimens of *Henia vesuviana* of about 7 cm in length were submerged in 2.5 % gluteraldehyde in 0.1 M cacodylate buffer. The centipedes were cut into pieces of 1 cm in length. A slit was made in the dorsal cuticle of each segment to facilitate penetration of fixatives. After two hours in gluteraldehyde, the material was post-fixed in 1 % osmium tetroxide in 0.1 M cacodylate buffer for one hour, dehydrated in a graded series of ethanols, and embedded in Spurr's low viscosity epoxy resin. Sections of 60 nm in thickness were cut onto water, picked up on uncoated copper grids, and stained with uranyl acetate and lead citrate. The specimens were examined in a JEOL 100S TEM operating at 80 kV.

2.2. Scanning Electron Microscopy (SEM):

Pieces of *Henia vesuviana* were submerged in 2.5 % gluteraldehyde in 0.1 M cacodylate buffer. A longitudinal cut was made immediately with fine scissors through the pore patches on each sternite to expose the internal structure (Figs 6, 8). After two hours in gluteraldehyde, the material was dehydrated in a graded series of ethanols, transferred to acetone, critical point dried, mounted on copper stubs, coated with gold and examined in a JEOL T300 SEM operating at 20 kV.

2.3. Light Microscopy (LM):

Sections of 1 µm in thickness were cut from blocks prepared for TEM and stained with an aqueous solution of 1 % toluidine blue and 1 % borax.

3. Results and Discussion:

Henia vesuviana conserves glue by secreting it only from segments that are stimulated (Fig. 3). Thus, a centipede is able to immobilise several predators if the attacks are made to different parts of its body. Henia vesuviana cannot, however, defend itself against swarms of ants (JONES et al. 1976). If a specimen is placed on the ground adjacent to the nest of the wood ant Formica rufa, the centipede is able to immobilise about a dozen ants. Eventually, however, its supplies of glue are exhausted and the centipede is killed and dragged into the nest (Hopkin, personal observation).

When a leg of a live centipede is stimulated, the segment to which it is attached momentarily shrinks in size, and a droplet of glue appears on the ventral surface (Fig. 3). Each gland is surrounded by an extensive network of muscles. Thus, it is probable that hydrostatic and/or muscular pressure acting on the gland forces glue out of the secretory cells to the surface (Fig. 4).

Each gland contains about 200 secretory cells. Each cell contains a huge sac which is surrounded by a thin layer of cytoplasm from which the glue is derived (Fig. 5). The sac narrows ventrally to form a duct which opens to the surface via a pore (Fig. 6). Directly beneath the pores, each duct is surrounded by a cuticular structure. This is formed into a valve which opens to allow glue to escape (Figs. 7, 8, 9). Such a structure is not present in the glue-secreting glands of *Pleurogeophilus mediterraneus* (MEINERT) in which the opening is sealed by a plug of hardened secretion (TURCATO & MINELLI 1990).

The cuticular part of the duct begins as a crescent-shaped structure in cross section (Fig. 10). The 'points' of the crescent meet nearer the pore to form a tube through which the glue passes (Fig. 11). Immediately below the pore, the tube 'pinches' together and forms the valve (Fig. 12). The outer side of this valve joins directly with the edge of the pore above it. However, the inner side 'crosses over' to the opposite edge of the pore (Figs 7, 8). Thus, the inner wall of the 'crescent' (Fig. 12) forms the 'cap' which seals the opening.

Interspersed among the glue-secreting pores are a number of smaller pores that are not sealed (Fig. 8). These appear to be connected to secretory cells that are located directly beneath the cuticle of the pore patches (Fig. 13). It is possible that these cells secrete 'anti-glue' to prevent the glue secreted from the main pores from sticking to the ventral surface of the centipede. However, further work is required before this suggestion can be substantiated.

The glue-secreting glands of *Henia vesuviana* are highly effective at repelling attacks from ground-dwelling predatory arthropods. Most geophilid centipedes possess similar structures but we know almost nothing about their importance as defensive organs. The ability of centipedes to produce defensive secretions may have much greater ecological significance than has hitherto been realised.

4. Literature:

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- TURCATO, A. & A. MINELLI (1990): Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (MEINERT) (Chilopoda, Geophilomorpha). In: A. MINELLI (ed.), Proceedings of the 7th International Congress of Myriapodology, E.J. Brill, Leiden: 165 173.

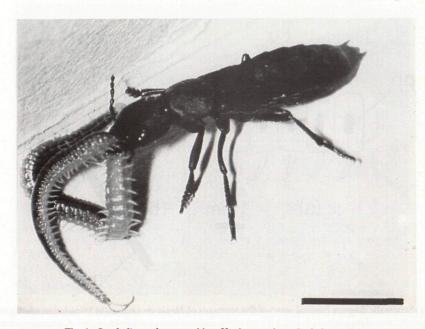


Fig. 1: Staphylinus olens attacking Henia vesuviana. Scale bar = 1 cm.

