FOLIA PARASITOLOGICA 43: 277–286, 1996

Ultrastructure of the gastrodermis and posterior gut pockets of *Concinnocotyla australensis* (Platyhelminthes, Monogenea, Polystomatidae) and comparison with another polystomatid, *Neopolystoma spratti*

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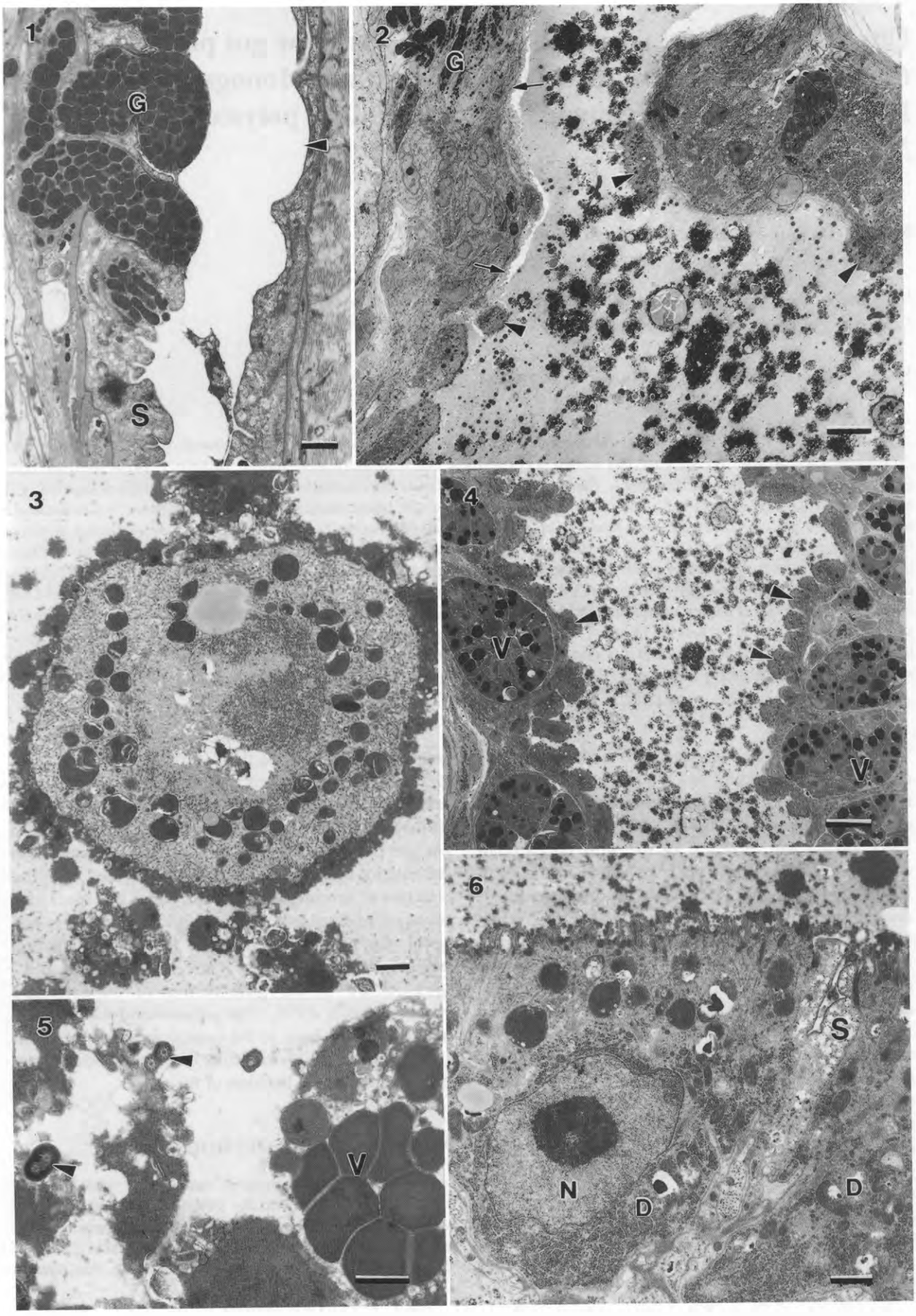
Key words: gastrodermis, ultrastructure, Polystomatidae, Platyhelminthes

Abstract. While the majority of polyopisthocotylean monogeneans feed on blood, some polystomatids infecting chelonians do not. This study examined the gastrodermis of two polystomatids, one – *Neopolystoma spratti* Pichelin, 1995 – from the conjunctival sac of a chelonian and the other – *Concinnocotyla australensis* (Reichenbach-Klinke, 1966) – from the oral cavity, gill arches and primary gill lamellae of a fish, and also found no evidence of blood feeding. However, the gastrodermal architecture in both species basically resembles that found in blood feeding polyopisthocotyleans, with alternation of lamellated digestive cells and an intervening syncytium. In *C. australensis*, oesophageal secretion appeared to be responsible for initial extracellular digestion and this was followed by pinocytotic uptake of partly degraded material in pits between the numerous apical lamellae of digestive cells. Posterior dorsolateral gut pockets unique to *C. australensis* were shown to be blind sacs separated from the external environment by a narrow cytoplasmic bridge, composed of a thin layer of tegument apposed to a thin layer of pocket syncytial epithelium. The pockets are lined with greatly folded syncytium and set in a "capsule" of tissue in which numerous protonephridial flame cells are embedded. It is suggested that the pockets have an osmoregulatory function related to the particular environment and evolutionary history of the host, the primitive lung fish (Dipnoi) *Neoceratodus forsteri* (Krefft, 1870).

