Insect Rectum

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Insect rectum

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[Plates 31 to 33]

An important function of the rectum in terrestrial insects is the removal of water from the faeces, which in some insects are in equilibrium with an atmosphere of 75 % relative humidity or less when they are voided.

Structural complexity in the insect rectum appears to have evolved along two main lines:

(*a*) The cryptonephric line; the ends of the Malpighian tubules are enclosed together with the rectum in a perirectal space.

(*b*) The rectal gland line; areas of thickened epithelium have a system of intercellular channels and spaces.

These two lines have in common that the perirectal fluid of (*a*) and the intercellular fluid of (*b*) are of higher osmolarity than the haemolymph, and it has been suggested that the reabsorption of water from the faeces is thereby facilitated.

Possible mechanisms are discussed, with special reference to the active transport of water.

Dr Maddrell has given an outline of the whole excretory system in insects, including the rectum and its role in reabsorption, and the only information I need to add to his account is that the hind-gut, which comprises the intestine and the rectum, is an invagination of ectoderm and is lined with cuticle similar to that which covers the external surface of the insect.

STRUCTURE

Whether there is any such thing as a simple insect rectum is becoming increasingly open to doubt; but if there is, then structural complexity has evolved along two main lines which I propose to call the cryptonephric line and the rectal gland line. I shall describe one example of each.

Cryptonephric line

In certain members of the orders Coleoptera and Lepidoptera the proximal (i.e. blind) ends of the Malpighian tubules are closely applied to the rectum and are enclosed together with the rectum in a kind of bag. The word 'cryptonephric' is applied to those parts of the Malpighian tubules which are enclosed within the bag and are thus hidden from view. The existence of cryptonephric systems has been known for nearly a hundred years.

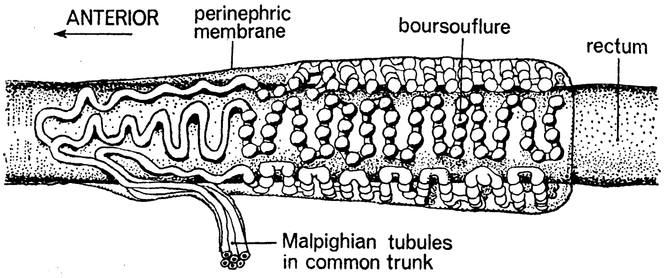

Figure 1. Diagram of the rectal complex of the mealworm. (From Grimstone *et al.* 1968.)

Figure 1 is a simplified drawing of the rectal complex of the mealworm, *Tenebrio*. It shows the proximal ends of the six Malpighian tubules closely applied to the rectum and enclosed within a membrane, the perinephric membrane, which is not so transparent as this drawing might suggest. It is in fact a complex membrane made up of several layers of flattened cells and is not unlike the myelin sheath of a nerve axon. The cryptonephric tubules are closely packed together

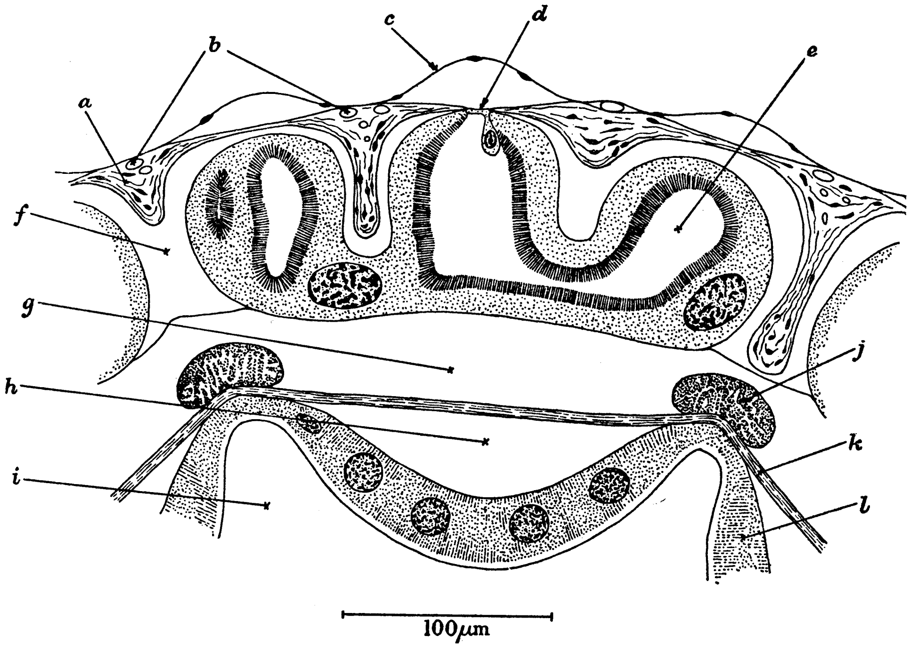

FIGURE 2. Transverse section of the rectal complex of the mealworm. *a*, perinephric membrane; *b*, tracheae; *c*, blister; *d*, leptophragma; *e*, lumen of perirectal tubule; *f*, artefactual space; *g*, *h*, perirectal space; *i*, rectal lumen; *j*, longitudinal muscle; *k*, circular muscle; *l*, rectal epithelium. (From Ramsay 1964.)

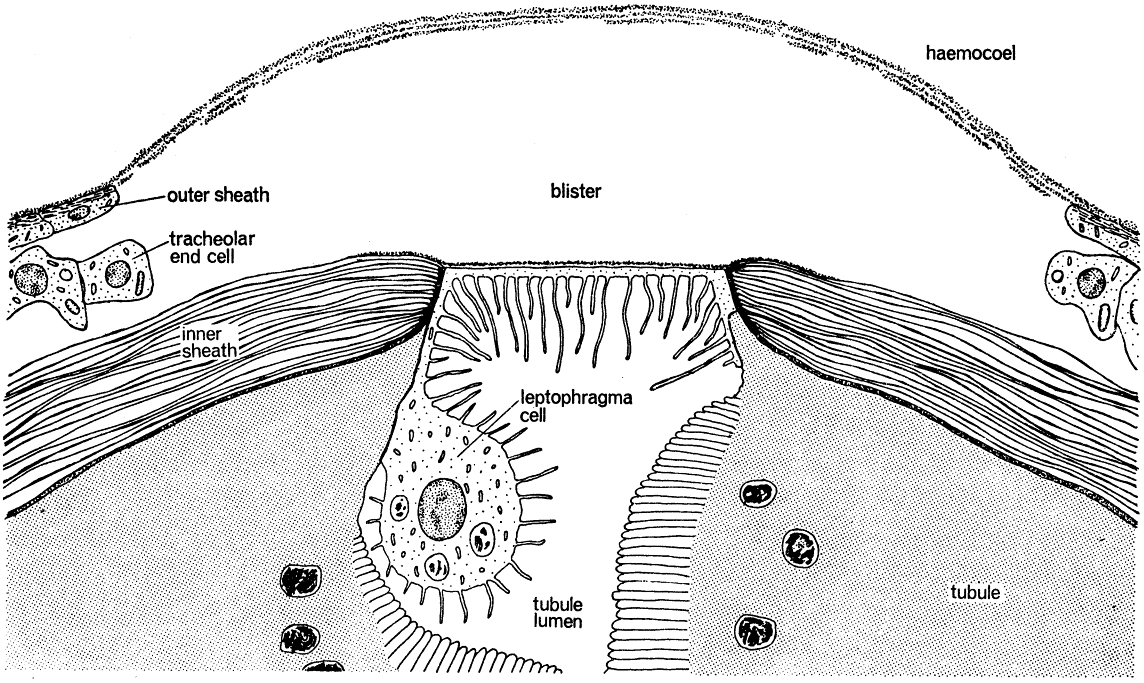

FIGURE 3. Diagram to illustrate the relations of a leptophragma. (From Grimstone *et al.* 1968.)

and folded like chinese crackers. Over the posterior region the tubules bear numerous small dilatations which Lison (1937) has called 'boursouflures'. The relations of these boursouflures are better seen in sections (figure 2). At each boursouflure the tubule bulges outwards to reach the perinephric membrane which is interrupted at the region of contact, and here the wall of the tubule is reduced to a very thin transparent window which Lison has called the 'leptophragma'. As may be seen from figure 3, the leptophragma is part of a small cell, the leptophragma cell, strikingly different from the large cells of the rest of the tubule. Beyond the leptophragma only an elevated portion of basement membrane lies between it and the haemocoel. The structure suggests, and physiological experiments confirm, that the perirectal space (in which the cryptonephric tubules lie) is isolated from the haemocoel by the impermeable perinephric membrane while translocation of material between tubule lumen and haemocoel is possible via the leptophragmata.

