Sensory Structure of the Tentacles
of the Slug, *Arion ater* (Pulmonata, Mollusca)

1. Ultrastructure of the Distal Epithelium, Receptor Cells
and Tentacular Ganglion

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Received January 22, 1974

Summary. The simple epithelium on the tentacle tips of the slug, *Arion ater* is composed, essentially, of supporting cells and sensory dendrites, and bears, at its distal surface, a brush-border of unusual structure. This brush-border is formed from the plasmatic extensions of supporting cells and the terminations of sensory dendrites. It is composed of two structurally distinct regions, an outer region containing "twig-like" extensions of the plasmatic processes, and an inner region containing the terminations of the sensory dendrites. No sensory terminations pass into the outer region.

Numerous receptor cells lie beneath the epithelium. There are two distinct morphological kinds, of which one kind contains dense-cored vesicles. Somato-dendritic synapses can occur between receptor cells.

The structure of the tentacular ganglion is somewhat similar to the procerebrum, but significantly different from that of other molluscan ganglia.

Key words: Tentacles — *Arion ater* — Receptor cells — Sensory ultrastructure.

Introduction

The non-optic nervous structure of the tentacles of pulmonate molluscs has been examined histologically on numerous occasions (Retzius, 1892; Samassa, 1894; Havet, 1899; Veratti, 1900; Schulz, 1938; Hanström, 1925, etc.) and on the basis of structural evidence the tentacle tips of a pulmonate mollusc are likely to have an important sensory role. There is a little evidence to suggest that chemoreception is the primary sense (Schulz, 1938; Kittel, 1955).

Ultrastructural studies on the non-optic nervous system of the tentacles of pulmonates have concentrated on the distal epithelium. This epithelium has been examined in the soleoliferan, *Vaginulus borellianus* (Renzoni, 1968a), in the helicaceans *Helix pomatia* (Schwalbach and Lickfeld, 1962) and *H. aspersa* (Lane, 1963; Rogers, 1971), and in the bassomatophorans, *Lymnaea stagnalis* and *Biomphalaria pfeifferi* (Zylstra, 1972). Only Renzoni (1968a) and Zylstra (1972) have examined the ultrastructure of sensory endings in the distal epithelium. Renzoni (1968a) has also examined the ultrastructure of the receptor cells in *V. borellianus*. No ultrastructural studies have been published, so far, on the tentacular ganglion.

* The author wishes to thank Dr. D. K. Roach and Mr. T. Davies for their helpful advice and Drs. D. Graham and U. Zylstra for proof-reading the manuscripts. This research was carried out during the tenure of an S.R.C. research studentship.
Ultrastructural studies on the distal epithelium of pulmonate tentacles are, however, somewhat inconclusive. In the stylommtophora *H. pomatia* Schwalbach and Lickfeld (1962) describe an unusual vacuolate structure in the distal epithelium, while Lane (1963) describes a somewhat different structure in *H. aspersa*. The epithelium does not appear to be vacuolate and the epithelial cells bear a complex surface specialization. Rogers (1971) confirms these observations of Lane for *H. aspersa* but is critical of several of Lane’s other conclusions. Renzoni (1968a) shows that a similar surface specialization to that of *H. aspersa* exists on the surface of the distal epithelium of the tentacles of the slug, *V. borellianus*.

The present paper describes the ultrastructure of the distal epithelium of the tentacles of the zonitacean pulmonate, *Arion ater*, and also includes a description of the receptor cells and tentacular ganglion. The ultrastructure of the free nerve endings in the distal epithelium of the tentacles of *A. ater* is described in a separate paper (Wright, in press).

Materials and Methods

Specimens of the common slug, *Arion ater* were obtained locally and kept in culture in polythene bowls. The slugs were supplied with moist air and fed on chopped carrot and potato. Excised tentacles of *A. ater* were prepared for the electron microscope using the following fixation procedures:

1. Ice-cold, 3% phosphate buffered glutaraldehyde with post-fixation in Millonig’s buffered osmium tetroxide (1961).
2. Warm (37°C), 3% phosphate buffered glutaraldehyde with post-fixation in Millonig’s buffered osmium tetroxide (1961).

Best general fixation was achieved after single-fixation in Millonig’s OsO₄ solution (method 3.) Fixation by methods one and two often resulted in massive vacuolation of the distal epithelium of the tentacles.

Fixed tentacle preparations were washed in phosphate buffer, dehydrated through a graded series of ethanols and embedded in Araldite. Thin sections were cut on an L.K.B. Ultratome, mounted on carbon-coated grids and examined on an A.E.I.E.M. 6 electron microscope. They were stained with uranyl acetate and lead citrate (Reynolds, 1963). Transverse serial sections were cut of the brush-border on the sensory epithelium of the superior tentacle.

"Thick" Araldite sections, for light microscopy, were stained in a solution of 0.5% toluidene blue in 0.5% borax at 80°C. Material for light microscopy was also silver stained to reveal neural structure using the method of Romanes (1946) and the Gregory (1970) modification of the Bodian protargol technique.

Results

Sensory Epithelium of the Tentacle Tip

In *Arion ater*, the surface of the tentacle tip is covered by a simple columnar epithelium. There are approximately $5 \times 10^4$ cells/mm². (This figure was determined from the number of nuclei in "thick" Araldite transverse sections of the epithelium). These epithelial cells are much taller than their counterparts on the tentacle wall (35–40 μm as compared to 6–7 μm for cells of the tentacle wall), and bear at their distal surface a complex specialization substantially different to the simple microvillar structure found on cells of the tentacle wall. Beneath the epithelium lies a network of muscle fibres.