Monopisthocotylean monogeneans are known to feed on host epidermal tissues and mucus (e.g. Kearn 1963) and the ultrastructure of their gastrodermis is simple, exhibiting only one cell type (Halton and Jennings 1965, Halton and Stranock 1976). Most polyopisthocotyleans, however, feed on host blood (Kearn 1963, Halton and Jennings 1965), and the gastrodermis is more complex, consisting of two distinct cell types, known as digestive cells and connecting syncytium. Representatives of the Polystomatidae infecting anuran amphibians also feed on blood, while those infecting chelonians and a mammal probably do not (Tinsley 1974). Allen and Tinsley (1989) investigated the gastrodermis of several polystomatid monogeneans infecting chelonians, using histochemistry, X-ray microanalysis and electron microscopy and concluded that these polystomatids have diverged nutritionally from all other polyopisthocotyleans so far studied, in that blood is not a significant part of their diet. Pichelin et al. (1991) erected a new subfamily (Concinnocotylinae) for the polystomatid *Concinnocotyla australensis* (Reichenbach-Klinke, 1966) Pichelin, Whittington et Pearson, 1991, which inhabits the oral cavity, gill arches and primary gill lamellae of the Australian lungfish. Pichelin et al. (1991) reported that there appeared to be no haematin in the gut of this species and they also described a unique pair of gut pockets, one joining each caecum posterior to the testes and communicating with the exterior by a dorsal duct. We investigated the ultrastructure of several regions of the gut of this species, to ascertain whether or not it is sanguinivorous and to discover the nature and possible function of the gut pockets. For comparison, we also briefly examined the ultrastructure of the gastrodermis of *Neopolystoma spratti* Pichelin, 1995. This polystomatid has a chelonian host but it lives in the conjunctival sacs, whereas those chelonian polystomatids previously studied inhabit the mouth and bladders of their hosts.

MATERIALS AND METHODS

Specimens of *Concinnocotyla australensis* were collected from a lungfish (*Neoceratodus forsteri* (Krefft, 1870)) found in Enogerra Creek, Queensland, Australia. The parasites were cut into pieces and fixed in 2.5 % glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.4 at 4°C for 6–8 h. Post-fixation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for 2 h in 1 % OsO_4 in buffer was followed by dehydration in ethanol and embedding in Spurr resin. Ultrathin serial sections were cut from three body regions: longitudinal sections through the pharynx, oesophagus and caeca to just below the level of the first testes; transverse sections through the mid body region including the two caeca, testes and vitellarium; and oblique transverse and longitudinal sections through the posterior body anterior to the opisthaptor and including the caeca and gut pockets.

Specimens of *Neopolystoma spratti* were removed from the conjunctival sacs of the freshwater turtle *Chelodina longicollis* (Shaw, 1794), collected in dams in the Armidale district (NSW, Australia) and fixed for 3 h at 4°C in 3 % glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.3). After buffer washing, specimens were post-fixed in 1 % OsO_4 in buffer for 1 h at room temperature, dehydrated in an alcohol series and embedded in Spurr resin. Ultrathin serial transverse sections were cut through the body in the region of the posterior pharynx, mouth canal to oesophagus to caeca, and continued through most of the testis and the adjacent caeca. Sections from both species were stained with uranyl acetate and lead citrate and examined with a JEOL 1200EX electron microscope at 60 kV.