The rectal epithelium itself is relatively unspecialized being not unlike the hypodermis of the general surface of the body; in this lack of specialization it stands in marked contrast to the rectal epithelium in the cockroach, next to be described.

Rectal gland line

The structure of the rectum in the locust, *Schistocerca* (figure 4), is essentially the same as in the cockroach, *Periplaneta* (Irvine 1966). The epithelium is thickened along six longitudinal bands, known as the rectal glands or rectal pads. These have been examined with the electron microscope by Oschman & Wall (1969). Figure 5*a* is a section through a rectal pad. On the apical side, i.e. the side adjoining the cuticle, the plasma membrane is infolded in an array of leaflets. At both apical and basal ends the lateral cell membranes come together in septate desmosomes. Over the region between the apical and basal desmosomes the lateral cell membranes are highly folded, weaving in and out between mitochondria. The spaces between the lateral membranes show occasional dilatations, and these spaces open out into sizeable intercellular sinuses which lie deep within the epithelium. The basal surfaces of some of the cells, which may be identified by the presence of the basement membrane, are deeply invaginated, carrying branches of the tracheal system well down into the epithelium and making contact with the intercellular sinuses. Between the basal surfaces and the muscle layer, over each rectal pad, is a subepithelial sinus, and this communicates with the haemocoel through a limited number of restricted openings which admit the tracheae.

What appears to be the most elaborate manifestation of the rectal gland line is to be seen in the rectal papilla of the blowfly, *Calliphora*. Figure 6, taken from a paper by Gupta & Berridge (1966), shows the conical rectal papilla in section. Two regions may be distinguished: a cortex which corresponds to the rectal epithelium, and a medulla which appears to be a supporting structure of connective tissue carrying the tracheal supply. The cells of the cortex are broadly similar to those already described in the cockroach; they have apical leaflets, apical and basal septate demosomes, and highly infolded lateral membranes, of which more in a moment. The tracheal system penetrates the epithelium, not haphazardly as in the cockroach but by invaginations around the rim of the papilla, and these invaginations extend laterally from cell to cell throughout the cortex. The spaces between the lateral membranes open into these in-invaginations. The invaginations are clearly extensions of a space which corresponds to the intercellular sinus of the cockroach; and this space is confluent with a system of spaces between cortex and medulla, corresponding to the subepithelial space of the cockroach, which eventually open into the haemocoel through narrow openings around the rim of the papilla, guarded by flap valves.

The relations between the lateral membranes and the mitochondria are formalized (Berridge & Gupta 1967). The lateral membranes are neatly folded into regular stacks with which the mitochondria are closely associated, forming conspicuous units (figure 7, plate 31). A magnesium-activated ATPase has been demonstrated in these membrane stacks (Berridge & Gupta 1968), on the cytoplasmic sides of the membranes (figure 8, plate 32).

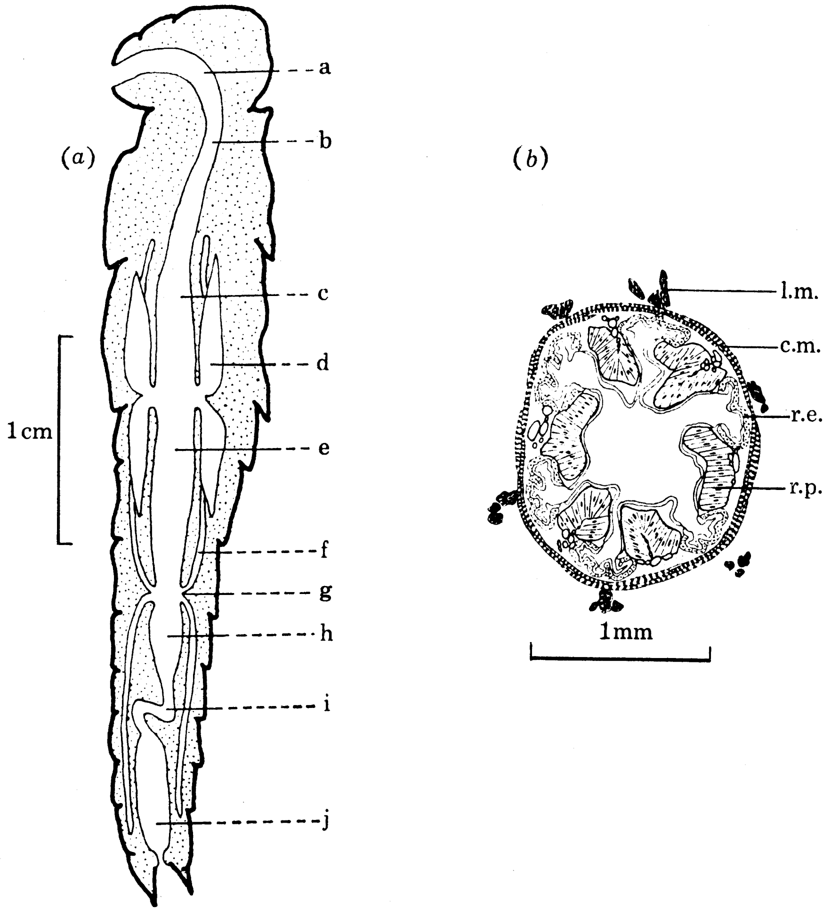

Figure 4. (*a*) The relative position and lengths of the components of the alimentary and excretory systems in the desert locust. *a*, pharynx; *b*, oesophagus; *c*, crop; *d*, caecum; *e*, ventriculus; *f*, Malpighian tubule; *g*, proctodaeal valve; *h*, ileum; *i*, colon; *j*, rectal sac. (*b*) Semi-diagrammatic cross-section of the locust rectum. *l.m.*, longitudinal muscle; *c.m.*, circular muscle; *r.e.*, reduced epithelium between rectal pads; *r.p.*, rectal pad. (From Phillips 1964.)

Reflecting upon these two very different lines of structural elaboration, we notice that what they have in common is a fluid compartment, the perirectal space in the cryptonephric line and the subepithelial space in the rectal gland line, which is separated from the lumen of the rectum by the epithelial cells and is in highly restricted communication with the haemocoel.

