MORPHOLOGICAL STUDIES OF THE RECTAL PAPILLAE OF THE MALE ORIENTAL FRUIT FLY, *DACUS DORSALIS* HENDEL, USING SCANNING ELECTRON MICROSCOPY[1]

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Wen-Yung Lee, Chien-Chung Cheng and Mei-Jung Lin (1990) Morphological studies of the rectal papillae of the male oriental fruit fly, *Dacus dorsalis* Hendel, using scanning electron microscopy. *Bull. Inst. Zool., Academia Sinica* **29**(3): 195-205. Four cone-shaped rectal papillae are located in the anterior part of the rectum in the *Dacus dorsalis* fly. The circular base of each papilla protrudes into the haemolymph, while the rest, a cone-shaped tip, extends into the rectal lumen. The base is covered with a basement membraneous layer, and the tip is sheathed within a cuticle. Sizes of the rectal papillae in these flies range from 0.58-0.64 mm in length, and 0.16-0.22 mm in width. There is no significant relationship between the variation in length of the rectal papillae and the age of the fly. The posterior part of a papilla will enlarge when a sexually mature male fly produces the sex pheromone, contrasting substantially with that of a fly which emerged only one to two days previously.

The internal structure of the rectal papilla comprises a cortex of columnar epithelial cells and a rod-shaped medulla. Between them, there is an infundibular space and many connecting trabeculae. Several tracheae extend into the papilla through the top of the medulla, running into the cortical epithelium and occupying intercellular space. Intercellular sinuses are distributed in the apical region of the rectal papilla. The physiological function of the rectal papillae in the fly, postulated to be a water and ion transport mechanism, is discussed.

Key words: Rectal papilla, Cortex, Medulla, Infundibulum, Intercellular space, Intercellular sinus, Trabeculae.

Structures associated with the recta of insects, such as rectal glands, have been demonstrated to regulate transport of water, amino acids and ions from the rectal lumen to the haemolymph by means of an osmotic mechanism (Phillips, 1970; Ramsay, 1971; Berridge and Oschman, 1972; Wall and Oschman, 1975; Noirot and Noirot-Timothee, 1976, 1977).

Morphological studies by scanning electron microscopy of insect rectal papillae or rectal pads have only been performed on certain orders of insects, such as the cavernicolous Trichoptera (Cianficconi *et al.*, 1984), *Stenophylex permistus* McL. of Trichoptera (Cianficconi *et al.*, 1985), and *Ceratitis capitata* of Diptera (Dallai *et al.*, 1985). Histological observations of the organ have already been described in several Dipteran insects using light microscopy and/or transmission electron microscopy (Gupta and Berridge, 1966a, 1966b; Wessing and Eichelberg, 1973;

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De Marza *et al.*, 1978; Dallai *et al.*, 1985).

The present study attempts to investigate, by means of scanning electron microscopy, the external and internal structure of the rectal papillae in the male oriental fruit fly, *Dacus dorsalis*, in order to hypothesize its physiological function.

MATERIALS AND METHODS

Male adult *D. dorsalis* flies were reared in the laboratory of the Institute of Zoology, Academia Sinica, with an artificial diet: a 1:3 mixture of peptone and sugar. Laboratory conditions were kept at 25±2°C and 70-80% RH. Both sexually immature and mature male flies were dissected between 16:00 and 17:00 each day in a buffer solution to obtain the recta. The rectal papillae were excised and fixed in 2.5% glutaraldehydrate with 0.05 M cacodylate buffer for 2 hours in cold, then transferred to the same buffer. After fixation, the sizes of the rectal papillae of each day's specimens, representing one to ten days old flies, were measured by a Wild M8 stereo-microscope.

After fixation, the rectal papillae were dehydrated by an ascending series of acetone. The specimens were dried in either air or a critical point dryer. After these treatments, the specimens for external study were mounted on stubs and coated with a gold membrane, using Ion coater type IB-2. Those specimens used for internal observations were opened in a longitudinal or a transverse direction with a razer blade, and then mounted on stubs and coated with a gold membrane. All these preparations were observed by a scanning electron microscope type Hitachi S-450.