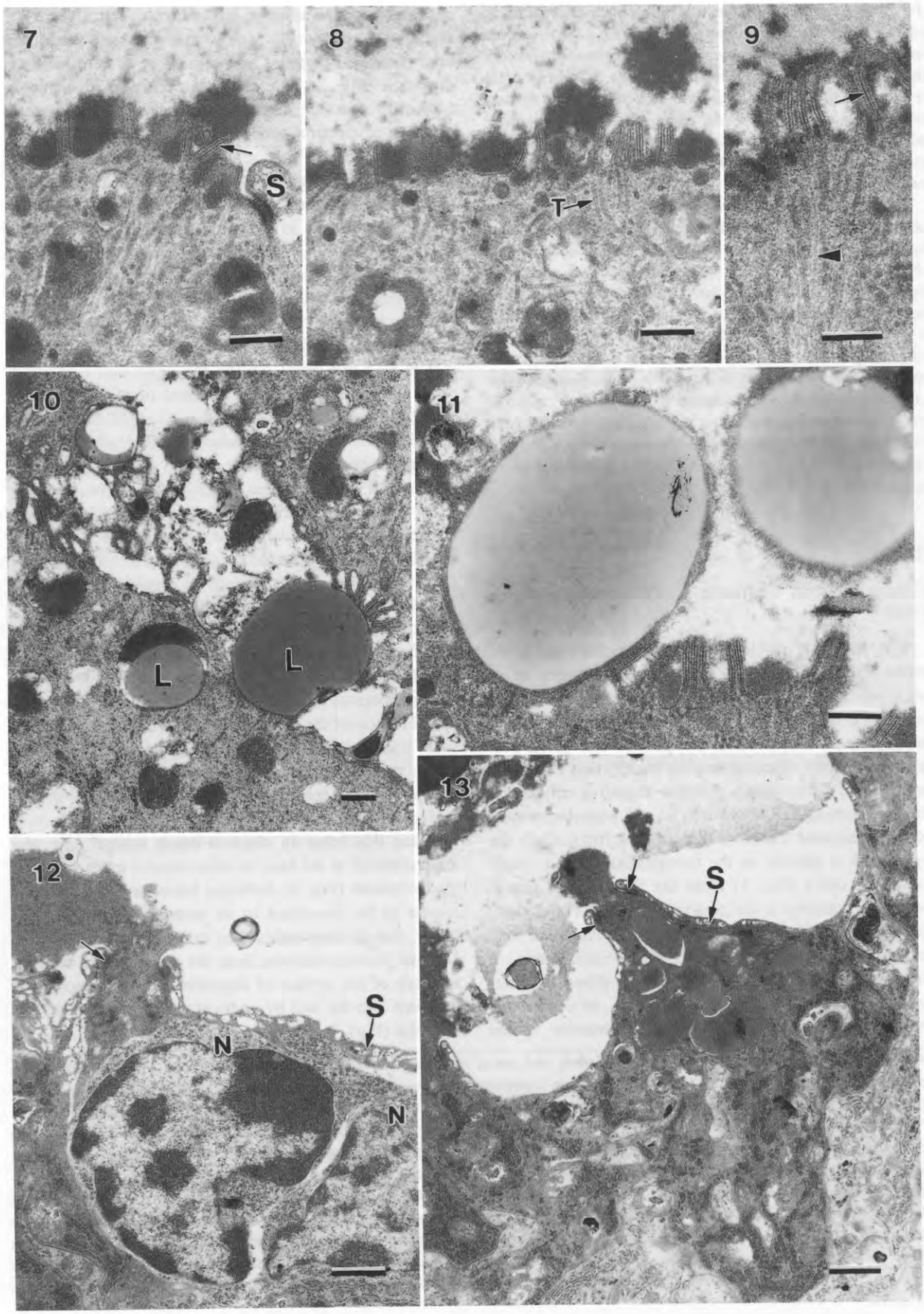
RESULTS

Concinnocotyla australensis (Reichenbach-Klinke, 1966)

The intestine of *Concinnocotyla australensis* comprises a short oesophagus and two tubular caeca which are confluent just anterior to the opisthaptor. Each caecum has a short anterior diverticulum near the pharynx and a conspicuous dorsolateral pocket near to its posterior extremity. Throughout the caeca, two cell types are present: conspicuous globular digestive cells and a thin intervening layer in which no cell boundaries were seen – presumed therefore to be a syncytium. Only the syncytium is present in the oesophageal region, punctuated by ducts (Fig. 1) from the oesophageal glands which lie posterior to the pharynx (Fig. 2). These gland ducts are lined with microtubules, and surrounded by a septate junction adjacent to the oesophageal lumen. In the specimen sectioned through this region, the ducts were not discharging and there were no contents in the lumen in this region (Fig. 1). Posterior to the oesophagus at the anterior end of each caecum, there are scattered digestive cells, and in this specimen the lumen here contained material in the process of extra-cellular digestion (Fig. 2). The contents consisted of aggregations of ingested material surrounded by numerous globules of electron-dense material with diffuse boundaries (Figs. 2–4). This material was present within a "soup" of much lighter appearance that was connected to the apical surfaces of all the digestive cells but remained unattached to the intervening syncytial surface (Fig. 2). Within the caeca proper the digestive cells become more numerous until there is very little space between them occupied by the syncytium. From the level of the vitellarium to the posterior confluence of the caeca, the lumen is surrounded by digestive cells attached to a thin basal lamina and separated from each other by a relatively small amount of syncytial cytoplasm (Fig. 4). Gut contents also changed further posteriorly, with more amorphous material visible, as well as some sperm and vitelline packets (egg shell granule clusters) in various stages of degradation (Fig. 5) posterior to the entrance of the genito-intestinal canal. Large droplets, presumed to be lipid, were also observed in the lumen, attached to the surface of digestive cells and within the cytoplasm of digestive cells (Figs. 10, 11).

The globular-shaped digestive cells (Figs. 2, 4, 6) each have a basal nucleus with prominent nucleolus surrounded by clumps of polyribosomes, mitochondria, Golgi apparatus and endoplasmic reticulum. The mid to apical region of the cell is filled with numerous vesicles with contents ranging from homogeneous electron-dense to heterogeneous with lighter regions, to condensed material resembling myelin bodies. The lumenal surface of these cells (Figs. 6–11) is covered with short lamellae that have an electron-dense central core and are connected at the base to microtubules extending into the cytoplasm (Fig. 9). Between lamellae, pitted regions appear to be connected to an extensive system of tubules, that in turn appears to connect to the vesicles. Diffuse globular material from the caecal lumen adheres to much of the surface of digestive cells and appears to be taken into the cell by endocytosis from pits between lamellae (Figs. 7, 8, 11).

