Tissue&Cell

Feeding behavior, epidermal structure and mucus cytochemistry of the scleractinian *Mycetophyllia reesi*, a coral without tentacles

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Abstract. The scleractinian *Mycetophyllia reesi* lacks even the vestiges of tentacles, but quickly captures particulate food by mucus entanglement. Mesenterial filaments emerge through the oral opening, collect the mucus-embedded particulates, and withdraw to the gastrovascular system within 15 min. Mucocytes dominate the outer epidermis with about 3000 cells/mm^2 and are capable of apocrine discharge *en masse*. Mucocytes are spumous, typically with web-like inclusions, which for the most part lack electron opacity with ordinary staining, and are only weakly PAS positive. In contrast, the mucus reacts strongly to diamine and other reagents that suggest an appreciable acidic mucopolysaccharide component. The strongest staining reaction occurs in the presence of high iron diamine, suggesting with other tests that the mucus contains significant quantities of sulfated polysaccharides. Cells with cilia anchored by spiriliform microvilli flank the mucocytes and possess small, spumous inclusions that contain acidic, sulfated, and neutral polysaccharides that do not appear to discharge during feeding. These support cells are closely intertwined with narrow, sinuous, secretory cells containing an electron-opaque cytoplasm of unknown composition that is discharged along with mucus during feeding. The outer epidermis also contains scattered cnidae, rather than the clusters or batteries typical of tentacles. The overwhelming abundance of mucocytes is consistent with their importance in feeding. Likewise, the small number of epidermal cnidae suggest they play a minor role in acquiring food. An inner epidermal layer associated with the mesoglea contains epitheliomuscular cells, nerve cells and pigment cells. The two epidermal layers form an essentially pseudostratified, architecturally simple epithelium.
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Introduction

The epidermis of anthozoans is covered with an array of ciliary cones, kinocilia, stereocilia, and microvilli that play

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critically important roles in sensory reception and in acquisition of food. This is particularly true for the tentacles, which are thought to be essential to prey capture, or at least, prey detection (Fautin & Mariscal, 1991). Thus many investigators have focused on the organization of tentacular cnidocytes, their attendant sensory cells, and their neural integration (e.g. Mariscal, 1973; Watson & Hessinger, 1989; Thorington & Hessinger, 1998; Westfall et al., 1998). While similar to other anthozoans in many respects, scleractinian corals may exhibit multiple modes of heterotrophy, including tentaculate plankton capture (e.g. Muscatine, 1973) and acquisition of suspended or benthic

particulate matter (e.g. Goreau et al., 1971; Sebens, 1987; Anthony, 1999) among other types of nutrition. Suspension feeding using mucus nets is also common. Lewis and Price (1975) found that most of the 35 species they examined used mucus to entrap food, either with or without tentacle capture, suggesting that in some coral species the tentacles may have other functions such as food detection. However, some specialized groups of scleractinians never develop tentacles. Among the few that have been examined, ciliary or mucociliary feeding appears to predominate; the mesenterial filaments, hereinafter referred to as digestive filaments (Goldberg, 2002) may also be employed, but primarily for extracoelenteric digestion (Yonge, 1930, 1973). Others have suggested that digestive filaments and cilia are unimportant compared to mucus entrapment and transport by water currents (Schlichter & Brendelberger, 1998). There are few scleractinian corals whose epidermal tissues have been examined at the ultrastructural level (Goreau & Philpott, 1956; Kawaguti, 1966; Van-Praët, 1977; Schlichter & Brendelberger, 1998) and none that focus on the cytochemistry of coral mucosecretory cells during feeding.

Mycetophyllia reesi (Wells, 1973) is an unusual western Atlantic scleractinian that lacks polyp tentacles (Lang in Wells, 1973). While this species appears to be absent from Florida and the Bahamas, *M. reesi* is widespread in the Caribbean, occurring sporadically on the deeper reefs of Jamaica (Wells, 1973), Cuba, the Cayman Islands, Aruba, Bonaire and Curacao (Chiappone et al., 1996), as well as in Belize, Cozumel (Fenner, 1999) and Roatan, Honduras (the current paper). This study examines the feeding behavior of this species, its mucosecretory cytochemistry, and the functional morphology of its epidermis.

Material and methods

Feeding

A single *M. reesi* colony was collected from 27 m at Rio Bueno, Jamaica in December, 1998 and placed for 2 days in a lightless, concrete tank equipped with running seawater. After the recovery period, freshly collected gastropods (*Nerita peloronta* and *Tectarius muricatus*) were collected from the upper intertidal of Discovery Bay, Jamaica. Their tissues were extracted and finely ground in a mortar and pestle with a small quantity of Cuprolinic blue dye (Polysciences, Washington, PA, USA). The mixture was filtered through a 0.1 mm mesh and applied with a syringe just above the colony after the flow of seawater was stopped. Photographs of the feeding process were taken at 5-min intervals. After 15 min, a portion of the colony was broken off, fixed as described later, and examined at both optical and electron microscope levels. A small piece was also anesthetized with menthol crystals for ~2 h before fixation to examine the digestive filaments. This fed and anesthetized material will be distinguished from unfed samples as described later.

Microscopy

A second colony of *M. reesi* was collected in Roatan, Honduras at 27 m by P. Humann, in August 1995. The entire specimen was anesthetized as mentioned earlier before fixation, but was not fed. Both colonies were fixed in 3% glutaraldehyde and 1% paraformaldehyde in seawater containing 0.1 M cacodylate buffered to pH 7.8 and were then stored at 4 °C in 0.2 M cacodylate buffer. Small pieces of the colonies were cut with a wet saw or were fractured with a Teflon-coated razor blade at the thin edge of the corallum. Samples were partially decalcified with a mixture of 5% glutaraldehyde and 5% citric acid buffered to pH 4.5 with sodium citrate. An EMS 820 laboratory microwave oven (Electron Microscopy Sciences, Inc., Ft. Washington, PA, USA) set with a temperature maximum of 30 °C accelerated the process. After 2 h the tissue other than the calicoblastic epithelium could be separated from the corallum with jeweler's forceps. Unless stated otherwise, material for transmission electron microscopy (TEM) was routinely post-fixed in 1% OsO_4 in 0.1 M cacodylate buffer for 1 h at room temperature, then dehydrated in ethanols and embedded in Spurr resin. Thick sections were stained with Toluidine blue O. Thin sections were stained with uranyl acetate (saturated in 50% ethanol) followed by 0.05% lead citrate, and were examined with a Philips EM 300 electron microscope at 60 kV. Some samples, noted specifically, were embedded in paraffin for optical microscopy. No substantive artifacts were detected using citric acid–glutaraldehyde compared to the ascorbic acid method (Dietrich & Fontaine, 1975) in this material, except that microtubule definition may have been compromised using the former method. Most of the TEM reported here employed citric acid decalcification. Photographs were digitized and labeled using Adobe Photoshop 5.5. Figure 9, a photomontage, was edited to reduce differential contrast and eliminate lines of contact between photographs.

Material for scanning electron microscopy (SEM) was typically prepared from glutaraldehyde-fixed, decalcified material either by dissection with iridectomy scissors or by ethanol cryofracture (cf. Humphreys et al., 1975) followed by critical-point drying (CPD) with CO_2 as the intermediate fluid. The anesthetized and fed material was kept at 4 °C and was not decalcified. The protruding digestive filaments were washed in commercial liquid detergent followed by a stream of ethanol to clear as much of the mucus as possible, then dehydrated for CPD. All samples were sputter coated with Au–Pd and examined with an ISI Super 3A scanning electron microscope operated at 10 or 15 kV.

Cytochemistry

Epidermal cells were examined after application of reagents that demonstrate protein, acidic and neutral carbohydrate, and acidic and neutral lipid at both the electron microscopic and optical levels. Aqueous 5% phosphotungstic acid at pH 2 *en bloc* was used to visualize acidic protein components (Silverman & Glick, 1969). Control tissue was stained with 5% PTA buffered to pH 7.8 with cacodylate. Paraffin sections were stained with mercuric Bromophenol blue to test for

protein and Adam's DMAB-nitrite for tryptophan (Pearse, 1968).