Physiology

Accepting Wigglesworth's (1932) idea that an important function of the rectum is the removal of water from the faeces we may begin by noting that the need to conserve water is more urgent

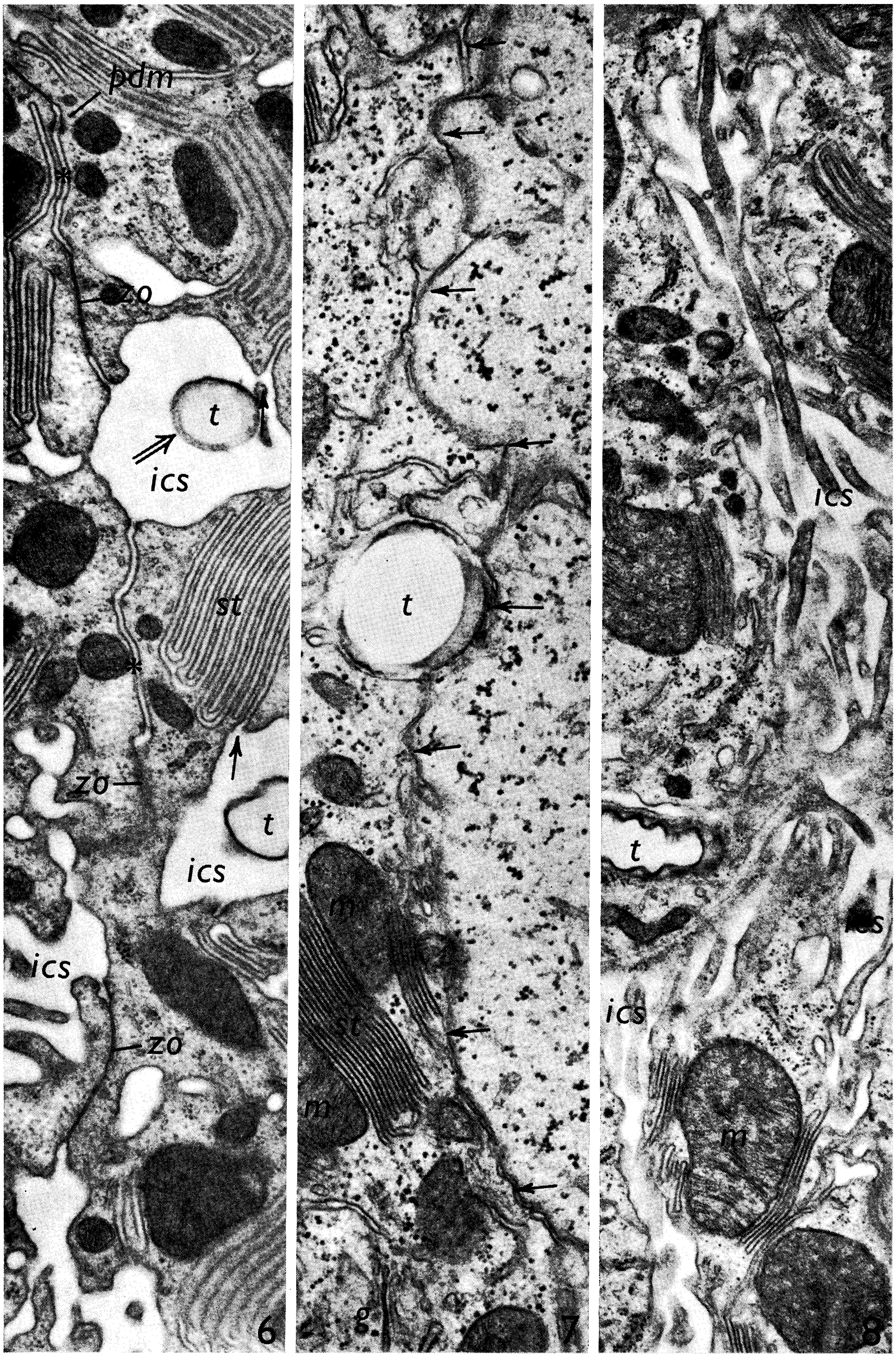

FIGURE 7. Fine structure of the epithelial cells from the rectal papilla of the blowfly. (6) 2-day-old fly with dilated intercellular spaces; single arrow, continuity of lateral plasma membrane with membrane stacks; double arrow, tracheoles lacking cell membrane. (7) Starved fly with intercellular spaces obliterated; single arrow, lateral plasma membranes. (8) Freshly emerged fly, with microvillus-like projections into intercellular spaces. *g*, dictyosome; *ics*, intercellular space; *m*, mitochondrion; *pdm*, desmosome-like densities; *st*, membrane stacks; *t*, tracheole; *zo*, occluded zones. (From Berridge & Gupta 1967, figures 6 to 8.)

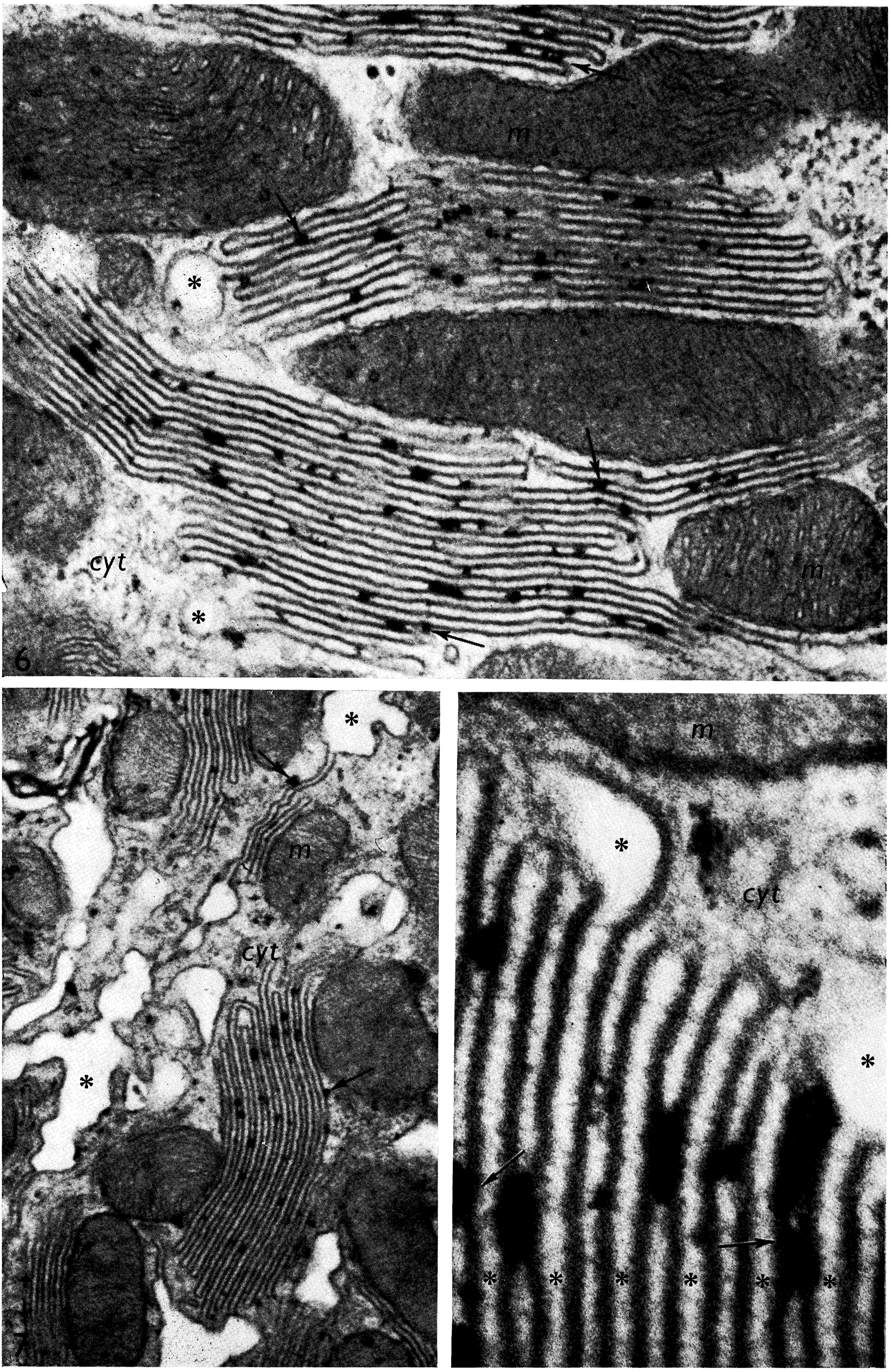

FIGURE 8. Fine structure of the membrane stacks from the rectal papilla of the blowfly, showing intracellular deposits indicating the presence of ATPase. *cyt*, cytoplasm; *m*, mitochondrion; arrows, indicating that the deposits develop in association with the cytoplasmic leaflet of the unit membrane; asterisks, marking the intercellular spaces. (From Berridge & Gupta 1968, figures 6 to 8.)