←**Figs. 1–6.** Electron micrographs of gastrodermis and caecal inclusions of *Concinnocotyla australensis*. **Fig. 1.** Oesophageal region showing gland ducts (G) filled with secretion penetrating the syncytial lining (S). **Fig. 2.** Longitudinal section of the anterior caecal region just below the oesophagus. Note ingested material surrounded by floccular globules (secretion granules?) in "soup" of lighter material that does not adhere to the syncytium (arrows) but is attached to the sparse digestive cells (arrowheads). Also note oesophageal glands (G). **Fig. 3.** An ingested particle completely surrounded by floccular globules assumed to be oesophageal secretion. **Fig. 4.** Longitudinal section of the caecum at the anterior level of vitellarium. Note gut contents and closely spaced digestive cells lining the lumen (arrowheads). Caeca at this level are completely surrounded by vitelline follicles (V). **Fig. 5.** Gut contents below the entrance of the genito-intestinal canal include sperm (arrowheads) and shell granule clusters (V) in various stages of degradation. **Fig. 6.** Part of two digestive cells (D) and intervening syncytium (S) resting on basal lamina. Note basal nucleus (N), surrounded by ribosomes, mitochondria and endoplasmic reticulum, numerous vacuoles with dense or condensed contents and numerous, short apical lamellae. Scale bars 1μm (Figs. 1, 3, 5, 6), 10 μm (Fig. 2), 20 μm (Fig. 4).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The syncytium separating digestive cells from one another also rests on the basal lamina of the gastrodermis. Very few nuclei of this layer were seen and the cytoplasm is electron-lucent with few organelles apart from many vesicles with scattered granular contents (Figs. 1, 6, 12, 13). The apical surface varies from relatively smooth in parts of the oesophagus (Fig. 1) and the main caecal regions (Fig. 6) to moderately folded in the lower oesophagus (Fig. 1) and anterior caeca (Fig. 2), to intensely lobed in the posterior gut pockets (Figs. 14, 15, 17, 18). The syncytial cytoplasm neither underlies nor overlies the digestive cell to any marked degree, and a ring septate junction surrounds each digestive cell at the apical boundary with the syncytium (Figs. 6, 7, 12, 13).

Several instances of apparent cellular extrusion were observed (e.g., Figs. 12, 13). In these situations the adjacent membranes of the syncytium were close together and cellular contents, mostly consisting of dense vacuoles and amorphous cytoplasm, appeared to be passing out through the narrow constriction. In one of these cases two cells resembling neoblasts lay beneath the extruding cell and similar unspecialised cells with large nuclei and little cytoplasm were seen scattered throughout the main intestinal region. However, in all the cases of apparent extrusion followed through serial sections, the cells were found, in fact, to be entire, and the apparent extrusion was due to a marginal view of the cell.