Epidermal cells containing PAS-positive material were stained according to the methenamine-silver method of Rambourg (1967) after oxidation by 1% periodic acid for 1 h. Controls were examined without periodic acid oxidation. Acidic and sulfated carbohydrate components were examined using Spicer's low iron diamine (LID); sulfated carbohydrate was localized using the high iron diamine (HID) variant of this technique (Spicer et al., 1978; formulations given in Hayat, 1993). Glutaraldehyde-fixed sheets of epidermis no thicker than 50 μm were stained overnight in freshly prepared HID and LID at room temperature, then osmicated as described earlier. Controls for HID and LID eliminated the diamine from the protocol. Some material was also examined after fixation with glutaraldehyde and osmium made up with 0.05% Ruthenium red. Paraffin sections were prepared with PAS to stain neutral carbohydrate and alcian blue at pH 2.5 and 1.0 to demonstrate acidic and sulfated carbohydrate, respectively. Schiff's reagent was prepared according to the deTomassi protocol (Pearse, 1968). Control procedures included elimination of periodate oxidation for PAS and the use of $1.0 \, M \, MgCl_2$ during Alcian blue staining to block the affinity of this dye for acidic tissue components.

Metachromatic responses to borax-buffered 0.1% Toluidine blue of Spurr-embedded material was also assessed as a means of distinguishing classes of carbohydrate. Metachromasia as referred to in this paper is always the gamma type (pink). Metachromatic tissues were also treated with 1% HCl in methanol at 60 °C for 1 h as a control to abolish
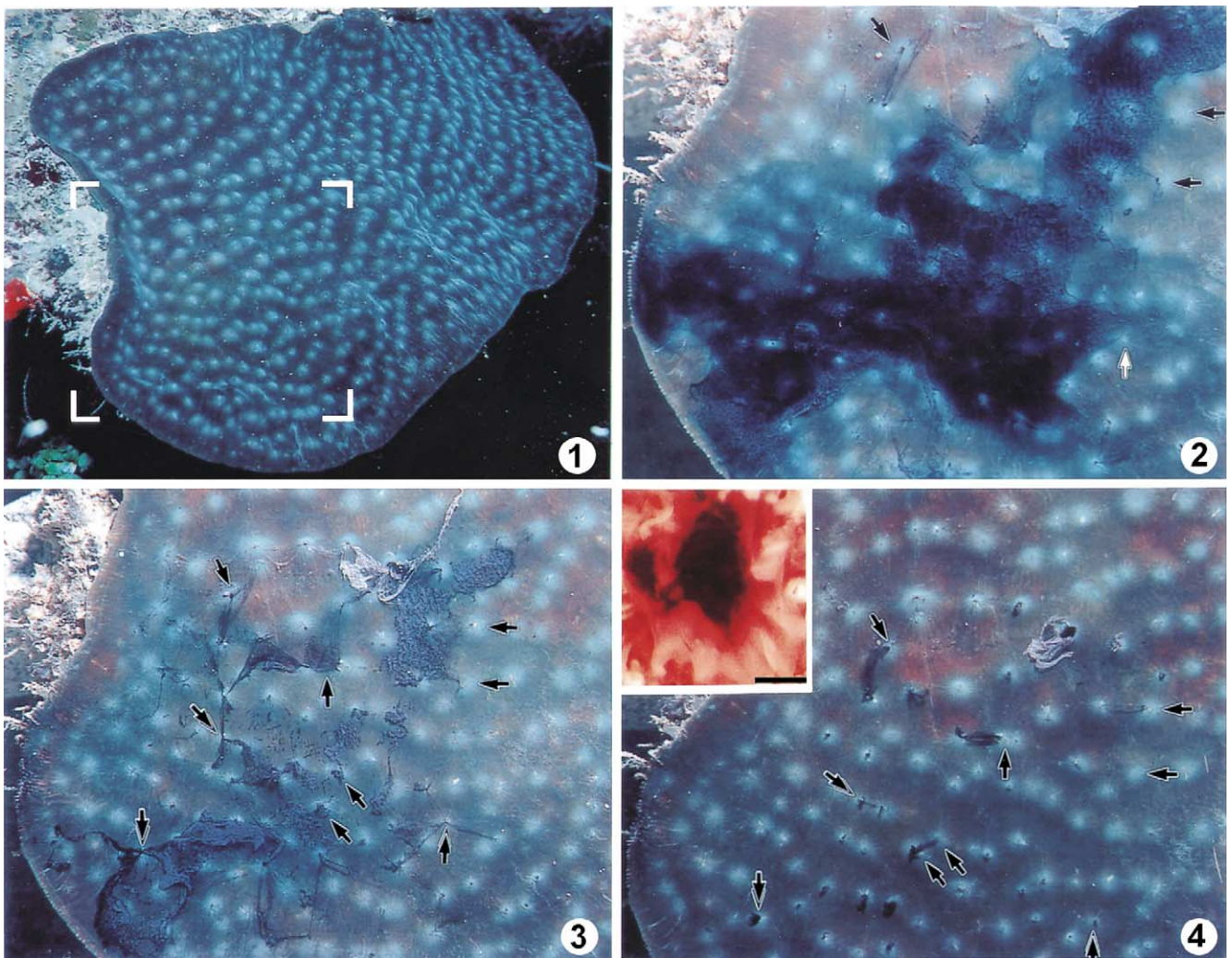
Figs 1–4 Colony morphology and feeding responses. **Fig. 1** Living colony of *M. reesi*, ca. 38 cm × 10 cm, at 27 m, Rio Bueno, Jamaica photographed prior to collection. The bracketed area is the approximate position of Figures 2–4. **Fig. 2** Colony in running seawater enclosure 1–2 min after application of dye and stained, particulate gastropod tissue. Arrows mark oral openings that can be seen in subsequent figures. **Fig. 3** Same area 5–10 min after application of dye; arrows mark oral regions that can be seen in Figure 4. Note concentration of stain in mucus nets and in digestive filaments (overlapped arrows). **Fig. 4** Food capture 10–15 min after dye application. Only digestive filaments and adherent mucus can be seen protruding from the oral openings as they begin withdrawal after feeding. There are no tentacles. The stained material cannot be seen through the circumoral pigment layer once filaments have withdrawn into the gastrovascular system. Inset: withdrawn, stained digestive filaments, food and mucus viewed from the polyp interior (scale = 1 mm).
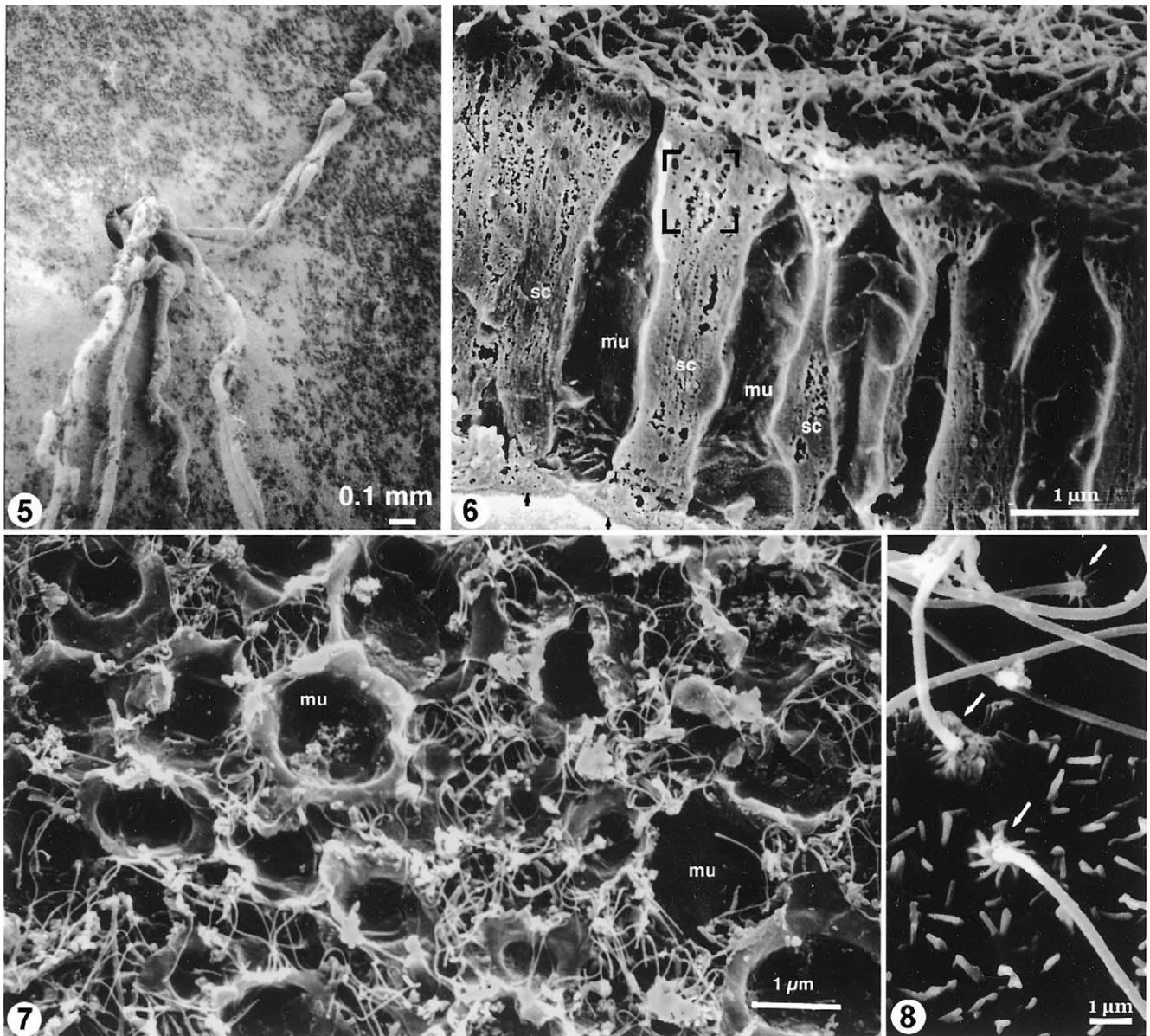
Figs 5–8 Digestive filaments and outer epidermis. SEM. **Fig. 5** Digestive filaments protruding through the oral opening in an anesthetized fed *M. reesi*. Some food particles remain attached to the filament surfaces. **Fig. 6** Freeze–fracture section through epidermal tissue. Support cells (sc) are columnar, contain numerous apical vesicles (e.g. bracketed area) and are flanked by mucocytes (mu). The epidermal surface is covered with cilia, almost all of which emanate from the support cells. The inner epidermal tissue (arrows) is composed of epitheliomuscular and nerve cells adjacent to the mesoglea (unanesthetized material). **Fig. 7** Surface view of discharged mucocyte (mu) field and surrounding support cell cilia. **Fig. 8** Ciliary bases are surrounded by spiraled microvilli (arrows). Note additional scattered microvilli on surrounding epidermal surface.