All terminology of the present study follows Graham-Smith (1934) and Gupta and Berridge (1966a).

RESULTS

I. External morphology of rectal papillae

Rectal papillae of *D. dorsalis* generally have a similar structure to those of other Dipterans (Gupta and Berridge, 1966a; Hopkins, 1967; De Marzo *et al.*, 1970; Wessing and Eichelberg, 1973; Dallai *et al.*, 1985). There are four circular bases protruding into the haemocoel at the anterior part of the rectum (Fig. 1, Rp.). The rest of papillae is embedded into the rectal lumen as a cone. An entire *D. dorsalis* rectal papilla appears as a rod with a circular base at the top (Fig. 2). In a mature fly during the mating period, the posterior part of the cone becomes enlarged, so that the rectal papilla can be divided into three parts: the base, the neck and the blunt tip (Fig. 3, B., N., T.).

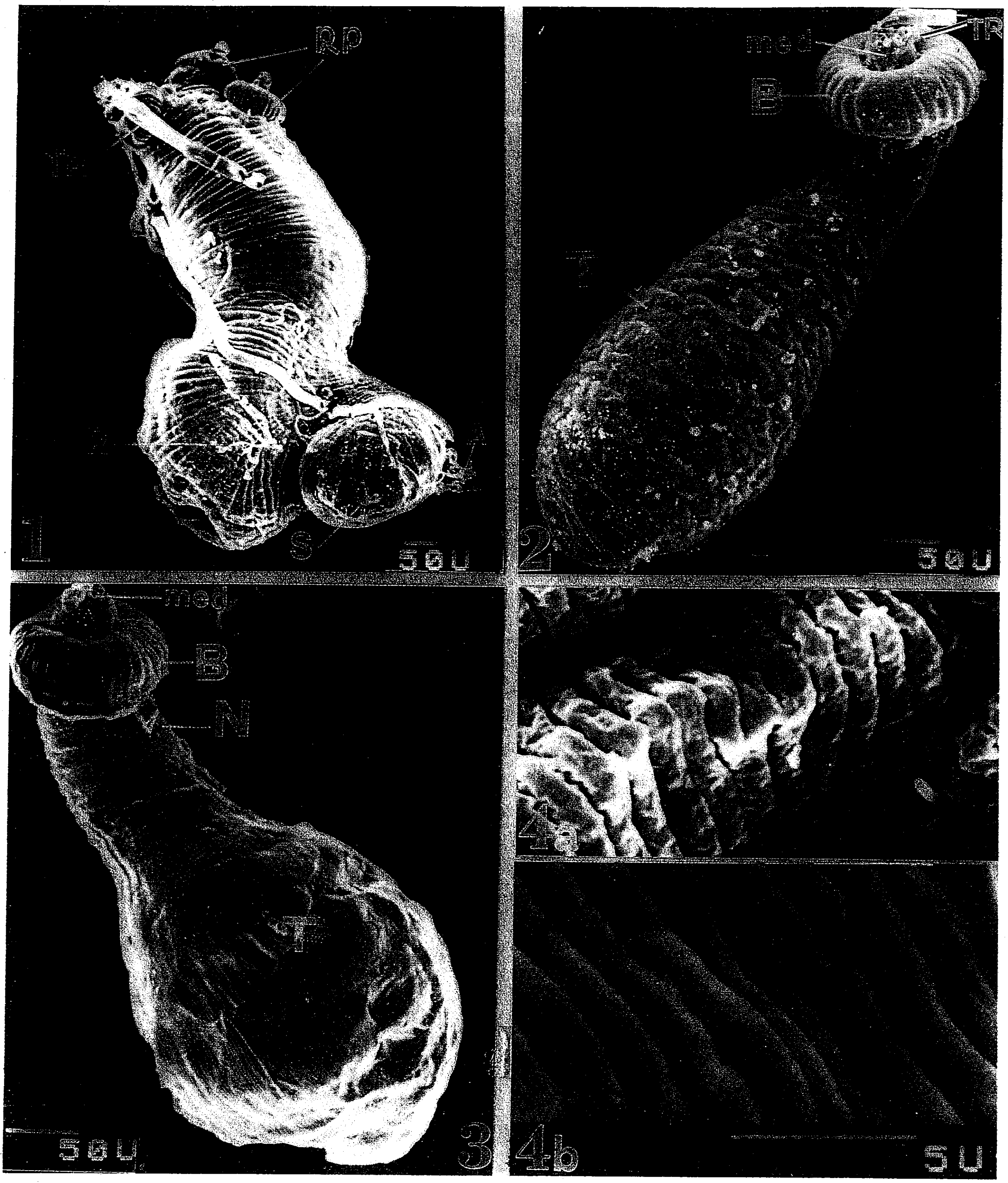
The base of the rectal papillae has a doughnut in shape, with about 35 or more segments in a radial arrangement (Fig. 5, Sg.). Several tracheae (TR) enter into a structure located in the central hole