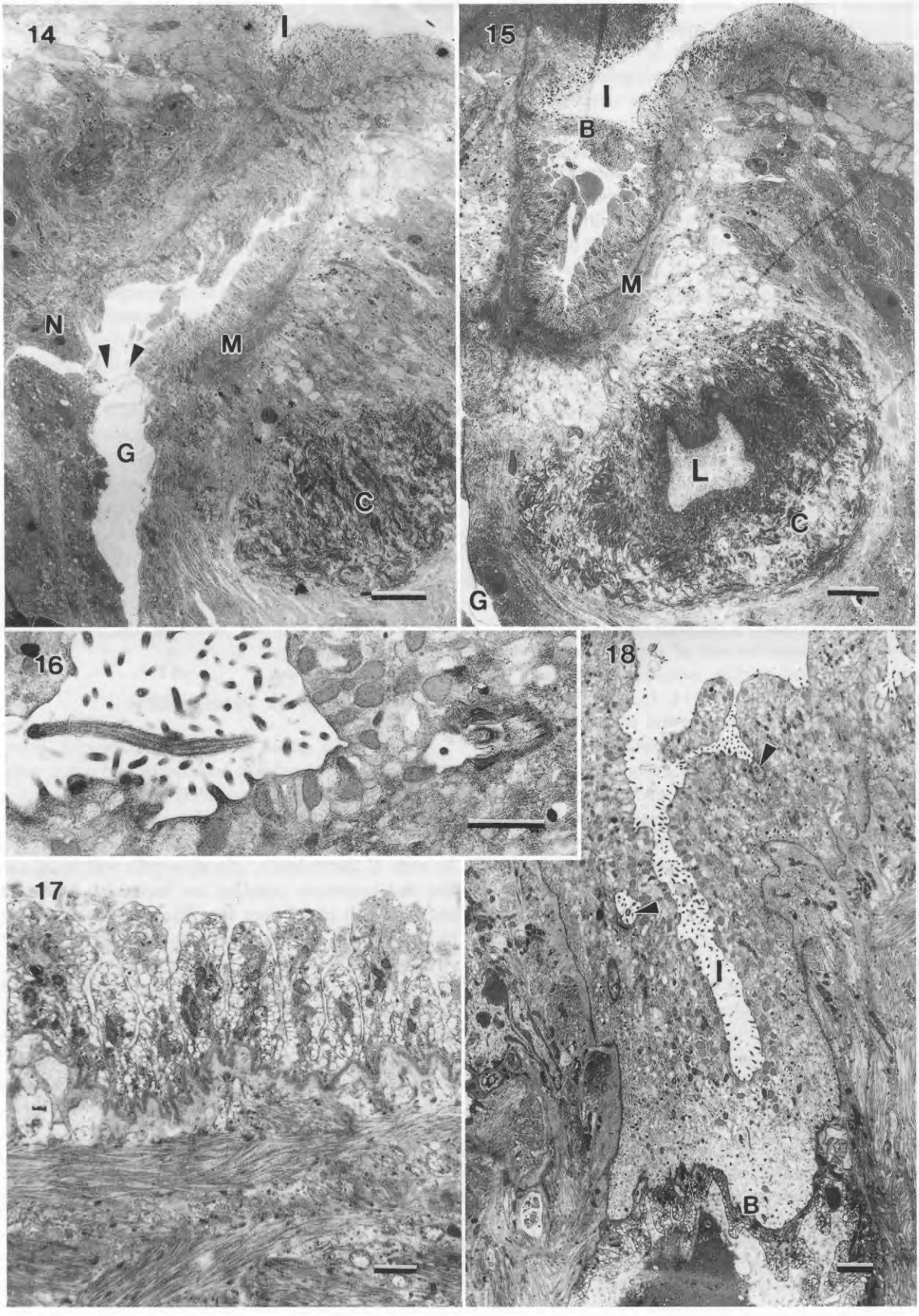
Near to the posterior end of each caecum, an enlarged dorsolateral pocket is connected through an opening to the caecum (Figs. 14, 15, 18). Each pocket has an irregular folded outline and is lined only with gastrodermal syncytium. The lumenal surface is also highly irregular, the syncytium being intensely folded and lobed thereby presenting an enormously increased surface area (Figs. 17, 19). Cytoplasm is packed with large numbers of vesicles, similar to those seen in much smaller numbers in the caecal syncytial cytoplasm, and mitochondria were seen in the basal cytoplasm. A nucleus was also present in the syncytium close to the pocket/gut boundary (Fig. 14). A portion of the pocket extends to close to the dorsal tegument. At this point the syncytial layer is extremely thin and is apposed to an equally thin layer of tegument within a deep invagination in the tegument (Figs. 15, 18, 19). This situation results in the appearance of a thin cytoplasmic bridge across what would otherwise be a canal leading from the caecum to the dorsal surface. Indeed, in light microscopic sections, it appears as a duct because the bridge is too thin for resolution. Two individuals were sectioned completely through this region with continuous serial ultrathin sections, proving unequivocally that there is no direct connection between the gut pocket and the exterior of the worm. Moreover, while there were contents in the pocket lumen, there was no cell debris or digestive remnants in the tegumental invagination or the adjacent external region. The region between the caecum and this bridge is surrounded by several layers of muscle fibres (Figs. 14, 15). The remainder of the gut pocket is not surrounded by muscles. Instead, the syncytium in these pockets rests on a thick basal lamina with a more dense region adjacent to the syncytium and with fingers from the outer, fibrous layer extending outwards from the pocket (Fig. 20). A distinct capsule is formed by the tissues surrounding the pocket – a layer comprising cellular processes rich in dense inclusions, and containing a large number of protonephridial flame bulbs (one visible in Fig. 20). Flame bulbs have a basal or lateral perikaryon, two rows of ribs (internal and external), internal and external leptotrichs and a pair of lateral cytoplasmic chords connected by a septate junction.