γ-metachromasia (Pearse, 1968). Loss of metachromasia due to methylation of carboxyl groups can be reversed by saponification. Metachromatic material was saponified for 20 min at room temperature in 0.5% KOH in 70% ethanol, then examined after restaining with Toluidine blue.

Neutral lipids were examined at the TEM level using the imidizole-OsO_4 technique of Angermüller and Fahimi (1982) and by applying phenylenediamine (PPD) after osmication during ethanolic dehydration according to Bosher et al. (1984). Parallel paraffin-embedded material was examined after staining with Oil red O or Sudan black B. Since the primary purpose of the light microscopy (LM) was

to compare with TEM preparations, no special precautions were taken to preserve lipid during dehydration, and unbound lipid was likely lost during processing.

Results

Colonies of *M. reesi* are thin and encrusting (cf. Wells, 1973; Humann, 1993) or may become thicker and shelf-like, especially on more vertical substrates (Fig. 1). The skeleton lacks collines and the colony appears flat except for the blue-green circumoral regions that project as small protuberances across

the corallum. There is typically less pigment between polyps and at the edge of the colony, revealing a yellow-brown color from gastrodermal zooxanthellae (Fig. 1).

Feeding

The application of dye and food to the colony obscures the coral's immediate reaction, but epidermal mucus is evident within seconds as it becomes stained; digestive filaments emerge from the oral opening within 1–2 min (Fig. 2). After 5–10 min, the mucus, filaments, and food are all stained and bound together (Fig. 3). Within 10–15 min, the stained material is found only on and in direct contact with the filaments, which begin withdrawal to the polyp interior (Fig. 4). Digestive filaments were only observed emanating from the oral opening (cf. Goreau et al., 1971); no other part of the polyp emerged during the entire feeding process.

Stained food, mucus and filaments were not visible once withdrawn into the digestive cavity. Since feeding could only be viewed intermittently to avoid disturbance, the digestive cavity contents were examined after fixation to confirm the ingestion of food. The gastric regions of several polyps contained digestive filaments coiled around clusters of food and mucus as suggested by Figure 4 (inset). Examination of the feeding process by close-up photography fails to show the digestive filaments clearly. Indeed the live filaments are thin, translucent, and are not easily distinguished from mucus strands. However, the anesthetized-fed polyps were fixed with filaments exsert as shown in Figure 5. No tentacles were found either on the corallum or around the polyps. There is no doubt that digestive filaments function, in part, as surrogate tentacles in this species.

The epidermis of *M. reesi* is typically 35–50 µm thick between polyps but may double in thickness periorally in anesthetized material. The unanesthetized specimen is half this thickness, and is obviously contracted. Seven cell types are found in this tissue. Four of these, cnidocytes, mucocytes, secretory and support cells are typical of the outer portions of the epidermis. Epitheliomuscular, nerve and pigment cells are typical of the inner epidermis, close to the mesoglea. The epidermis, described more fully later, is essentially a simple pseudostratified epithelium. All cells (except the cnidocytes) are in contact with the mesoglea, but only some of them reach the surface.

Outer epidermal cells

The outer epidermis is dominated by mucocytes and the ciliated cells that separate them (Fig. 6). The mucocytes are the largest and most prominent cells of the epidermis, most often measuring 6–7 µm wide and 30 µm long in anesthetized tissue. These cells appear to lack microappendages at their apical surfaces, but since much of the epidermis is obscured by adjacent, ciliated cells, this conclusion must be tentative. Undischarged mucocytes appear to have a narrow, restricted opening, 1 µm or less in diameter (Fig. 6), followed by an irregular shape that extends deep into the epidermis; there are no goblet-shaped mucocytes that narrow toward the base as described from a pennatulid by Crawford and Chia

(1974). Mucus cell density can most easily be determined in areas where mucus discharge has occurred and the pores have become enlarged and crater-like (Fig. 7). Discharged mucocytes open by pores 5.3 ± 0.8 (SD) µm in diameter (range 2–10 µm, $n = 20$). A mean of 2906 ± 441 (SD) of these cells occurs per mm^2 of epidermal surface (range 2381–3741), determined by LM measurements in 10 discharge fields.

The mucocytes contain large, spumous chambers (loculae) whose partitions break down as mucus is released. During discharge, the apical cell membrane is breached and the contents of the cell are released (Figs 9 & 13). The mucosecretory material is the product of Golgi cisternae that form vesicles containing flocculent material, especially in the vicinity of the typically mediolateral nuclei (Fig. 9, inset). There is little development of rough endoplasmic reticulum in these cells. Consistent with this, the secretory products contain no cytochemically reactive protein either with PTA or mercuric Bromophenol blue. Similarly, no tryptophan is detected in these cells. In a small portion of some mucocytes, electron-opaque regions stain with $PPD–OsO_4$, suggesting the presence of lipid as a minor component. The mucosecretory material is PAS positive in TEM but only after periodate oxidation, as would be expected of vicinal glycols. The distribution of silver is diffuse within the cell, suggesting that neutral carbohydrate is omnipresent but not concentrated in any one area (Fig. 10). In LM preparations, the mucus stains as wisps of both PAS-positive and alcianophilic (at pH 2.5) strands. Some of the loculae contain a dense Alcian blue-positive reaction product, suggesting an acidic polysaccharide component. Correspondingly, mucosecretory material is more clearly and coarsely stained with LID, revealing concentrations of secretory product within the cell (Fig. 11).