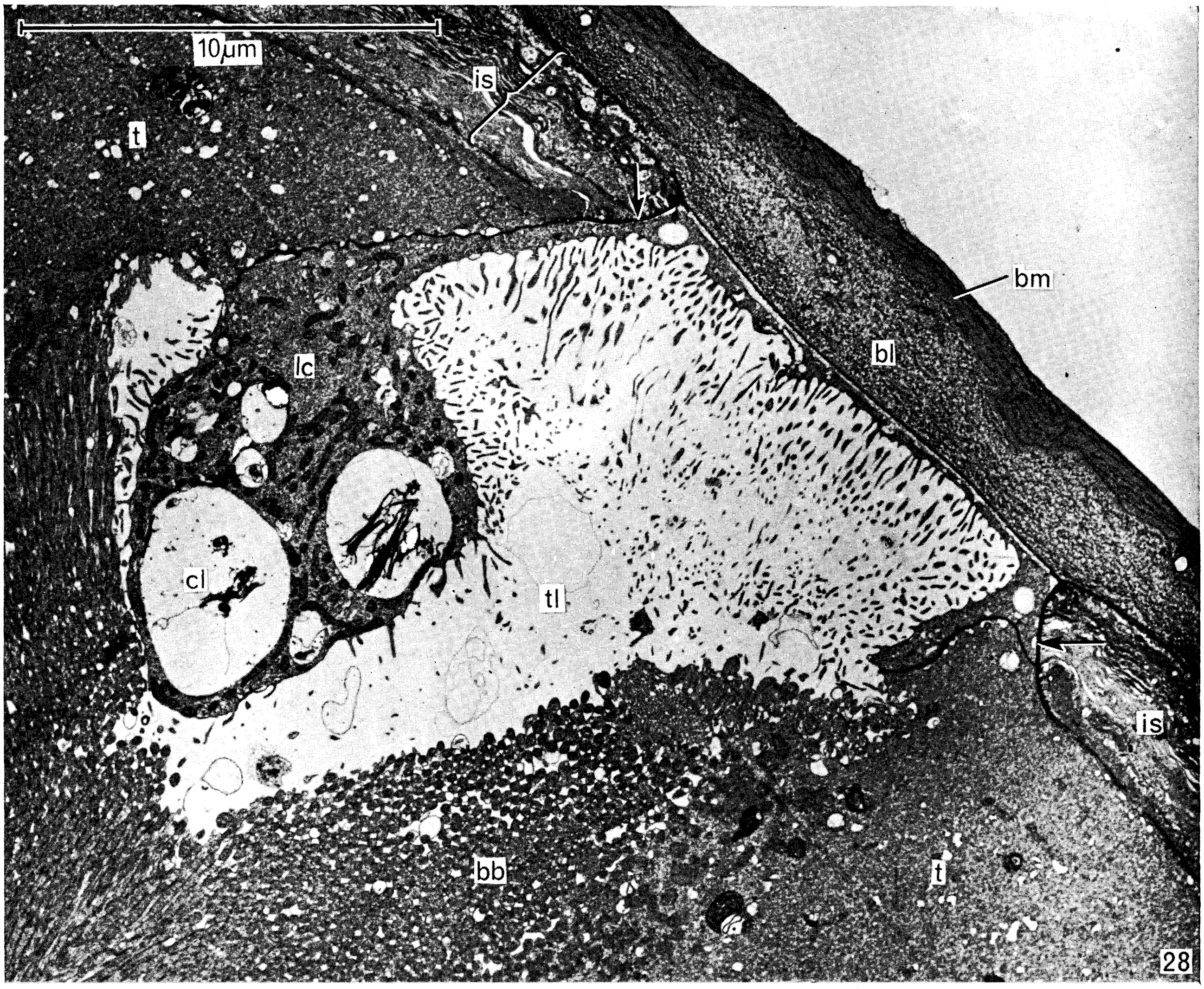

FIGURE 11. Electronmicrograph of a leptophragma. *bb*, brush border of tubule cell; *bl*, blister over leptophragma; *bm*, basement membrane; *cl*, cytolysome; *is*, inner sheath of perinephric membrane; *lc*, leptophragma cell; *t*, tubule cell; *tl*, tubule lumen. (From Grimstone *et al.* 1968, figure 28.)

in some insects than in others; it is more urgent in the mealworm which lives in stored products without having access to liquid water than it is in the cockroach or the locust which live on moist food. The maximum osmolarity which has been recorded for the rectal contents of the cockroach, allowed access to food but deprived of liquid water, is 1.0 osmol/l (Wall & Oschman 1970); and for the locust this also seems to be about the highest concentration which can be reached (Phillips 1964). But in the mealworm the drying process is carried much further, and