Cytoplasm of the tegumental invagination leading to the bridge resembled that of the adjacent tegument, with many vesicular inclusions and scattered microvilli. Two ciliate receptors with a number of electron-dense collars were seen about midway down in the invagination (Figs. 16, 18).

Neopolystoma spratti Pichelin, 1995

Neopolystoma spratti has a short oesophagus, bifurcate intestine not confluent posteriorly, and caeca without diverticula (Pichelin 1995). Although lacking diverticula, the caecal lumenal surface is greatly enlarged by multiradiate longitudinal grooves (Fig. 21). As with *C. australensis*, digestive cells with basal nuclei and numerous lamellae are separated from one another by an intervening syncytium with smooth surface (Figs. 21, 23, 24). Digestive cells contain many Golgi apparatus and mitochondria and are rich in vacuoles of irregular outline, with dense contents and some clear regions (Fig. 22). The apical surface is covered with numerous lamellae that have a similar dense core but are much longer than those of *C. australensis.* (Figs. 23, 24). They are also frequently seen to be loops connected at both ends to the cytoplasm (Fig. 24).

←**Figs. 7–13.** Electron micrographs of gastrodermis of *Concinnocotyla australensis*. **Figs. 7–9.** Details of the apical lamellae of digestive cells showing dense core of lamellae (arrows), microtubules attached to lamellae (arrowhead), partially digested material being taken in between lamellae, tubules (T) extending from the surface into the cytoplasm, and septate junction with adjacent syncytium (S). **Fig. 10.** Presumed lipid droplets (L) attached to and within digestive cells. **Fig. 11.** Presumed lipid droplet apparently being engulfed by digestive cell. **Figs. 12, 13.** Micrographs which appear to show cellular extrusion but serial sections revealed that these were marginal views of entire digestive cells. Note septate junctions (arrows) with syncytium (S), and unspecialised cells (N) (neoblasts?) beneath the syncytium in Fig. 12. Scale bars 500 nm (Figs. 7–11), 1 μm (Figs. 12, 13).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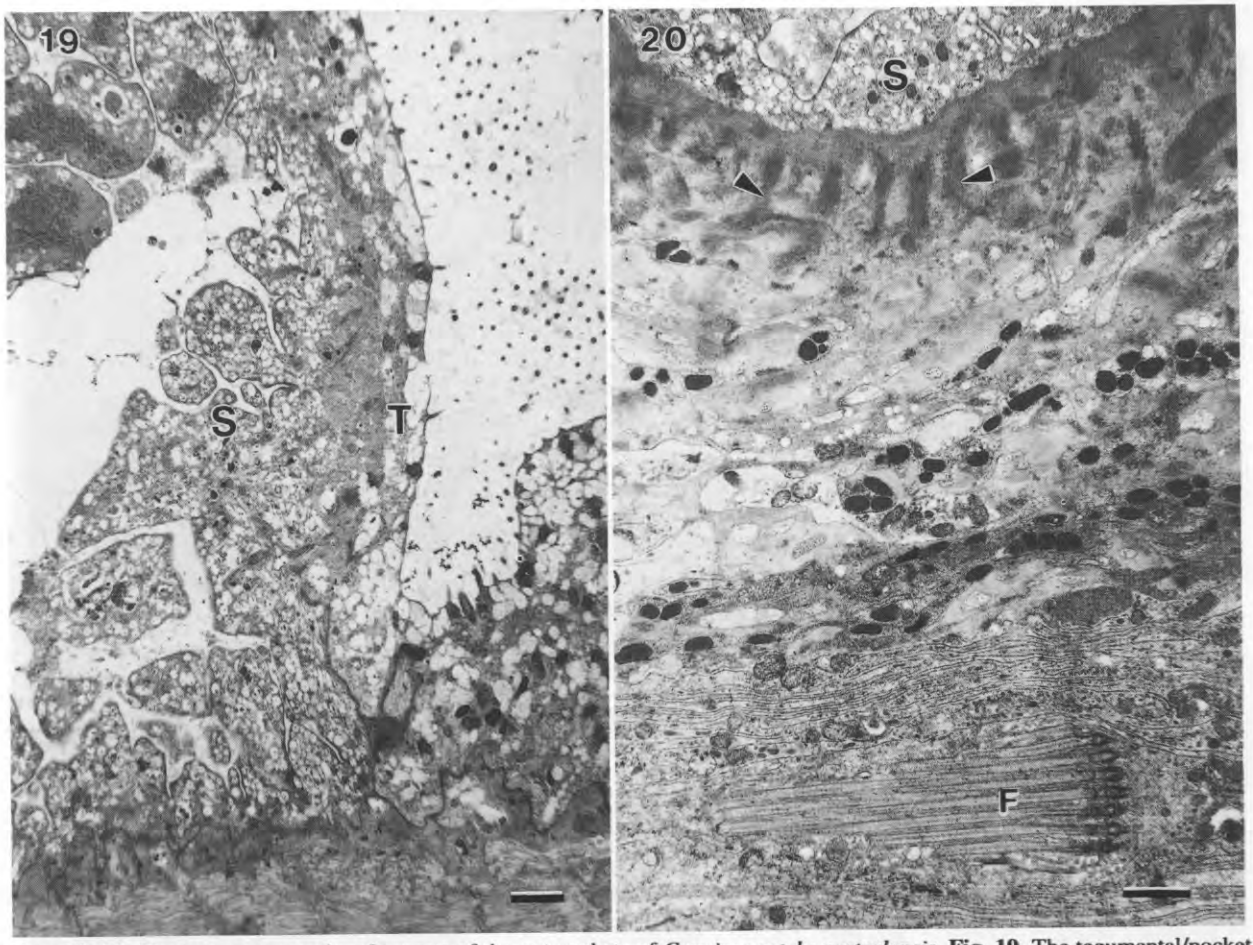


Figs. 19, 20. Electron micrographs of aspects of the gut pockets of *Concinnocotyla australensis*. **Fig. 19.** The tegumental/pocket bridge at its most narrow region. Note thin layer of tegument on the right (T) and folded syncytium (S) on the left with only the less electron-dense component of the basal lamina between them. **Fig. 20.** Section from the syncytial lining (S) of the pocket proper through part of the surrounding capsule which is extremely rich in flame cells (one shown – F). Note dense fingers (arrowheads) from the basal lamina extending into the surrounding tissue. Scale bars = 1 μm.