The most prominent reaction occurs with HID, which makes the mucus strongly electron opaque, revealing its fine, microfibrillar structure. Tissue without diamine in the medium fails to stain, while material treated with Ruthenium red is essentially indistinguishable from that treated with HID. Before discharge, the HID-reactive material occurs in zones of varying opacity (Fig. 12) but during discharge the mucus tends to stain more darkly and uniformly, taking on a net-like appearance on contact with the external environment (Fig. 13). LM sections of mucocytes stain lightly with Alcian blue at pH 1.0 and give a metachromatic pink response to Toluidine blue. Taken collectively, these staining reactions strongly suggest polyanionic materials in the mucus, most likely acid mucopolysaccharides. The metachromasia with Toluidine blue is abolished by N-HCl–methanol and cannot be reversed by saponification. This reaction indicates that sulfate esters are a key element in the metachromasia of the mucus, and together with strong HID positivity, suggests sulfated polysaccharides as a prominent component.

The cnidae occurring in the outer epidermis are generally sparse with 469 ± 34 (SD) of them per mm^2 of epidermis (range 405–503) determined from ten 5000–8000 $µm^2$ fields. This number includes both mature and immature developmental stages from the epidermal subsurface, both of which stain deeply with Toluidine blue. Their capsules are
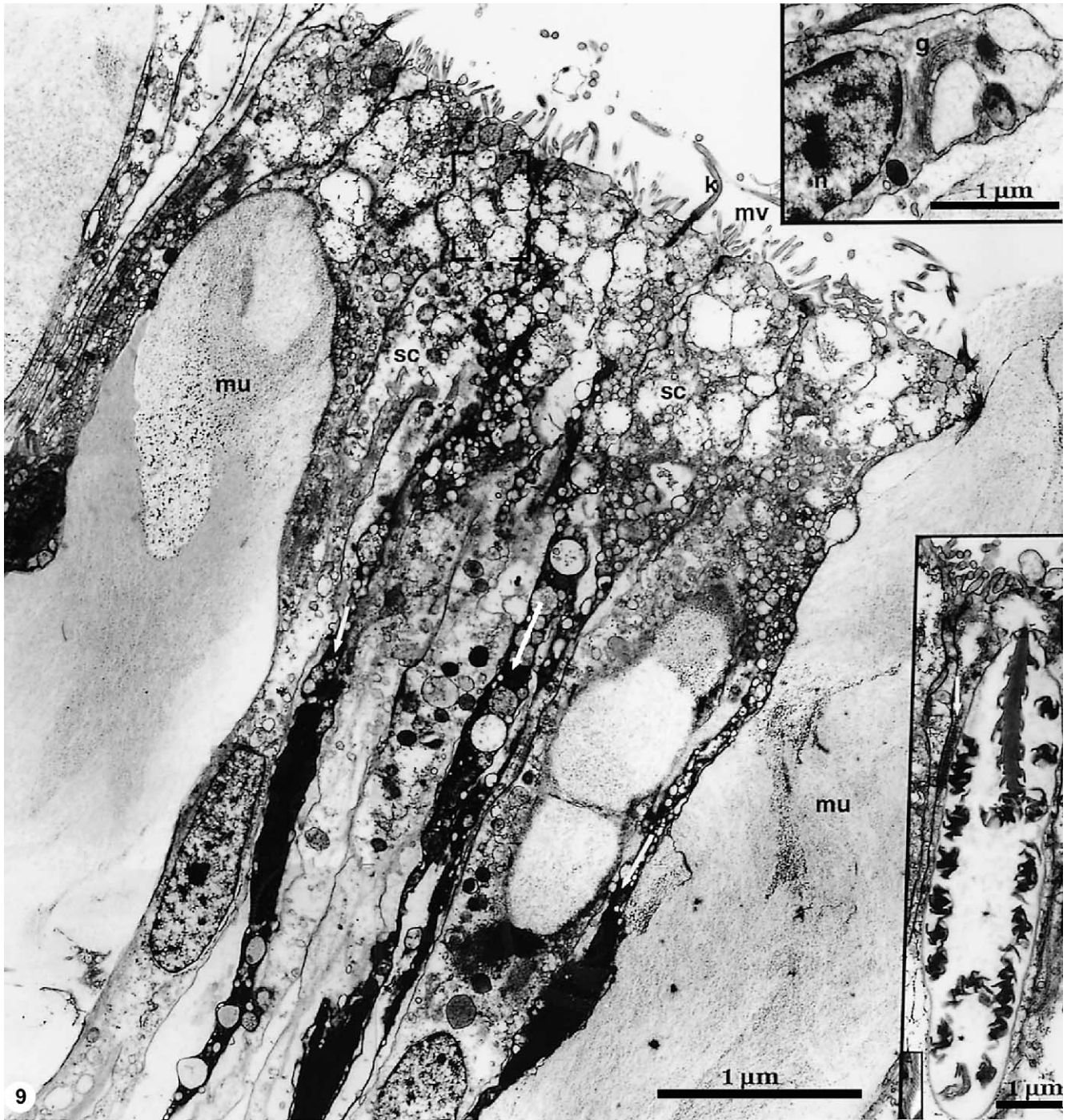
Fig. 9 Six-part TEM photomontage of support cells (sc) with intervening mucocytes (mu). Mucocyte contents typically stain weakly (as shown) with uranyl acetate and lead citrate. Note apocrine mucocyte discharge at right. Support cells contain a single apical kinocilium (k) surrounded by microvilli (mv). Larger apical vesicles (e.g. bracketed area corresponding to that shown in Fig. 6) contain a variety of carbohydrate materials. Dark staining, vesiculate cytoplasm (arrows) are apical extensions of secretory cells. Inset lower right: longitudinal section of spirocyst-like cnida with serrated capsule (boxed area = 2.5 × inset magnification) and tangential portion of the ciliary rootlet (arrow). The tubule is not subdivided into rodlets as is typical of spirocysts. These cnidae are isolated and scattered in the epidermis. Inset upper right: mucocyte with nucleus (n) and Golgi (g) during synthesis of mucus droplets.