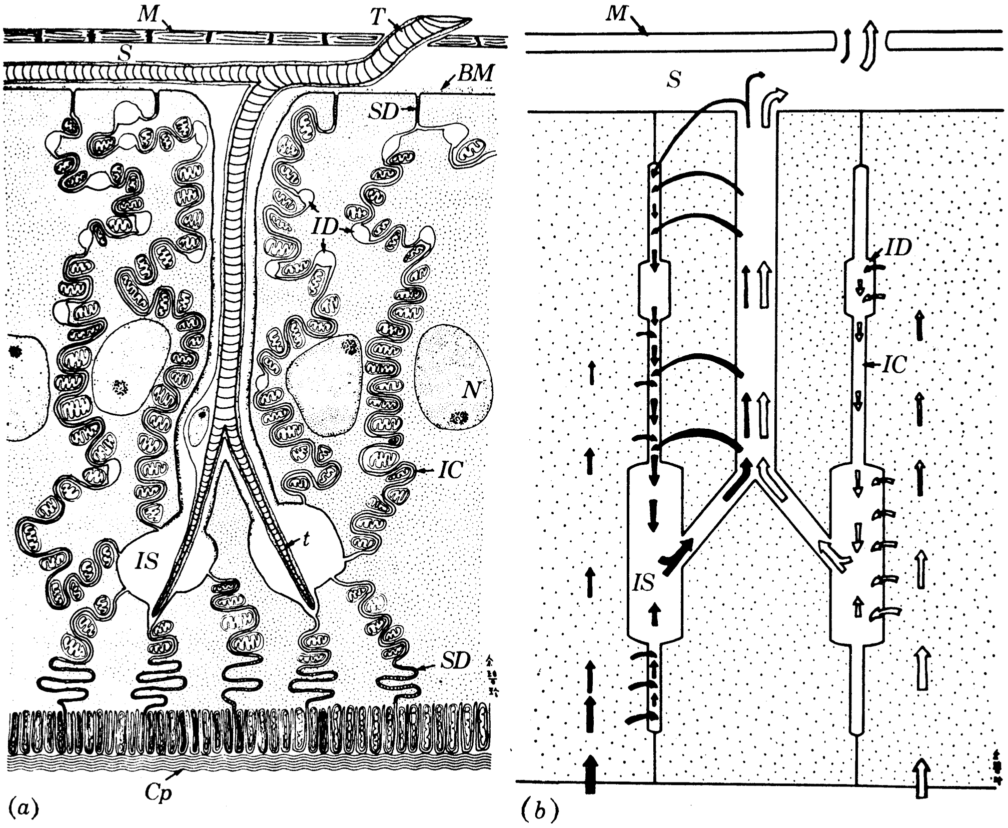

FIGURE 5. (*a*) The general organization of the rectal pad of the cockroach. (*b*) Diagram illustrating the functional significance of this organization. *BM*, basement membrane; *Cp*, cuticle; *IC*, intercellular dilatations; *IS* intercellular sinus; *M*, muscle; *N*, nucleus; *S*, subepithelial sinus; *SD*, septate desmosomes; *T*, trachea; *t*, tracheole; open arrows, flow of water; solid arrows, flow of solute. (From Oschman & Wall 1969).

in the posterior part of the rectum the faecal pellets are in an air space. In order to obtain a measure of the drying power of the rectal complex one has to find the relative humidity of the atmosphere with which the faecal pellets are in equilibrium. This has an average value of 88 % relative humidity, and values as low as 75 % have been recorded. Notionally, a solution in equilibrium with an atmosphere of 75 % relative humidity would have a concentration of over 13 osmol/l and a freezing-point depression of about 25 °C. So by any physiological standard the ability of the mealworm to remove water from its faeces must command respect.

The point has already been stressed that what the cryptonephric line and the rectal gland line have in common is the third fluid compartment lying between the haemocoel and the rectal lumen. Saini (1962, 1964) measured the freezing-point depression of perirectal fluid in four species of insect belonging to the cryptonephric line. In all cases he found that the perirectal fluid was more concentrated than the haemolymph and less concentrated than the rectal contents, and he suggested that by increasing the osmolarity of the perirectal fluid the insect reduces the work to be done by the rectal epithelium in extracting water from the faeces and so makes possible a more thorough extraction. More recent work confirms Saini's results and extends them to include one insect, the cockroach, belonging to the rectal gland line.

I shall now discuss possible mechanisms involved in the reabsorption of water from the rectum.

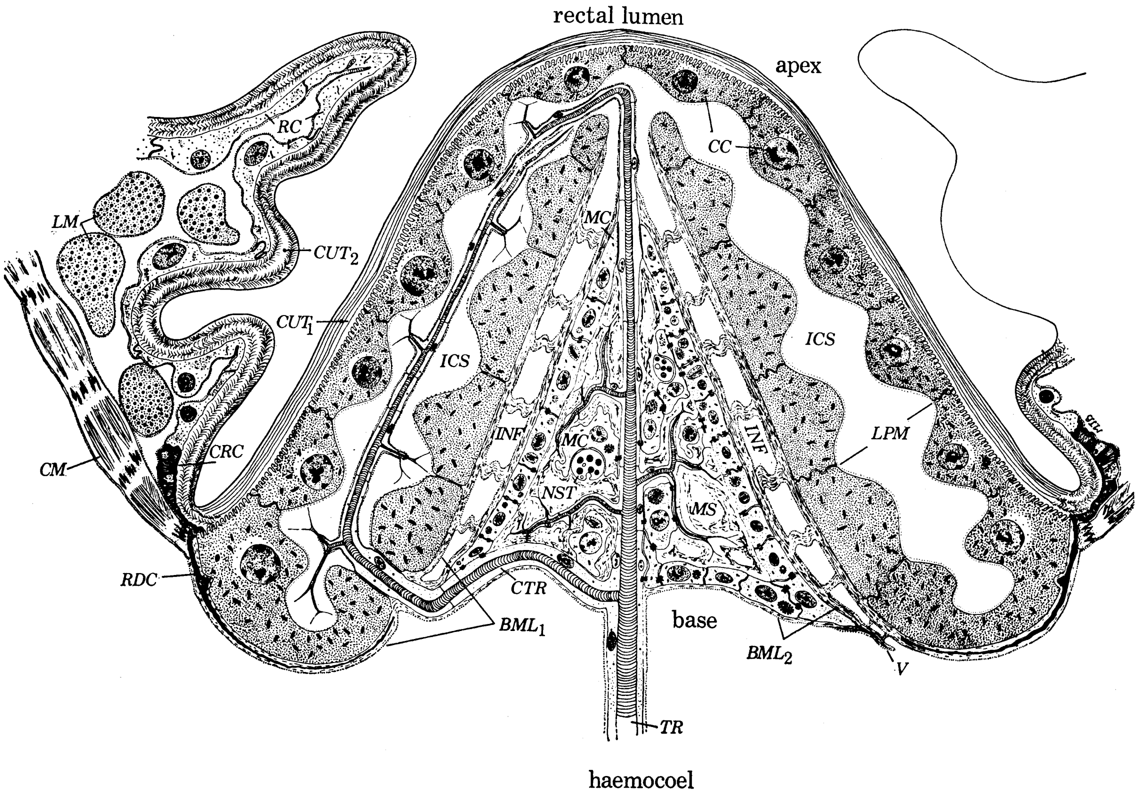

FIGURE 6. General organization of the rectal papilla of the blowfly. BML_1, BML_2, basement lamellae of cortex and medulla respectively; *CC*, cortical epithelial cells; *CM*, circular muscle; *CRC*, junctional cell; *CTR*, cortical trachea; CUT_1, CUT_2, cuticular intima of the papilla and rectal pouch respectively; *ICS*, intercellular space; *INF*, infundibulum; *LM*, longitudinal muscle; *LPM*, lateral plasma membranes of the cortical epithelial cells; *MC*, medullary cells; *MS*, medullary space; *NST*, neurosecretory terminals; *RDC*, radial cell; *TR*, tracheal trunk; *V*, medullary or infundibular valve. (From Gupta & Berridge 1966.)

The mealworm

Figure 9 is a diagram of the rectal complex of the mealworm reduced to its bare essentials and showing the osmolarities measured in different parts of the complex. The general level of osmolarity increases from anterior end to posterior end in all compartments including the cryptonephric tubules whose contents are not far from isosmolar with perirectal fluid at all levels. The input from the intestine is at a concentration of 0.55 osmol/l, more or less isosmolar with the haemolymph; an average figure for the (notional) osmolarity of the faeces leaving the rectum would be 5.5 osmol/l. Likewise, the osmolarity of the perirectal fluid increases from 1.0 osmol/l at the anterior end to 2.5 osmol/l at the posterior end. Water, and some solutes, are reabsorbed through the rectal epithelium and presumably the water leaves the rectal complex either through the cryptonephric tubules or by escaping under the anterior end of the perinephric membrane (which closely invests, but is not fused with, the intestine) or by both routes.

At this point in the story we encounter an irritating little problem of the conservation of matter. What enters the rectum is a fluid which is isosmolar with haemolymph; what leaves by the anus is faeces which are hyperosmolar to haemolymph. For this to be possible it seems that the rectal complex must reject, by some other route, a fluid which is hypo-osmolar to haemolymph. But the fluid which may be rejected by either of the two routes we have considered is hyperosmolar to haemolymph is both cases (Ramsay 1964).

A possible way out of this difficulty is provided by the discovery (Grimstone, Mullinger & Ramsay 1968) that the rectal complex is able to take up potassium chloride from the haemolymph. If this salt uptake is not accompanied by water uptake the phenomenon is saved. But where does the salt uptake occur?