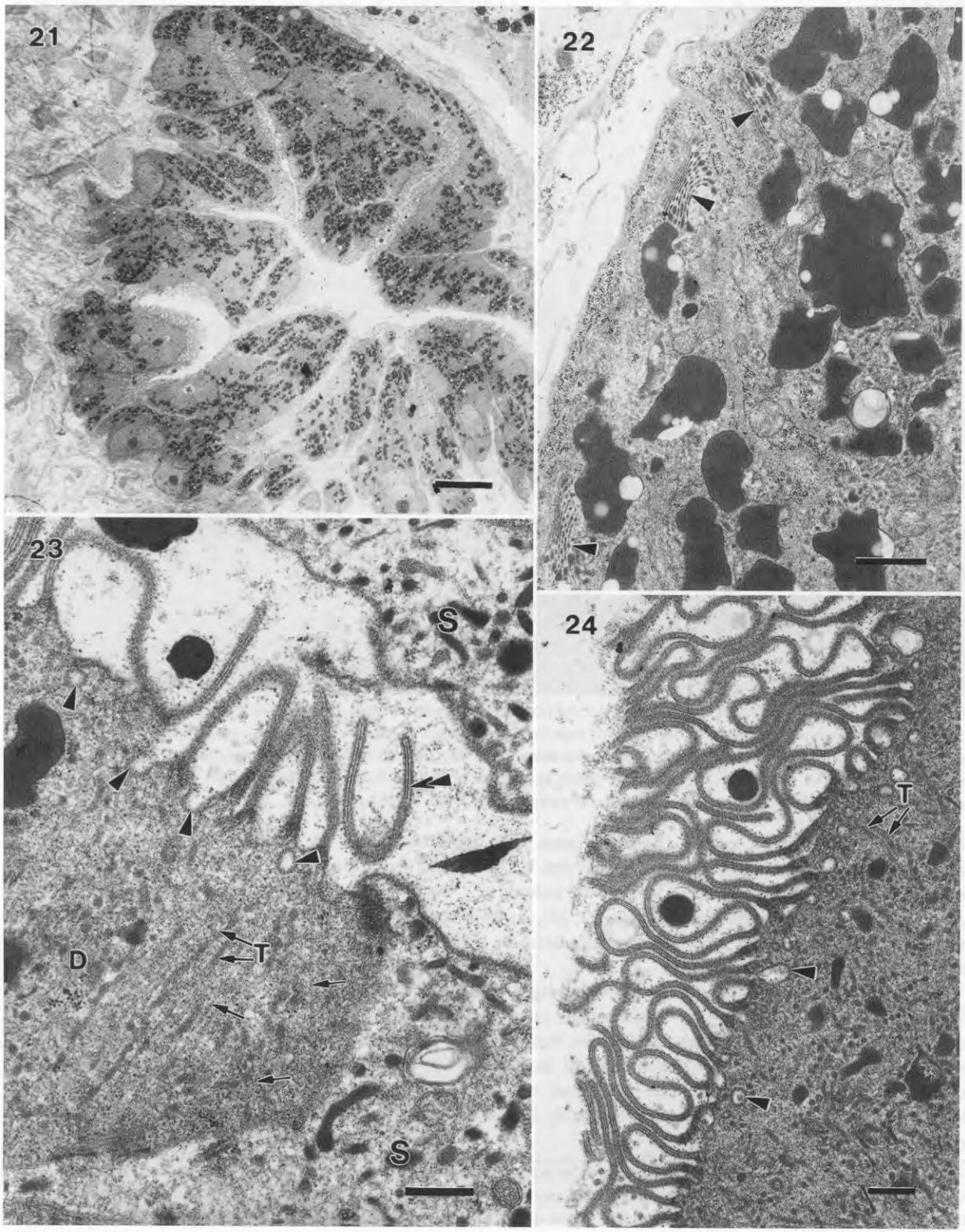
Conspicuous microtubules extend from the bases of microvilli deep into the cytoplasm, and coated pits between microvilli appear to bud off to become the coated vesicles present just below the surface (Figs. 23, 24). As in *C. australensis*, numerous tubular bodies also extend from the surface into the cytoplasm.

The syncytial cytoplasm does not overlie the digestive cells, and is joined to them by apical septate junctions. Syncytial cytoplasm is much lighter than that of digestive cells, and contains mitochondria and many dense elongate bodies (Fig. 23). The individual sectioned had almost no gut contents so presumably had not recently fed.

DISCUSSION

Observations from the oesophagus to the hind gut suggest that digestion in *Concinnocotyla australensis* is initially extracellular, by the action of oesophageal secretion, followed by intracellular, after uptake of degraded material in pits between lamellae on the apical surfaces of the digestive cells. It is also likely that whole lipid droplets are engulfed between lamellae. Alternatively, the presumed lipid droplets could be in the process of being excreted from the cells, but this explanation seems less probable, considering the specific association of the droplets with lamellae, and the

←**Figs. 14–18.** Electron micrographs of aspects of the dorsolateral gut pockets of *Concinnocotyla australensis*. **Fig. 14** shows the connection (arrowheads) between the caecum (G) and the part of the pocket which leads to the tegumental invagination (I). Note the nucleus belonging to the syncytium (N), layers of muscles (M) and tangential view of the capsule (C) surrounding the pocket. **Fig. 15.** A different section through the same pocket, showing part of the pocket lumen (L), the canal lined with muscles (M) leading to the tegumental/pocket bridge (B) and the tegumental invagination (I). Note the caecum (G). **Fig. 16.** One of the ciliate collared receptors in the tegumental invagination. **Fig. 17.** Extensively folded, villus-like syncytial lining of the pocket. Note numerous vesicles, underlying basal lamina and muscle layers. **Fig. 18.** Tegumental invagination (I) leading to the tegument/pocket bridge (B). Note two ciliate receptors (arrowheads) and lumen contents on pocket side of the bridge. Scale bars 1 μm (Figs. 16, 17), 2 μm (Fig. 18), 10 μm (Figs. 14, 15).