thin walled like spirocysts (Fig. 9, inset), but the tubules do not appear to contain the rodlets or similar substructures typical of these cnidae (e.g. Fautin & Mariscal, 1991; Goldberg & Taylor, 1996). No other types of cnidae are present. Discharged cnidae could not be distinguished with certainty in the epidermis of the fed colony, and could not be found in unfed material. While the apical cell surface characteristics of the cnidocyte have not been determined with certainty, there appears to be a striated rootlet and microvilli associated with these cells. These are the only epidermal cells without connection to the mesogleal basement layer.
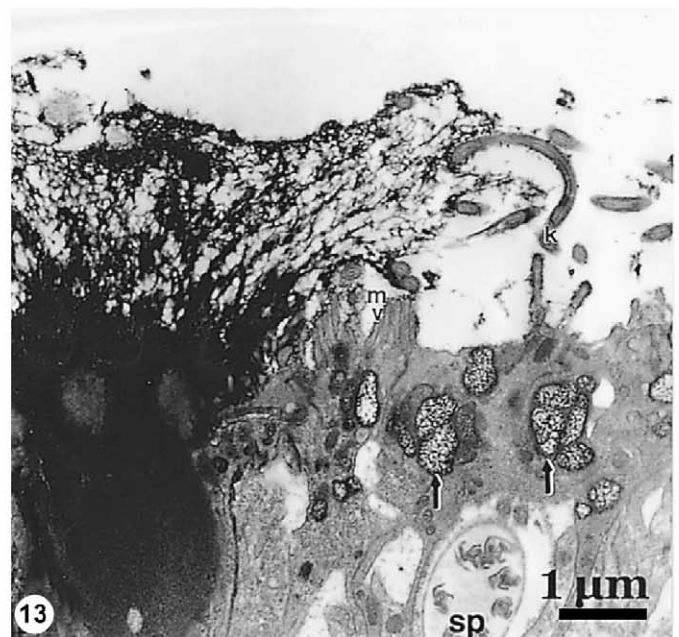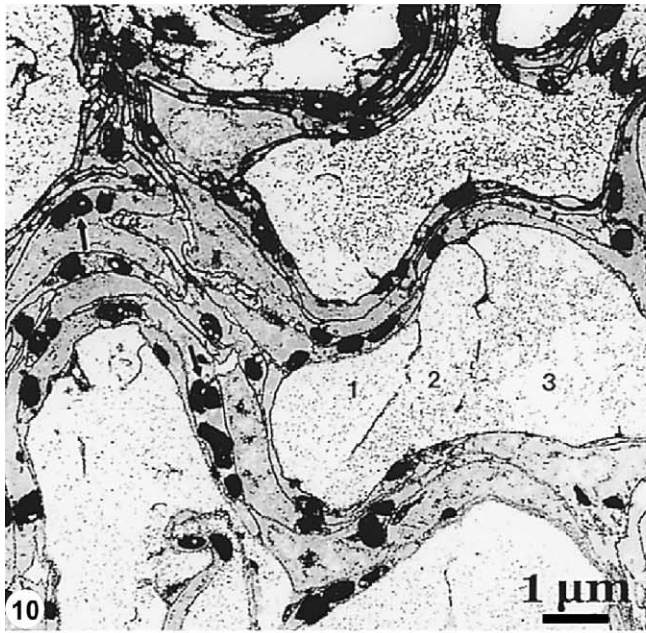
Figs 10–13   Carbohydrate cytochemistry of the epidermis. TEM. **Fig. 10** PAS reaction with methenamine-silver in tangential section of epidermis. Note scattered and generally weak reaction in mucocytes. Most dense silver deposits are confined to vesicles of surrounding support cells (e.g. arrows). Only traces of locular structure within the mucosecretory material are demonstrated (e.g. 1–3). The tissue is not osmicated. **Fig. 11** LID reaction of undischarged mucocyte (longitudinal section). Mucus stains as a dark, coarsely fibrous network; dark and thickened regions suggest locular compartments. Small vesicles in apical portions of support cells (arrows) are also stained; nuclei (n) stain in both experimental and control material. mes, mesoglea. **Fig. 12** HID preserves and stains mucus locular structure and contents, seen as regions of differing density of microfibrillae within the secretory material (tangential section). Note stain also occurs in apical vesicles of support cells (arrow) and in nuclei (n) as a false-positive reaction. Spirocyst-like cnida (sp). **Fig. 13** HID-treated mucus cell in explosive apocrine discharge. Note loss of locular definition, uniformity of stain, and formation of mucofibrils as secretory material discharges from the apical cell surface. Adjacent support cell with microvilli (mv) and kinocilium (k) containing diamine-positive vesicles (arrows) are not discharged. Spirocyst-like cnida (sp).
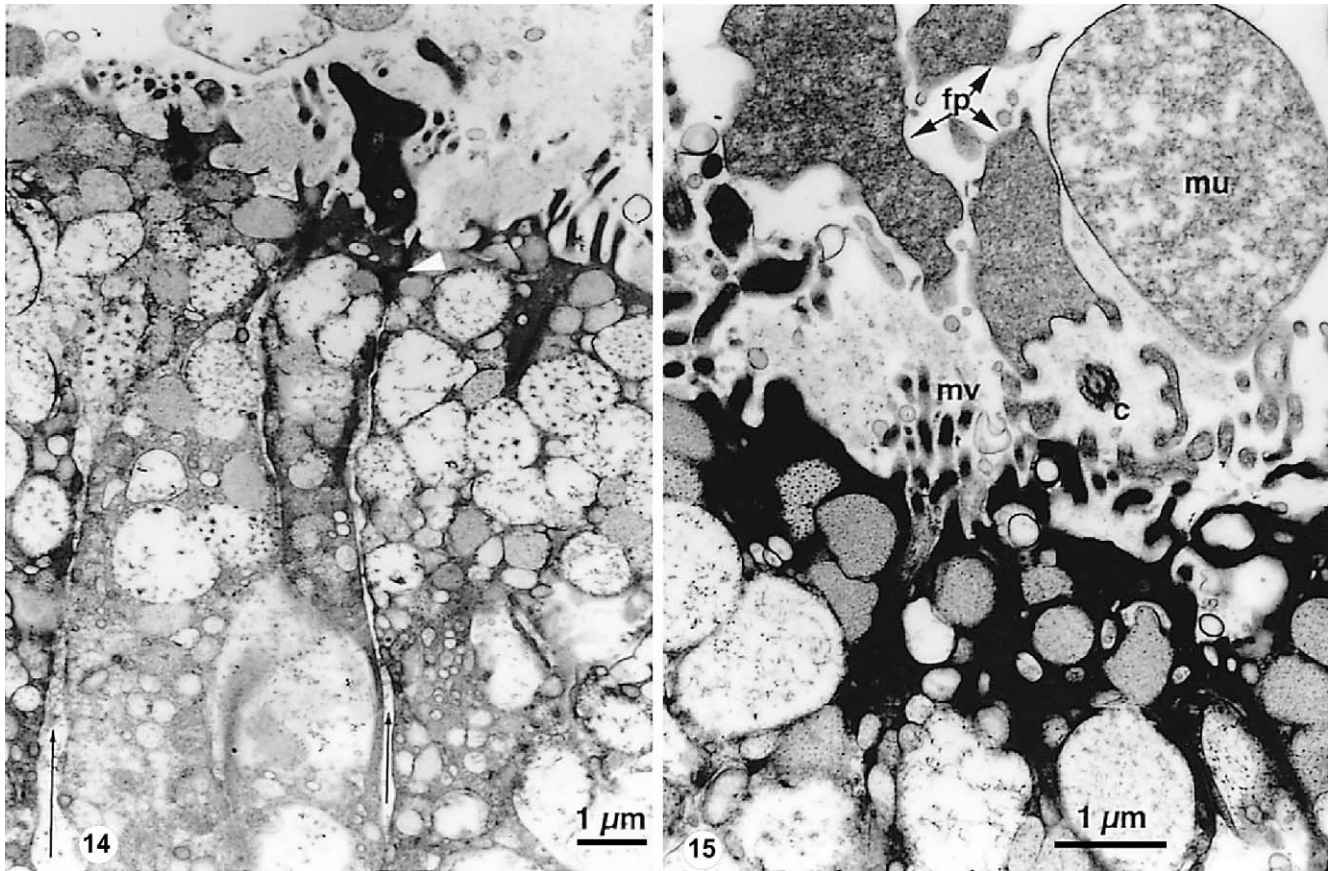
Figs 14 & 15   Discharge of electron-opaque substance in cross-sections of unanesthetized fed material. TEM. **Fig. 14** Electron-opaque, cytoplasmic channels of secretory cells (cf. Fig. 9) appear to be empty (arrows) coincident with discharge of electron-opaque material onto the epidermal surface. Tight junctions of support cells (e.g. arrowhead) are intact; discharge point of secretory cell material is unknown. **Fig. 15** Discharged electron-opaque substance coats the microvilli (mv) and cilia (c) of the epidermal surface. Mucus discharge (mu) and food particles (fp) stained with Cuprolinic blue are also adjacent to the epidermis.

The dense ciliation typical of the epidermis appears to be due almost entirely to a single type of cell with a short rootlet and a kinocilium 10–15 μm long (Fig. 9) surrounded basally by a spiral circlet of microvilli (Fig. 8). Microvilli also appear over much of the apical surface of these cells, in addition to those around the cilium. The role of these microappendages in feeding remains to be evaluated. The cytoplasm stains orthochromatically with Toluidine blue, unlike the mucus cells. The apical portions contain a variety of small vesicles containing diffuse flocs (Fig. 9), which are strongly PAS positive and also react strongly with both LID and HID (Figs 11–13). These inclusions did not appear to discharge during the feeding episode, but a secretory function cannot be ruled out. The ciliated cells are therefore referred to tentatively as support cells.

The ciliated cells are usually intertwined with narrow, sinuous cells with an electron-opaque cytoplasm containing strands of vesicles. These cells are often less than 1 μm wide (Fig. 9) and their contents do not react strongly with any of the cytochemical reagents used. When the colony is stimulated with food, electron-opaque material of unknown composition is discharged to the surface, covering cilia and microvilli (Figs 14 & 15). The dark cytoplasm, while closely associated with the ciliated cells, is separate from them as shown later.

Inner epidermal cells

The inner epidermis is associated primarily with the mesoglea, although outer epidermal cells are anchored therein as well. Epitheliomuscular cells (EMCs) become prominent basally and expand as they become embedded in the mesoglea (Fig. 16). The cytoplasm is vesiculate and muscle filaments are weakly developed. Their nuclei can be found a few microns above the mesoglea (Fig. 16, inset), but beyond that, the cells become attenuated and difficult to follow with certainty. In no case could EMC be distinguished near the epidermal surface.

