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The ultrastructure and histology of the perinotal epidermis and defensive glands of two species of *Onchidella* (Gastropoda: Pulmonata)

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ABSTRACT

Histology and electron microscopy were used to describe and compare the structure of the perinotal epidermis and defensive glands of two species of shell-less marine Systellommatophora, *Onchidella capensis* and *Onchidella hildae* (Onchidiidae). The notum of both species is composed of a layer of epithelial and goblet cells covered by a multi-layered cuticle. Large perinotal multi-cellular glands, that produce thick white sticky mucus when irritated, are located within the sub-epidermal tissue. The glands are composed of several types of large secretory cell filled with products that stain for acidic, sulphated and neutral mucins, and some irregularly shaped support cells that surround a central lumen. The products of the secretory cells are produced by organelles that are basal in position. The entire gland is surrounded by a well-developed capsule of smooth muscle and collagen, and in addition smooth muscle surrounds the cells within the glands. Based on the size of the gland cells, their staining properties, and the appearance of their stored secretions at the transmission electron microscope level, five different types of secretory cells were identified in *O. capensis* and four in *O. hildae*. The products of these cells, which are released by holocrine secretion, presumably mix in the lumen of the duct as they are forced out by contraction of the smooth muscle. The structural similarity of these glands to those of siphonariids, suggest that they have a common ancestry.

1. Introduction

The Onchidioidea, of the sub-order Systellommatophora, are a superfamily of mainly marine intertidal, shell-less pulmonates (Britton, 1984), although there has been debate as to their higher taxonomic placement (Marcus and Marcus, 1956; Jensen, 1992; Dayrat, 2009). Current phylogenies place the Onchidioidea within the Pulmonata (Mordan and Wade, 2008; Dayrat, 2009). One family, the Onchidiidae, with 19 genera, one of which is *Onchidella*, is currently recognised within the Onchidioidea (Dayrat, 2009).

Members of the Onchidiidae are usually 10–70 mm long, oval in shape with a broad, large foot (flanked by the hyponotum) and a papillate or tuberculate notum. The notum is covered by a cuticle that may also contain siliceous spicules (Marcus, 1979; Smith and Stanisic, 1998). Although the Onchidiidae are common in some habitats, little is known about their biology and ecology. Most onchidiids live amphibiously in the eulittoral zone of sandy, muddy and rocky shores as well as estuaries, where they probably feed on the organic film of algae, diatoms and bacteria on the surface of the substratum (e.g. Arey and Crozier, 1921; Watson, 1925; Fretter, 1943; Wägele et al., 2006; Dayrat, 2009). *Onchidella* spp. avoid direct sunlight and prefer to forage at low tide when the sky is overcast (Arey and Crozier, 1921; Pepe and Pepe, 1985; Weiss and Wägele, 1998). The Onchidiidae are chiefly found throughout the tropics of the Pacific and Indian oceans (Stringer, 1969; Kenny and Smith, 1987; Barker, 2001; Dayrat, 2009). The genus *Onchidella*, however, whilst having an extensive global distribution including temperate habitats, is absent from the tropical Indo-West Pacific (Dayrat, 2009).

Like other shell-less molluscs, the Onchidiidae are potentially vulnerable to attack by predators. *Onchidella* spp. appear to avoid predation, however, by producing secretions from glands sited along the edge of the notum. Because of their position these glands have been referred to as perinotal glands (Watson, 1925; Marcus, 1979). These glands may also be situated in erectile papillae which are not obvious in the undisturbed animal, but are readily distinguished when it is disturbed (Arey, 1937; Arey and Barrick, 1942; Young et al., 1986). In response to stimulus (physical, chemical and electrical) the glandular secretions are discharged simultaneously or singly, the secretion being released as a stream of milky fluid (Fretter, 1943) which is acidic and burning to the taste (Arey and Barrick, 1942). Young et al. (1986) showed that the secretion from the repugnatorial perinotal glands of *Onchidella borealis* repelled intertidal predatory asteroids, and whilst intertidal crabs ate dead *O. borealis*, they did not consume live ones that are capable of

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releasing their defensive secretion. Chemical analysis of secretions from *Onchidella binneyi* and six species of the genus *Onchidium* has revealed that the glands contain isomeric polypropionates (Ireland and Faulkner, 1978 and see Darias et al., 2006 for review), and it is likely that these are the compounds that deter predators. Relatively little is known about the structure and histology of the glands of onchidellids. Most studies to date on gland structure are brief light microscope descriptions or illustrations mainly using routine histological stains. Joyeux-Laffuie (1882) was the first to describe epidermal glands in his study of *Onchidella celtica* (as *Oncidium celticum*). Von Wissel (1898) described similar glands in *Onchidella marginata* and *Onchidella juan-fernandeziana* (as *Oncidiella* spp.). Other light microscope studies of glands of *Onchidella* include those of Watson (1925) on *Onchidella pulchella* and *Onchidella capensis*, Arey and Barrick (1942) on *Onchidella floridana* (as *Onchidium floridanum*), Fretter (1943), Gabe and Prenant (1950) as well as Binot (1965) and Weiss and Wägele (1998) on *Onchidiella celtica*, Marcus (1979) on six species of *Onchidella* (*O. celtica*, *O. incisa*, *O. indolens*, *O. accrensis*, *O. capensis* and *O. philippei*) and Young et al. (1986), Weiss and Wägele (1998) and Wägele et al. (2006) on *Onchidella borealis*. Whilst Arey and Barrick (1942) observed that the glands of *Onchidella floridana* were composed of seven different types of cells, Binot (1965) only recognised five types in *Onchidella celtica* (as *Onchidiella*).