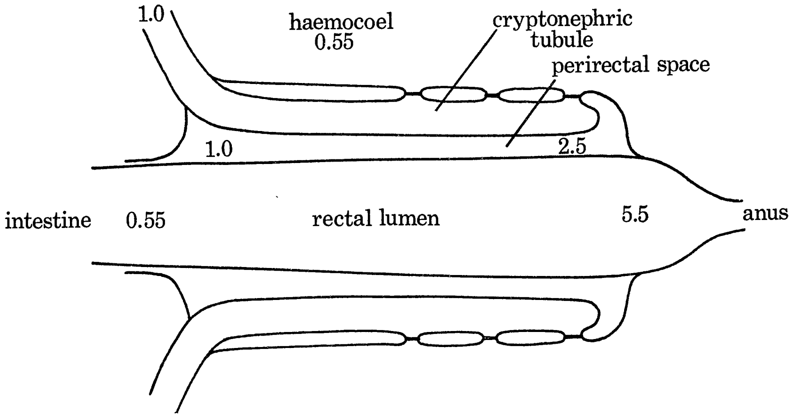

FIGURE 9. Diagram to illustrate the distribution of osmolarity in the rectal complex of the mealworm.

If salt uptake does not take place through the leptophragmata it is very difficult to imagine where the site of uptake can be. Lison (1937) demonstrated that the leptophragmata are permeable to chloride. The tubular fluid from the cryptonephric tubules is almost pure potassium chloride; concentrations of up to 2 mol/l have been measured directly, and from freezing-point depression concentrations of as high as 3 mol/l may be inferred. The difference of electrical potential between tubular lumen and haemocoel is such as to indicate that potassium must be actively transported while chloride may move passively.

The mechanism proposed for the rectal complex of the mealworm is shown in figure 10. The fluid entering with the faeces is mostly reabsorbed at the anterior end, first into the perirectal space and then into the cryptonephric tubules. The high osmolarity at the posterior end arises from the secretion of potassium chloride from haemolymph to tubular fluid through the leptophragmata, which must be relatively impermeable to water. On the other hand, the walls of the cryptonephric tubules facing the perirectal space must be relatively permeable to water so that the high osmolarity produced by the uptake of potassium chloride is communicated to the perirectal fluid; this is in line with other observations upon Malpighian tubules, which do not in general maintain substantial differences in osmolarity across their walls. The osmolarity of the posterior perirectal fluid is always lower than the (notional) osmolarity of the faeces leaving the rectum; and since the faeces are in an air space at the posterior end of the rectum only water vapour (and no solute) can be taken up. The mechanism proposed therefore envisages the active uptake of water from the rectal lumen to the perirectal space.

The mechanism proposed for the rectal complex places upon the leptophragma cell the

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burden of transporting potassium ion against a concentration difference of the order of 2 mol/l and against a potential difference of the order of 75 mV. Figure 11, plate 33, is an electron micrograph of this cell, and it is difficult to think of it as adequate to this task.

The cockroach and the locust

Coming now to the rectal gland line I wish to refer to a very elegant study made by Phillips (1964) on the rectum of the locust. Phillips isolated the rectum *in situ* by ligating the intestine. He then introduced various solutions via the anus, and at intervals he recorded changes in volume of solution and changes in the concentrations of solutes. In the course of these experiments he filled the rectum with solutions of sugars to which the rectal wall was impermeable and he was able to show that water was removed from the rectum against a concentration difference of 0.5 osmol/l; and since in these experiments there was no movement of solute across the rectal wall in either direction this was a clear case—the first clear case—of the active transport of water between two fluid-filled compartments.

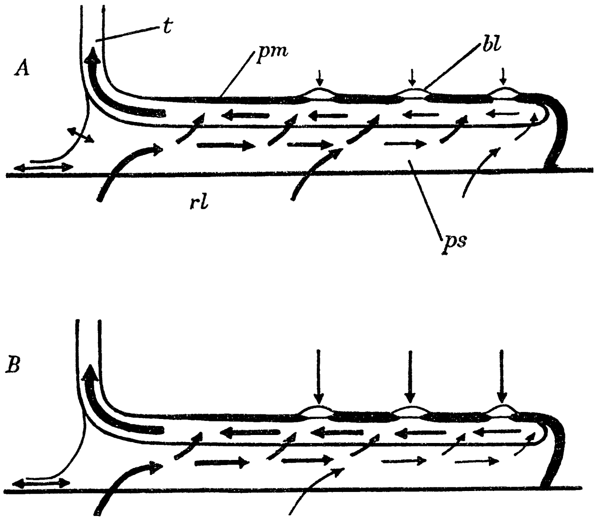

FIGURE 10. Model proposed for the mechanism of the rectal complex. A, movements of water; B, movements of potassium. *bl*, blister over leptophragma; *pm*, perinephric membrane; *ps*, perirectal space; *rl*, rectal lumen; *t*, tubule. (From Grimstone *et al.* 1968.)

But this demonstration of the active transport of water was not allowed to go unchallenged. Gupta & Berridge (1966) have pointed out '...that the osmotic and electrochemical gradients governing the flow of ions and water from the rectal contents are to be measured between the rectal lumen and the intercellular sinus and not the haemolymph as has been done by Phillips. Only then would it be possible to measure the absorptive activities of the rectal papillae.' I could agree with this if for 'rectal papillae' were substituted the words 'rectal epithelium', for Phillips's conclusion that water can be actively transported by the rectal papilla (or pad or gland), between rectal lumen and haemocoel seems to me to be well founded.

Gupta & Berridge propose a mechanism for the transport of water which is based upon the active transport of ions and does not require that water be actively transported as well. This line of thought has been further developed by Wall & Oschman (1970), who have proposed for the cockroach rectum a mechanism which envisages recycling of solutes between cells and sinuses, as indicated in figure 5*b*. The effect of this recycling should be to set up a concentration gradient within the epithelial cells such that the apical regions of the cells are hyperosmolar to the basal regions; and in confirmation of this hypothesis Dr Wall and her associates have successfully performed the technical feat of collecting fluid from the intercellular sinuses and have shown that this fluid can be hyperosmolar to the rectal contents (Wall, Oschman & Schmidt-Nielsen 1970).

I admit the truth of the testimony. We are not compelled to believe that water is actively transported across the rectal epithelium of the cockroach. But I am not ready to agree that this evidence disposes of the possibility of the active transport of water by the insect rectum; and in conclusion I propose to make some observations upon the active transport of water in general.

As far as terrestrial arthropods are concerned their ability actively to transport water from the atmosphere into the haemolymph cannot be doubted. It has long been known that some arthropods can reduce the relative humidity of an air space far below the value which would be in equilibrium with their body fluids. The record is at present held by the firebrat, *Thermobia*, which can reduce the relative humidity of the air space to 45 % (Beament, Noble-Nesbitt & Watson 1964). Until recently it had been supposed that the site of uptake was the general body surface, but recently Noble-Nesbitt (1970) has found that uptake of water vapour by the firebrat is prevented by occlusion of the anus. This indicates that the site of uptake in the firebrat is the rectum; and still more recently Noble-Nesbitt (personal communication) has shown that this is also the case in the mealworm. These are cases of the active transport of water from a gas-filled compartment to a fluid-filled compartment, but we should also call to mind the demonstration by Phillips, mentioned earlier, of the active transport of water between two fluid-filled compartments. What all these examples of the active transport of water have in common is the involvement of an epithelium which is covered by a chitinous cuticle; I do not know of any comparable case where the active transport of water across a naked epithelium has been demonstrated. One cannot but wonder whether the active transport of water is possible only in the situation where the epithelium is covered with a chitinous cuticle, and (more importantly) where the chitinous cuticle in turn is covered with an oriented layer of wax molecules. Beament (1964) has given much thought to the asymmetrical permeability of such oriented wax layers to water and its possible importance for the active transport of water.