Opaque cytoplasmic strands, extensions of the secretory cells, can be seen especially well in anesthetized material, extending to the mesoglea, then expanding laterally as they anchor themselves within it (Fig. 16). The same material appears to take a circuitous route around the mucus cells and can be traced close to the epidermal surface near the support cells where they discharge. The point of discharge has not been determined. The nuclei of these electron-opaque secretory cells are located above the mesoglea near those of the EMC and neurons (Fig. 17, inset).

The inner epidermal layer of the oral region is significantly different from the rest of the epidermis in the development of the nervous system. The nerve cell nuclei (Fig. 17),
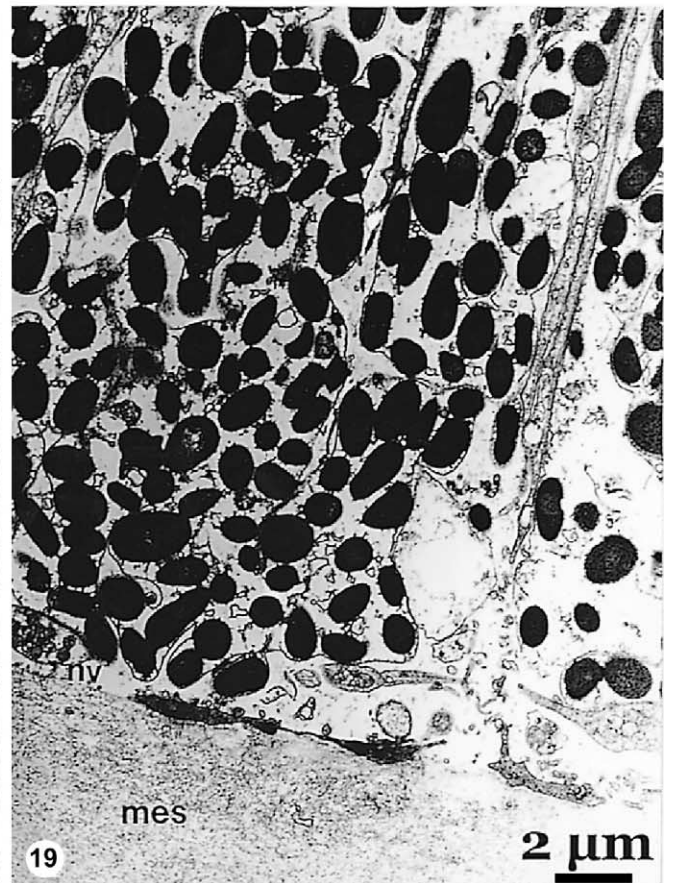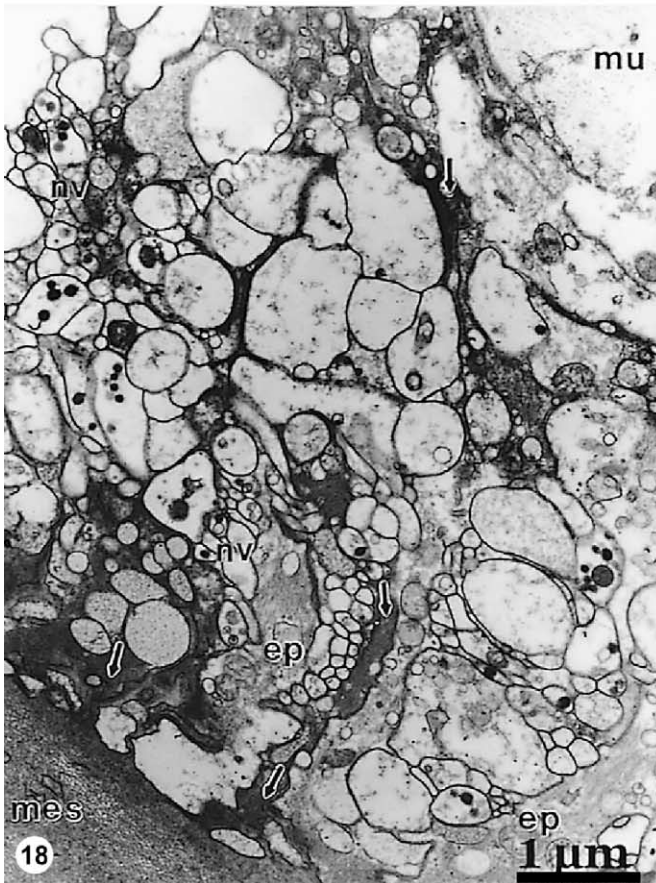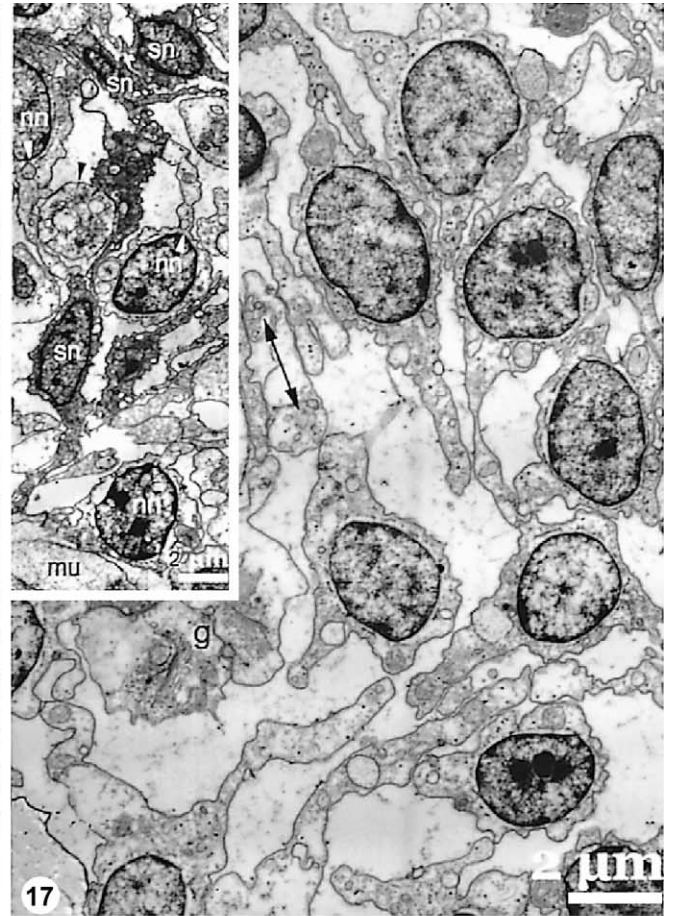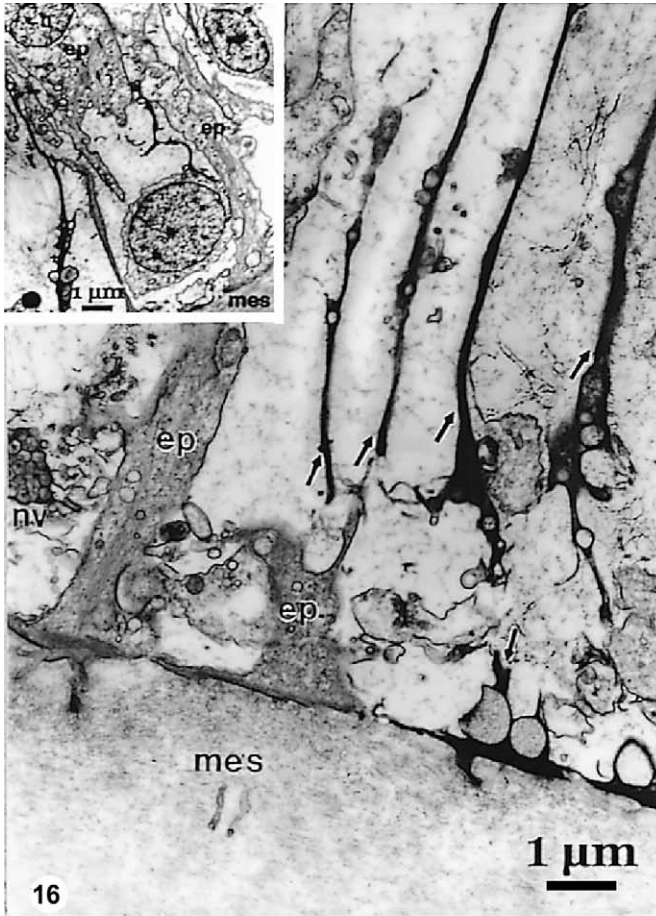
Figs 16–19   Cell structure of the inner epidermis. TEM. **Fig. 16** Inner epidermis longitudinal section showing bases of epitheliomuscular cells (ep) and electron opaque extensions of secretory cell cytoplasm (arrows) some of which display mesogleal anchorage. Neurites with dense-cored neurosecretory vesicles (nv) can be found but are not prominent here. mes, mesoglea. Inset: epitheliomuscular cells and nuclei (n) are closely associated with mesogleal layer. Anesthetized unfed material. **Fig. 17** Cluster of nerve cell nuclei (cross-section) several microns above the mesoglea showing neurite origins. Clear vesicles (double arrow) at neuro-neuronal contact. Golgi (g). Inset: nuclei of sinuous secretory cells (sn) with surrounding dark cytoplasm, and those of adjacent nerve cell nuclei (nn) are common near the basal regions of mucus cells (mu). Neurites are at arrowheads. **Fig. 18** Nerve plexus tengential section in the oral region of the inner epidermis showing neurites containing neurosecretory vesicles (nv). Basal processes of secretory cells (arrows) and epitheliomuscular cells (ep) traverse the plexus but synapses are not clearly delineated. Mucus cell (mu) mesoglea (mes). Unanesthetized-fed material. **Fig. 19** Longitudinal section of electron-opaque pigment granules in inner oral epidermis. mes, mesoglea; nv, neurosecretory vesicles.