Figs. 21–24. Electron micrographs of the caecum of *Neopolystoma spratti*. **Fig. 21.** Transverse section of the caecum showing multiradiate lumen surrounded by digestive cells that are separated from one another by a thin layer of syncytium. **Fig. 22.** Part of a digestive cell showing several Golgi apparatus (arrowheads) and numerous irregular-shaped vacuoles with dense contents. **Fig. 23.** Part of a digestive cell (left) and adjacent syncytium. Note microtubules extending in from the bases of lamellae (arrows)

partially degraded appearance of vacuoles containing lipid in Fig. 10. The function of the intervening syncytial layer is unclear. In both the polystomatid species examined here, it covers only a very small portion of the lumen surface and does not overlap the digestive cells, in contrast to the situation observed in blood-feeding polystomatids (Tinsley 1974) and other polyopisthocotyleans (e.g., Halton et al. 1968, Halton and Stranock 1976). The role of skeletal support for haematin-laden digestive cells postulated for the blood-feeding polystomatids (Tinsley 1973) and other polyopisthocotyleans (Halton 1976) therefore does not seem to apply to these non-blood feeders, although as suggested by Allen and Tinsley (1989), its presence may reflect its ancestry among blood feeders. In *C. australensis*, the "soup" of partially digested material in the lumen was seen to be connected to the digestive cells but not to the syncytial surface. This suggests that the syncytium is not involved in uptake of particulate matter, but it does not rule out uptake of soluble products across the membrane. Syncytial cytoplasm in *C. australensis* and *N. spratti* contained mitochondria and numerous vesicles (vacuoles?) but the function of the latter is unclear and no evidence of secretory activity in the syncytium was seen.

While some digestive cell vacuoles contained myelin bodies indicative of breakdown products, no direct evidence of elimination of these bodies by cellular defaecation was seen. It may of course be a cyclic activity with these individuals in an uptake phase. Several instances were seen where whole cells appeared to be in the process of being extruded from the gastrodermis. The contents of these cells appeared to be passing into the lumen through a narrow constriction between adjacent syncytial surfaces. However, when these cells were traced through serial sections all were found to be normal intact digestive cells and the views suggesting extrusion were merely marginal sections through the cell bodies. This does not rule out the possibility that some cellular extrusion occurs, and the presence of undifferentiated cells beneath the gastric surface suggests that there may be some replacement of digestive cells. If some sloughing of cells does occur, the syncytium may function to physically seal the wound until a new digestive cell is differentiated at that position.

No traces of haematin crystals were seen in the digestive cells of *C. australensis* or *N. spratti* and it is concluded that neither feeds routinely on host blood. The vacuoles in the digestive cells of *N. spratti* were irregular in outline and much more electron-dense but bore no resemblance to the crystalline haematin accumulations in the vacuoles of such blood feeders as *Pricea multae* Chauhan, 1945 and *Pseudothoracocotyla indica* (Unnithan 1956) (personal observations). Thus the gastrodermis of the two species studied here conforms in all significant details to that of the polystomatids infecting chelonians and a mammal examined by Allen and Tinsley (1989) and shown by histochemistry and X-ray microanalysis to lack haematin in the gastrodermis. Their study included two species of *Polystomoides* (from chelonians) that Rohde (1973) had also earlier examined and, by analogy with other polyopisthocotyleans, considered may contain haematin in dark vacuoles.

The gut pockets of *C. australensis* are an intriguing and unique feature, not found in any other polystomes and with no apparent homologues in any other monogeneans. Pichelin et al. (1991) speculated that they may serve as twin ani (believing that they were continuous with the exterior) but noted that although gut contents were seen to circulate around the caeca of living worms, nothing was seen to be extruded from the dorsal pores. They also mentioned the possibility that the tegumental pores act as vaginae. We believe that neither of these functions apply. The massive increase in surface area of the pocket brought about by villus-like folding of the syncytium suggests a fluid exchange function. In combination with the presence of a large number of protonephridial flame bulbs in the surrounding capsule, it appears more likely that the gut pockets have an important osmoregulatory function. The ciliate receptors in the tegumental invagination may be chemoreceptors detecting osmotic pressure or solute concentration of the surrounding environment, and linked to the regulation of uptake of fluid or solutes from this posterior region of the gut. Lying near to the furthest extremity of the digestive system, the pockets could be filled with products of extracellular digestion from the remainder of the caecal regions, and the layers of muscles underlying the basal lamina of part of the pockets could enable control over their filling and emptying from the caeca.

Lungfish inhabit freshwater and are thus subject to much greater fluctuations in their environment than are marine species. Osmotic conditions of streams and billabongs vary enormously from very low osmotic pressure after influx of rainwater through to high osmotic pressure as evaporation and drought reduce water bodies to stagnant pools. Lungfish are capable of surviving stagnation by gulping air into the lungs. Furthermore they are believed to have evolved in shallow marine environments (Campbell and Barwick 1986) where wide fluctuations in salinity and hence osmotic

← which have a dense core (double arrowhead), coated pits and coated vesicles (arrowheads) and tubules (T) in the digestive cell (D), and mitochondria and small dense vesicles in the syncytial cytoplasm (S). **Fig. 24.** Apical surface of a digestive cell showing long lamellae, frequently looped back to the surface, coated pits and vesicles (arrowheads) and numerous tubules (T). Scale bars 10 μm (Fig. 21), 1 μm (Fig. 22), 500 nm (Figs. 23, 24).

pressure would also be experienced. *C. australensis* is the only polystomatid known to infect a fish, the remainder being parasites of tetrapods, and the enigmatic gut pockets may have developed to enable it to survive these wide fluctuations along with its host. Other polystomatids have migrated to less exposed sites in their hosts including nasal cavities, lungs, intestines, cloacal and urinary bladders, and conjunctival sacs, and some have developed life cycle strategies to evade desiccation.

Acknowledgements. The work was supported by an Australian Research Council grant to Klaus Rohde and microscopy was carried out at the Electron Microscope Unit of the University of New England, Armidale.

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Received 24 April 1996

Accepted 17 July 1996