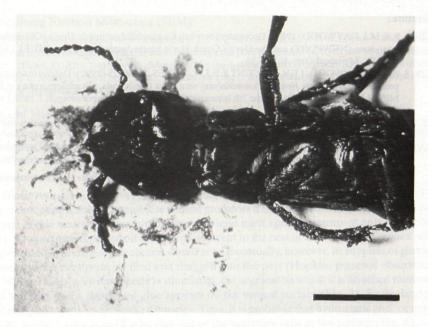


Fig. 2: The mouthparts of the beetle are stuck together with glue secreted by the centipede. The beetle remained in this position with its head glued to the substrate for 20 minutes before it was able to mount another attack. Scale bar = 0.5 cm.

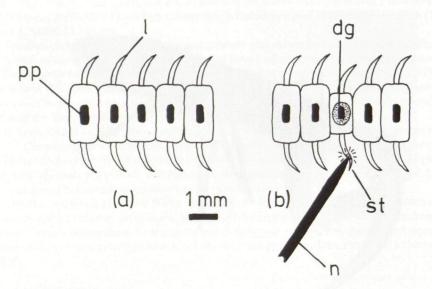


Fig. 3: (a) Schematic diagram (ventral view) of five segments of *Henia vesuviana*. (b) Stimulation of a leg results in rapid contraction of the segment to which it is attached, and secretion of a droplet of glue. Adjacent segments do not respond to the stimulation. a) 1 = leg; pp = pore patch. b) dg = droplet of glue; n = needle; st = stimulus.

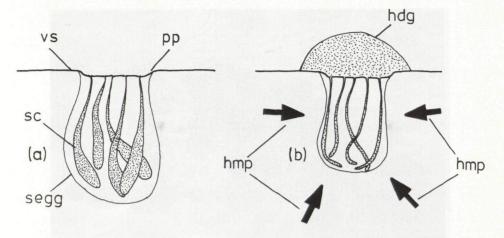


Fig. 4: (a) Schematic diagram (not to scale) of a cross section through a glue-secreting gland of *Henia vesuviana* (for simplicity, only five secretory cells are shown rather than the 200 actually present). (b) The gland is 'squeezed' by surrounding muscles and glue is forced to the surface. a) sc = secretory cells; segg = sac enclosing glue gland; pp = pore patch; vs = ventral surface. b) hdg = hemispherical droplet of glue; hmp = hydrostatic and/or muscular pressure.

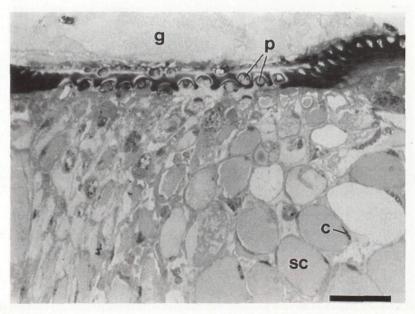


Fig. 5: Light micrograph of a section cut obliquely through a pore patch and associated glue-secreting gland. Each pore (p) is supplied by its 'own' secretory cell composed of a huge sac of glue (sc) surrounded by a thin ring of cytoplasm (c). Solidified glue (g) is attached to the ventral surface. Scale bar = 30 μm.

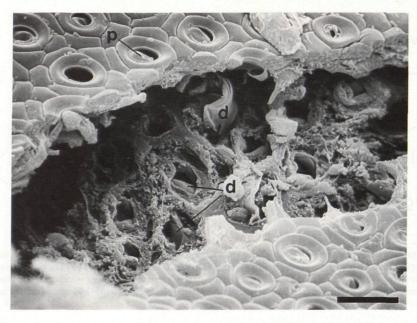


Fig. 6: Scanning electron micrograph of a fracture through a pore patch. Each pore (p) is supplied with glue via its 'own' secretory duct (d). Scale bar $=10~\mu m$.

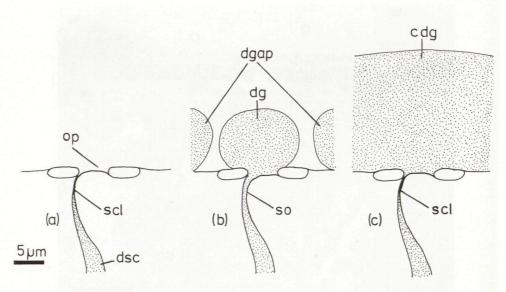


Fig. 7: (a) Schematic diagram of the valve associated with each pore in the closed position. (b) The valve opens to allow glue to escape. (c) The valve closes again, resealing the pore. a) dsc = duct from secretory cell; scl = seal closed; op = opening of pore. b) dg = droplet of glue; dgap = droplets of glue from adjacent pores; s = seal open. c) cdg = coalesced droplets of glue; scl = seal closed.