like those of the epitheliomuscular cells, lie a few microns above the mesoglea. The number of processes per cell has not been determined, but neurite contacts with the basal and medial regions of the secretory and mucus cells are common (e.g. Fig. 17, inset). Golgi and 1.5–2.0 nm vesicles occur frequently within the neurites, but most of the contacts are '*en passant*'; clearly defined synaptic connections appear to be uncommon but have not been sought specifically with serial sections. Neurotubules are rarely observed in this material.

Cross-sections of the oral regions of the inner epidermis are characterized by well-developed neurite clusters in contact with EMC and secretory cells (Fig. 18). Small, dense-cored, electron-opaque and electron-lucent vesicles typical of cnidarian neurosecretory granules (van Marle, 1977; Goldberg & Taylor, 1989; Westfall & Sayyar, 1997) are also present. Since the nervous system has not been the primary focus of this paper, it is unclear whether the neurosecretory cells are distinct from ganglion cells, hence these terms are not used. The EMC near the oral region, while more numerous than elsewhere in the epidermis, contain similar thin and poorly developed myofibrils.

The inner epidermis of the oral region is also characterized by clusters of electron-opaque granules 2.0 ± 0.2 µm long and 1.1 ± 0.1 (SD) µm wide ($n = 20$). These have a fibrous core and become electron opaque with osmium used in conjunction with imidizole and phenylenediamine, or when osmium is followed with uranyl acetate and lead citrate (Fig. 19). They also stain with acidic PTA, perhaps suggesting that they contain lipid and protein. These granules are not HID or LID positive, and are only occasionally PAS positive and therefore may not contain large amounts of carbohydrate. Granules are most abundant in the oral region, and are most likely the pigment responsible for the blue-green, circumoral color seen in living material. Similar pigment granules have been described in the lower epidermis of another deep water coral species (Schlichter & Brendelberger, 1998), and in the gastrodermis of a second species, where they are closely associated with zooxanthellae (Schlichter & Fricke, 1991).

Discussion

The feeding experiments were conducted in a concrete enclosure without flowing seawater. It was clear that material settling onto the colonial surface was trapped in mucus and gathered as described. It does not appear that digestive filaments remain outside the animal long enough to employ them primarily for extracoelenteric digestion as suggested by Yonge (1930), but they might with larger food particles than those tested. Other feeding modalities might be employed on the reef. It is possible that *M. reesi* can suspension feed by projecting filaments and/or mucus nets above the colony into the reef boundary layer. Further observations should be made of feeding behavior under natural conditions.

Seven types of cells have been recognized so far in *M. reesi*, although others, e.g. sensory cells, remain to be identified. Overall, the architecture of the epidermis is simple, as summarized in Figure 20. Much of the simplicity may be attributable to the complete absence of tentacles and the loss of nematocysts, including the attendant sensory cells, their surface microappendages and neural connections. How the structure of *M. reesi* compares to other species of *Mycetophyllia* is not clear. Rows of polyp tentacles and their nematocysts have been described generally in the type species of this genus, *M. lamarckiana* (Matthai, 1928). However, a skeletal specimen deposited by Matthai in the U.S. National Museum (USNM 95480) was identified as *M. danaana* by S. Cairns (pers. comm.). Unfortunately, the colony from which Matthai took histological samples has been misplaced. A photograph of *M. danaana* (Veron, 2000a) clearly shows rows of tentacles associated with the polyps, suggesting that Matthai was examining that species when he found type II (microbasic mastigophores) and type I (spirocysts) cnidae differentially distributed within small batteries. This interpretation of Matthai's cnidae types is in agreement with that made by Lang and Chornesky (1990). Tentacles in *M. lamarckiana* appear to be confined to the margin of the colony and are not associated with the polyps (Cairns, 1982). Tentacular nematocysts in that species and in the other species of *Mycetophyllia* have not been described.

The atentaculate *M. reesi* may be unique among western Atlantic corals, although there have been suggestions that this condition may exist in a few Indo-Pacific species. The agariciid *Leptoseris fragilis* Edwards and Haime and the pectiniid *Mycedium elephantotus* (Pallas) have been reported as atentaculate (Schlichter, 1991; Schlichter & Brendelberger, 1998). However Veron (2000b; personal communication) has observed that most members of these genera have tentacles that appear only at night, including *M. elephantotus* specifically. Thus Schlichter and Brendelberger's finding that *M. elephantotus* epidermis contains an abundance of mucocytes and near absence of nematocysts may have to be re-evaluated. Similarly, Yonge (1973) could find no trace of tentacles in the agariciid *Pachyseris speciosa* (Dana), but
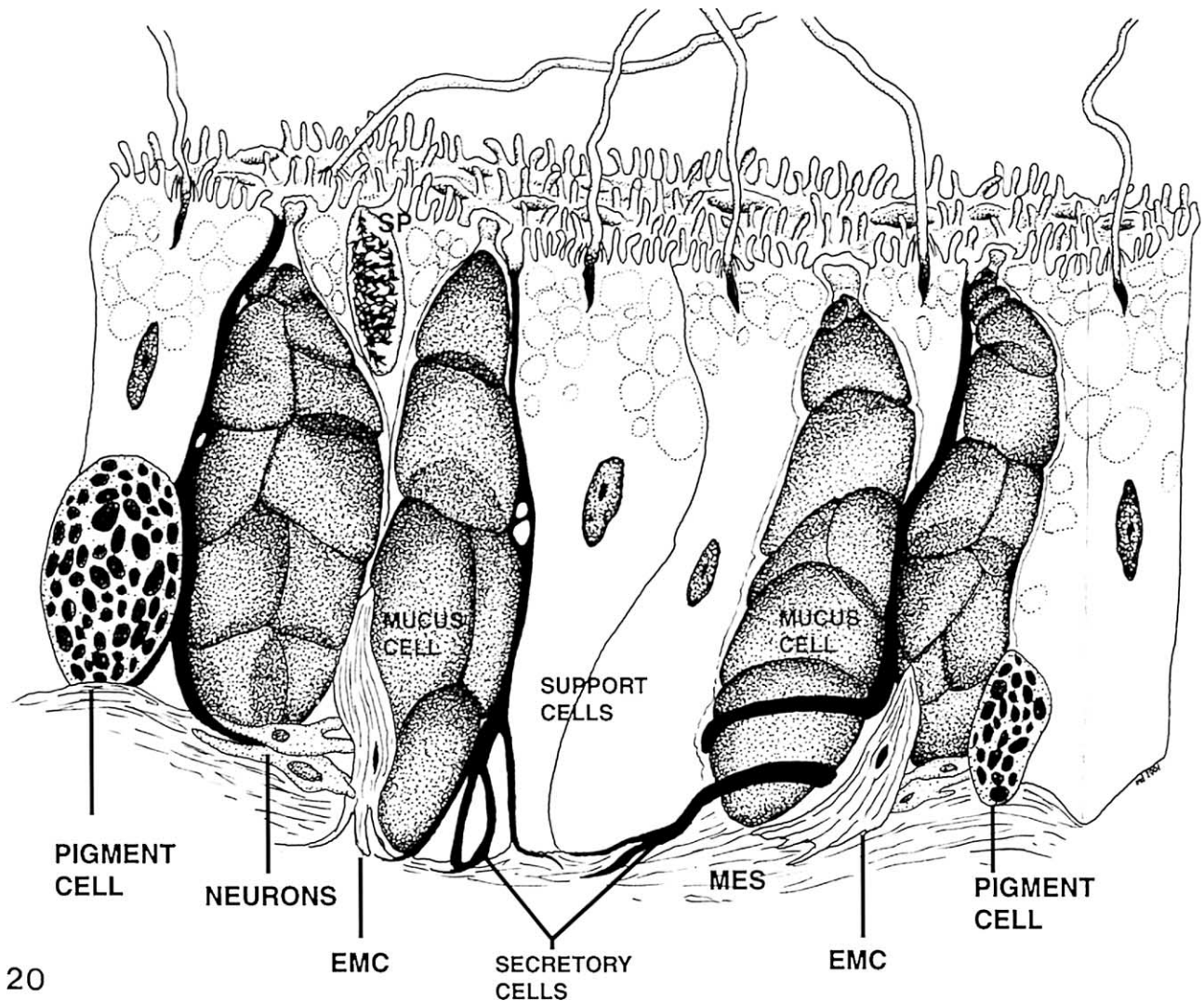
Fig. 20 Illustration of *M. reesi* epidermis showing approximate position and relationships of cell types. sp, spirocyst-like cnida. emc, epitheliomuscular cell. mes, mesoglea.