I do not suppose that there would be any hesitation about admitting the possibility, even the likelihood, that water can be actively transported were it not for the controversy which has grown up around this idea in other areas of study. Some years ago the non-equilibrium distribution of water between cells and body fluids was the subject of claims and counterclaims (Robinson 1953). This background of controversy and the lack of any decisive evidence of active transport of water in animals other than arthropods, may well account for the urge which drives some people to seek alternative explanations. Schmidt-Nielsen (1969) dissociates himself from this attitude. ‘Water transport as such is an alternative that in my opinion should not be dismissed just because it is *possible* to explain the phenomenon on a different basis.’ I agree, notwithstanding that I myself am the person whom Schmidt-Nielsen is taking to task in this passage.

The principle seems to have gained acceptance that the accused is presumed to be guilty until he can be proved to be innocent—the onus of proof is placed upon those who support the view that water is actively transported. And the course of justice is likely to be further perverted by the system of appeals. If it is demonstrated with full thermodynamic rigour that water is actively transported across the rectal wall the prosecution will then require it to be demonstrated that water is actively transported across the rectal epithelium. If this is established they will then submit that water might move passively in consequence of solute movements within some limited region of the epithelial cell—and so on until the case is transferred from the jurisdiction of thermodynamics to the jurisdiction of quantum mechanics.

I would like to ask those who are unwilling to accept the idea of the active transport of water to spell out the evidence they would require in order to be convinced.

For myself, I find great difficulty in believing that the lowering of relative humidity such as has been recorded can ever be completely accounted for by active transport of sodium or potassium. If active uptake of water, reducing the relative humidity of an air space to 45 %, is to be explained on the basis of recycling of these ions, then the following data are relevant. At 25 °C the relative humidity in equilibrium with saturated potassium chloride is 85 %, and for sodium chloride it is 75 % (Winston & Bates 1960). I leave this problem as an exercise for the reader.

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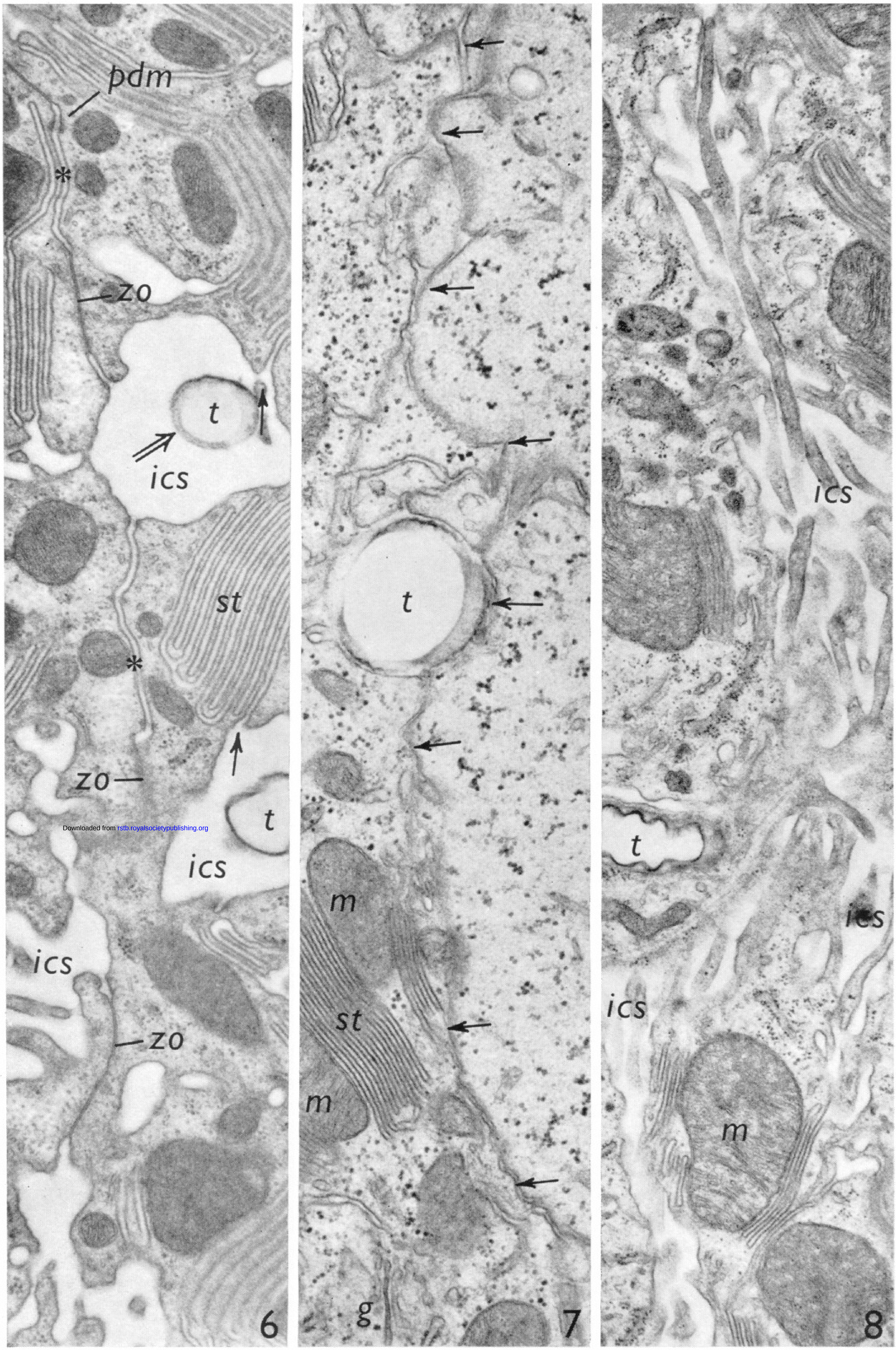
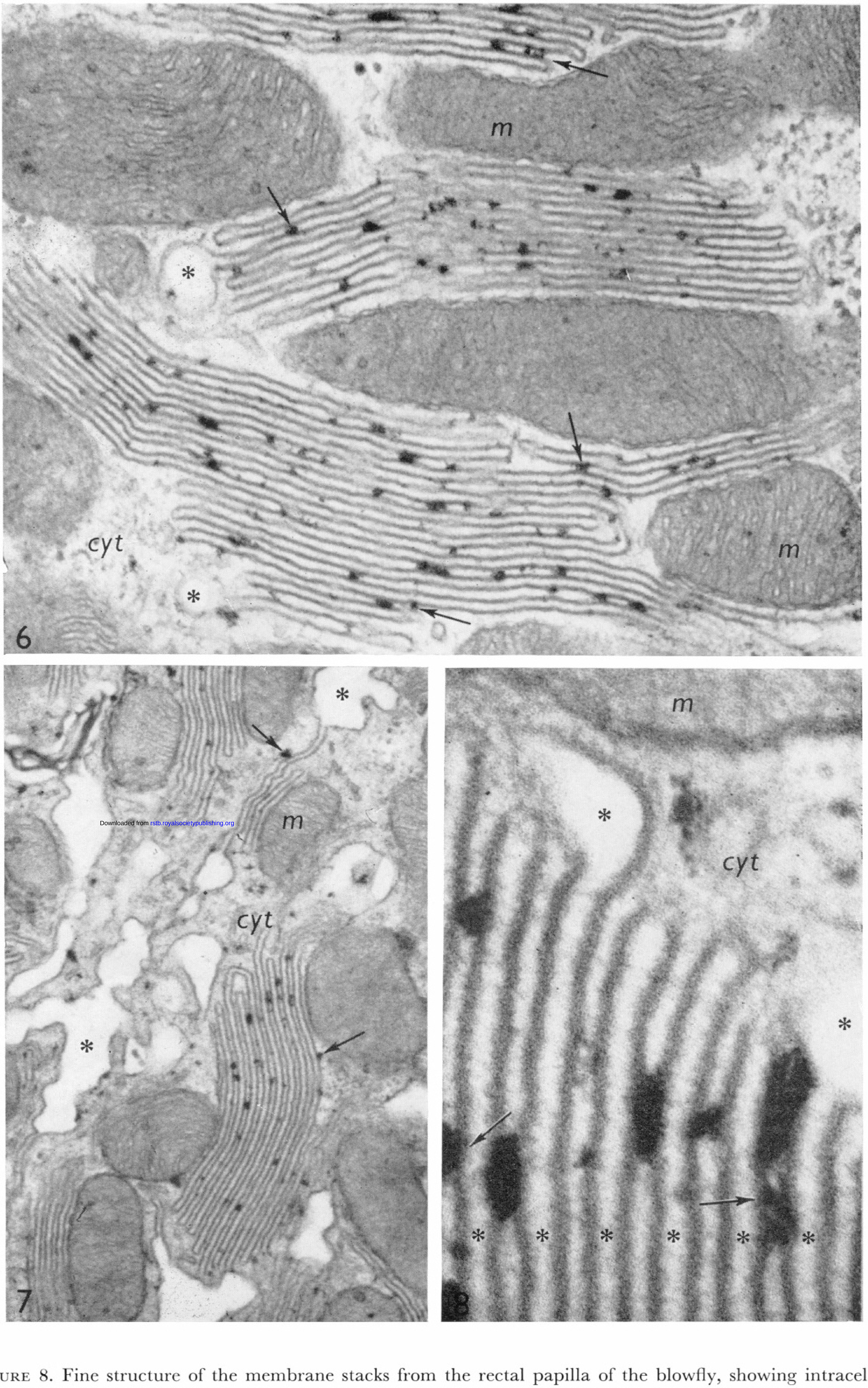