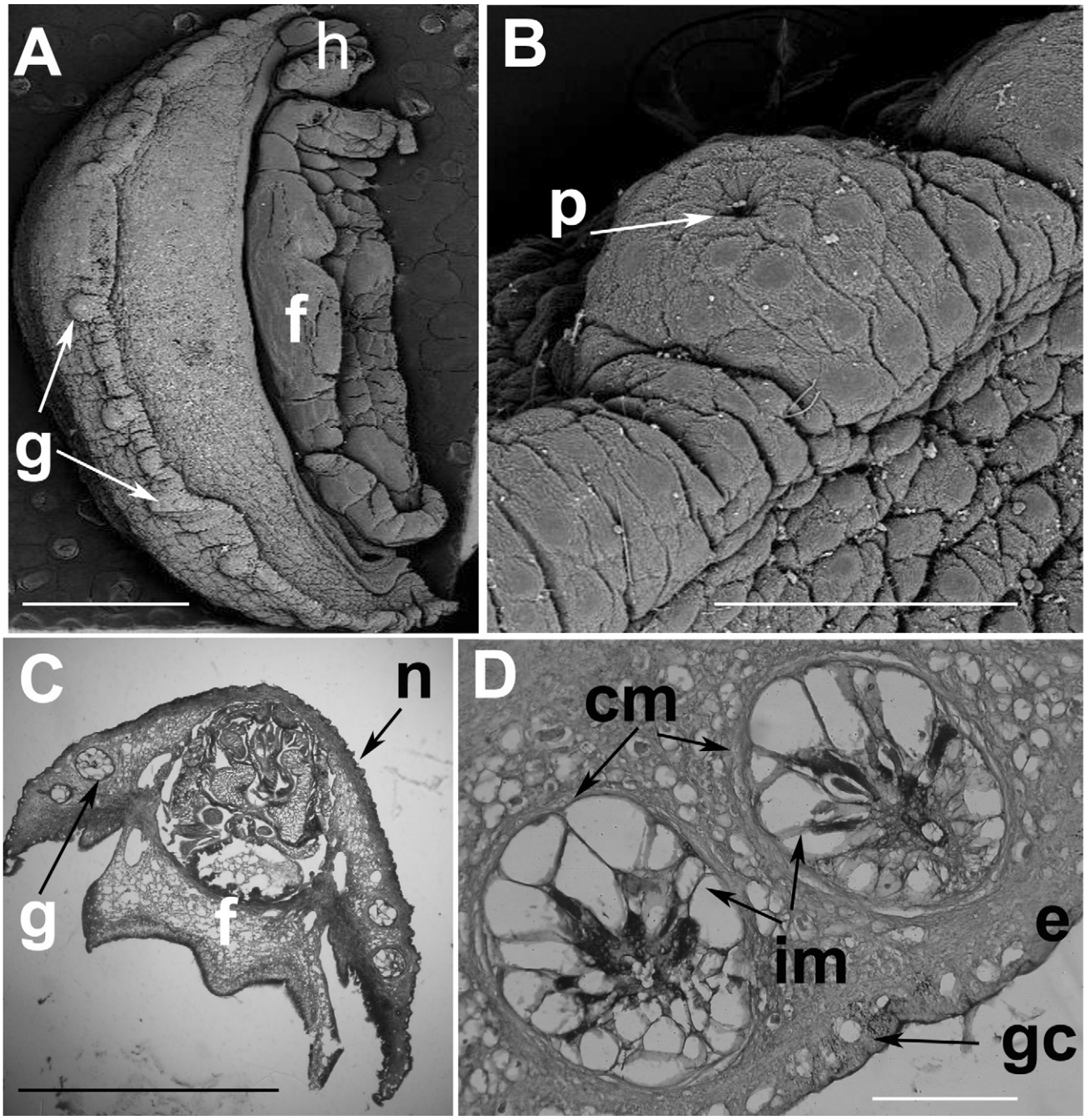

Fig. 1. Scanning electron microscopy and light microscopy of *Onchidella capensis*. (A) Lateral view; SEM image of the perinotal glands (g, gland; h, head; f, foot). (B) A higher magnification image of an individual papilla and gland pore (p). (C) Light micrograph of a mid-transverse section showing the position of the glands embedded in the perinotal region (g, gland; n, notum; f, foot), stained with toluidine blue. (D) Light micrograph of the glands stained with aldehyde fuchsin (cm, capsule muscle; im, intra-gland muscle; gc, goblet cell; e, epidermis). Scale bars: A = 2 mm; B = 200 μm; C = 5 mm and D = 100 μm.