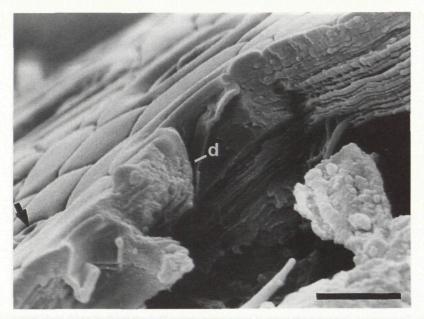


Fig. 8: Scanning electron micrograph of a fracture through a pore. One side of the duct (d) from the secretory cell 'crosses over' to the opposite wall forming the valve. Other smaller pores (arrow) are also present. These may secrete a substance that prevents the glue from sticking to the ventral surface of the centipede. Scale bar $= 5 \mu m$.

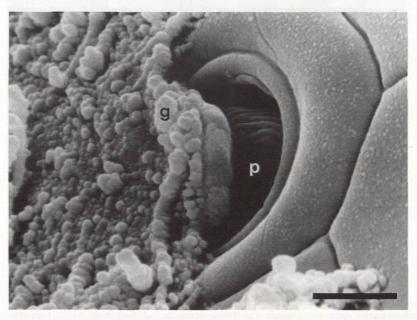


Fig. 9: Scanning electron micrograph of a pore (p) after secretion of glue (g) under 2.5 % gluteraldehyde. The glue has polymerised immediately after secretion (similar to a 'pillow lava'), and has retained the shape of the pore after becoming detached from the cuticle. Scale bar $= 2 \mu m$.

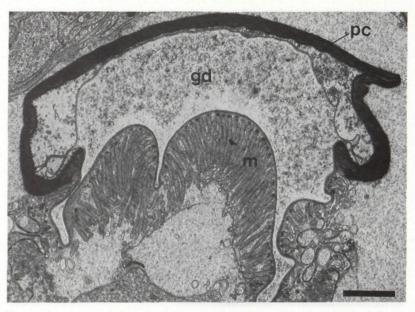


Fig. 10: Transmission electron micrograph of a transverse section through the duct which leads from a secretory cell. The duct through which the glue flows (gd) is surrounded on three sides by pore cuticle (pc) which encloses the duct nearer to the ventral surface (Fig. 11) and forms the valve (Fig. 12). The function of the complex of membranes (m) adjacent to the duct is not known. Scale bar = 1 μ m.

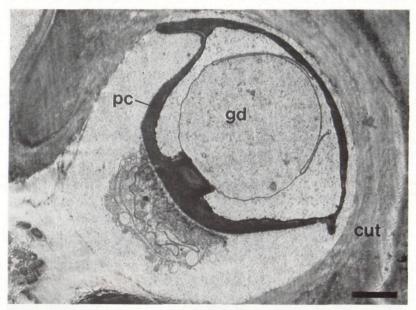


Fig. 11: Transmission electron micrograph of an oblique section through the duct which leads from a secretory cell and which passes through a hole in the sternal cuticle (cut). The section is intermediate to those shown in Figs 10 and 12. The glue duct (gd) is completely surrounded by pore cuticle (pc) which 'pinches together' near the ventral surface to form a valve (Fig. 12). Scalebar = $1 \mu m$.

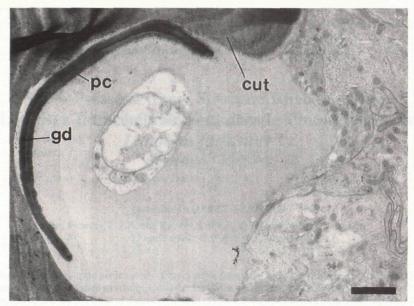


Fig. 12: Transmission electron micrograph of an oblique section through the valve which controls the release of glue from the secretory cell. The pore cuticle (pc) completely surrounds and seals the duct (gd) which passes through a hole in the sternal cuticle (cut). Scale bar $-1 \mu m$.

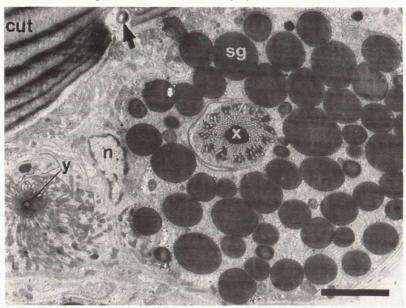


Fig. 13: Transmission electron micrograph of an oblique section through a cell adjacent to the sternal cuticle of a pore patch. The cell contains a small nucleus (n) and large numbers of secretory granules (sg). These may represent 'antiglue' which is secreted onto the ventral surface via the structure in the centre of the cell (x), and the narrow duct (arrow – see also Fig. 8). The identity of the structure on the left (y) is not known, but may represent structure x sectioned in a plane nearer to the sternal cuticle. Scale bar = 5 μm.

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