cautioned that full expansion may not have been observed. After observing full expansion in an aquarium specimen, Veron (personal communication) found that *P. speciosa* does indeed possess tentacles. Although aquarium observations are still needed to confirm its external morphology, *M. reesi* has been recorded at night and after anesthetization, and appears to be an unusual, atentaculate scleractinian.

Types of mucus cells

Marine invertebrate mucus cells have a diversity of structures, inclusions, and secretions (e.g. Storch & Welsch, 1972). Epidermal mucus cells among hydrozoans and scyphozoans are limited in their occurrence among species, restricted in their distribution within species, and appear to occur only in spumous form. Spumous mucus cells are common in planula larvae (reviewed by Thomas & Edwards, 1991) and in the integument of polyps (Hentschel & Hündgen, 1980).

In contrast, anthozoan mucocytes appear to be characteristic of the epidermis, although few studies have examined their ultrastructure. These studies suggest that mucus cells are of two general types. Those with large, polygonal spumous inclusions such as in *M. reesi*, are most easily recognized although some cells exhibit smaller, more condensed versions of foamy secretory material (Kawaguti, 1966; Lyons, 1973; Goldberg & Taylor, 1989). Histochemical reactions to Toluidine blue or PAS suggest their contents may include either acidic or neutral carbohydrate components.

Other anthozoan mucocytes contain several types of intracellular, electron-opaque granules that stain histochemically as a mixture of neutral and acidic components (Crawford & Chia, 1974). Lyons (1973) described three types of granular secretory cells in addition to the spumous type in a planula larva. Two of these were filled with granules that were either uniformly or variously electron opaque. The granules in both cases displayed metachromasia with Toluidine blue and were PAS positive suggesting that they contained mucopolysaccharide. These electron-opaque cells cannot generally be distinguished from other secretory types without

cytochemical characterization. Considering the dramatic differences in carbohydrate histochemistry reported in the present study, it would be instructive to examine coral mucus cells routinely with diamine stains.

Secretion mechanisms

Three types of secretory processes are often distinguished.

In merocrine extrusion or exocytosis, vesicles fuse with the cell membrane, discharging their contents with no membrane discontinuity. In apocrine extrusion the apical membrane is breached and some cytoplasm is lost along with secretory material. Holocrine secretion is characterized by the breakdown and release of entire cells or discharge of their cytoplasm and secretions (e.g. Welsch & Storch, 1973). Vertebrates typically secrete mucus exocytotically, while pulmonate molluscs discharge by apocrine secretion, and hagfish by holocrine mechanisms (Deyrup-Olsen & Luchtel, 1998). Apocrine secretion has been suggested as a means of mucus cell discharge in hydrozoans (Thomas & Edwards, 1991). Judging from the details given in this study, it would appear that apocrine secretion describes the process in *M. reesi* as well.

Secretory products and functions

Coral mucus, like mucus generally, contains a variety of proteins, carbohydrates, and lipids. Although several investigators have examined the composition of coral mucus (Ducklow & Mitchell, 1979; Daumas et al., 1981; Coffroth, 1990), few have included the contribution of acidic glycans. Meikle et al. (1988) found that while the mucus of all six species they studied contained acidic and sulfated glycans, their overall contribution was minor compared to neutral sugars and protein. On the other hand, Krupp (1981, 1985) found the polysaccharide component to be the dominant fraction in the mucus of *Fungia scutaria* Lamarck, with sulfated polysaccharide as the most prominent type. Krupp (1985) further suggested from immunological cross-reactivity, that such materials may be an important component of coral mucus. Mucocyte inclusions have also been characterized histochemically as acidic carbohydrate by Goreau (1956) and Van-Praët (1977). Goreau's work is particularly significant in that he examined the epidermis of 32 coral species by optical microscopy and found the mucus inclusions to be PAS negative, but intensely metachromatic, suggesting that acid mucopolysaccharides are a more ubiquitous component of coral mucus than is indicated by the chemical analyses cited earlier. Moreover, his description of acidic mucus secretion as 'typical of corals' is consistent with that of *M. reesi* given here.

Histo-/cytochemical analysis of *M. reesi* while not quantitative, suggests that the acidic component is an important part of mucus secretion. Ruthenium red is often employed to fix acidic polysaccharides, and while it is not specific for them, it does seem to display a higher affinity for sulfated polysaccharides (Eisenstein et al. in Hayat, 1993). Cellular components that react with the LID reagent are likely to be acidic or sulfated mucosubstances and while reactivity does not distinguish the two, LID does not bind to neutral polysaccharides (Spicer, 1965). Traditional Alcian blue staining at different pH levels also supports the presence of both components. The HID method, on the other hand, is allegedly specific for sulfated glycans (Spicer et al., 1978; Hayat, 1993) and does not react with sialic or hyaluronic acid or neutral mucosubstances.

While the characterization of mucus secretion into neutral, acid or sulfated polysaccharide is helpful in a biochemical comparison of properties, the functional distinctions are unclear. It has been suggested that acidic mucopolysaccharides may raise the viscosity of mucus (Bubel, 1984) or may function as ion barriers, either selectively or by buffering abrupt external environmental changes (Welsch et al., 1984).

Mucus secretion by corals is known to have a number of functions. Yonge (1930), Abe (1938) and Lewis and Price (1975) have made clear the taxonomically broad role mucus plays in the entrapment of food. Additional functions include a role in extracorporeal digestion (Tiffon, 1975), cleansing and removal of sediment (Duerden, 1906; Schumacher, 1977; Telesnicki & Goldberg, 1995; Reigl & Branch, 1995), protection against desiccation (Krupp, 1984), UV radiation damage (Drollet et al., 1997), and resistance to changes in salinity and temperature (Marcus & Thorhaug, 1982; Kato, 1987). It has been suggested that mucus discharge may accompany bioluminescence in some species (Crawford & Chia, 1974) and may play a role in recognition of self (Tidball, 1984) or function as an immune cloaking device (Bigger, 1976). Toxic–paralytic substances may also occur in mucus, as in certain ctenophores (Horridge, 1974). The toxicity of coral mucus has been suggested as a means of interspecific competition among some corals, and cytotoxicity has been demonstrated using purified preparations (Fung et al., 1997). An analysis of coral mucus from an ecochemical perspective should provide a clearer understanding of its manifold roles.

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