FIGURE 7. Fine structure of the epithelial cells from the rectal papilla of the blowfly. (6) 2-day-old fly with dilated intercellular spaces; single arrow, continuity of lateral plasma membrane with membrane stacks; double arrow, tracheoles lacking cell membrane. (7) Starved fly with intercellular spaces obliterated; single arrow, lateral plasma membranes. (8) Freshly emerged fly, with microvillus-like projections into intercellular spaces. *g*, dictyosome; *ics*, intercellular space; *m*, mitochondrion; *pdm*, desmosome-like densities; *st*, membrane stacks; *t*, tracheole; *zo*, occluded zones. (From Berridge & Gupta 1967, figures 6 to 8.)



GURE 8. Fine structure of the membrane stacks from the rectal papilla of the blowfly, showing intracellular deposits indicating the presence of ATPase. *cyt*, cytoplasm; *m*, mitochondrion; arrows, indicating that the deposits develop in association with the cytoplasmic leaflet of the unit membrane; asterisks, marking the intercellular spaces. (From Berridge & Gupta 1968, figures 6 to 8.)

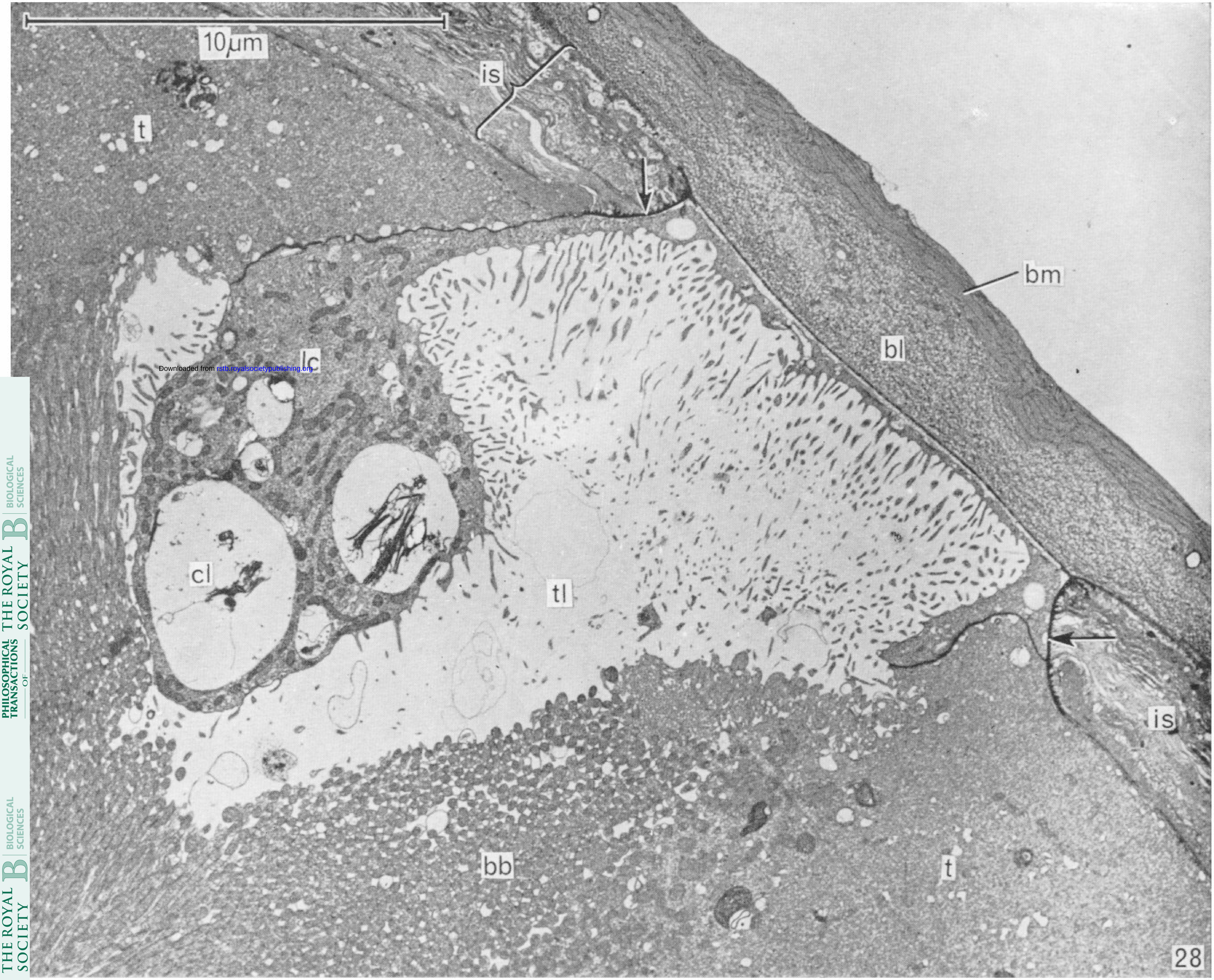


FIGURE 11. Electronmicrograph of a leptophragma. *bb*, brush border of tubule cell; *bl*, blister over leptophragma; *bm*, basement membrane; *cl*, cytolysome; *is*, inner sheath of perinephric membrane; *lc*, leptophragma cell; *t*, tubule cell; *tl*, tubule lumen. (From Grimstone *et al.* 1968, figure 28.)