Fig. 1. The rectum of the male *Dacus dorsalis*. Four circular bases of the rectal papillae (Rp) protrude from the anterior part of the rectum. A: Anal tube; R: Reservoir; S: Secretory sac.; TR: Tracheae.

Fig. 2. Micrograph of a rectal papilla which is comprised of the base (B) and the tip (T). med: Medulla, TR: Tracheae.

Fig. 3. The micrograph shows the rectal papilla of the mature male fly. Its posterior part is enlarged. Therefore, the whole papilla can be divided into three parts: the base, (B); the neck, (N); and the tip, (T).

Fig. 4. External structure of the rectal papillar tip. 4a, the texture of the cuticle of the normal fly. 4b, the texture of the cuticle while the rectal papilla is enlarged.



Rp
S
1
50U
med
TR
B
T
2
50U
med
B
N
T
50U
3
4a
4b
5U

of the base. This structure is the top of the medulla (med). There are a number of bridged structures connecting the doughnut base to the medulla, giving the top of the medulla a star-like shape.

The membrane system of the papilla differs in the base and the tip. The base is covered by a smooth membrane (Fig. 5, Sg.), while the tip is enclosed in a cuticle, which looks like scales at lower magnification (Fig. 2). The cuticle forms longitudinal strands with waving folds under high magnification (Fig. 4a). However, these waving folds disappear (Fig. 4b) when the papilla enlarges.

Comparison of the rectal papillae of the flies at various ages, i.e. from one- to ten-day old, has shown no significant difference in size (see Table 1). They range from 0.58 to 0.64 mm in length, and from 0.16 to 0.22 mm in width. However, they become substantially wider upon sexual maturation, i.e. four to ten days after emergence, compared to those at the younger stage, i.e. one to three days after emergence.

Table 1
The length and width of rectal papillae of the male adults of *Dacus dorsalis*

Age of flies (days)	Length (mm) Mean±SD	Width (mm) Mean±SD
1	0.62±0.009 ab	0.17±0.002 b
2	0.64±0.002 a	0.17±0.0001 b
3	0.62±0.003 ab	0.16±0.0001 b
4	0.61±0.004 ab	0.20±0.002 ab
5	0.58±0.002 b	0.20±0.005 ab
6	0.60±0.004 ab	0.20±0.005 ab
7	0.63±0.004 ab	0.18±0.002 ab
8	0.61±0.0006ab	0.19±0.003 ab
9	0.61±0.006 ab	0.22±0.0004a
10	0.59±0.002 ab	0.20±0.004 ab

Data analyzed by Duncan's New Multiple-Range Test. Means with the same letter are not significantly different at $\alpha=5\%$.

II. Internal structure of rectal papillae

The internal structure of *D. dorsalis* rectal papillae is comprised of epithelial cells, collectively named the cortex (COR), and the tube structure of the medulla (med).

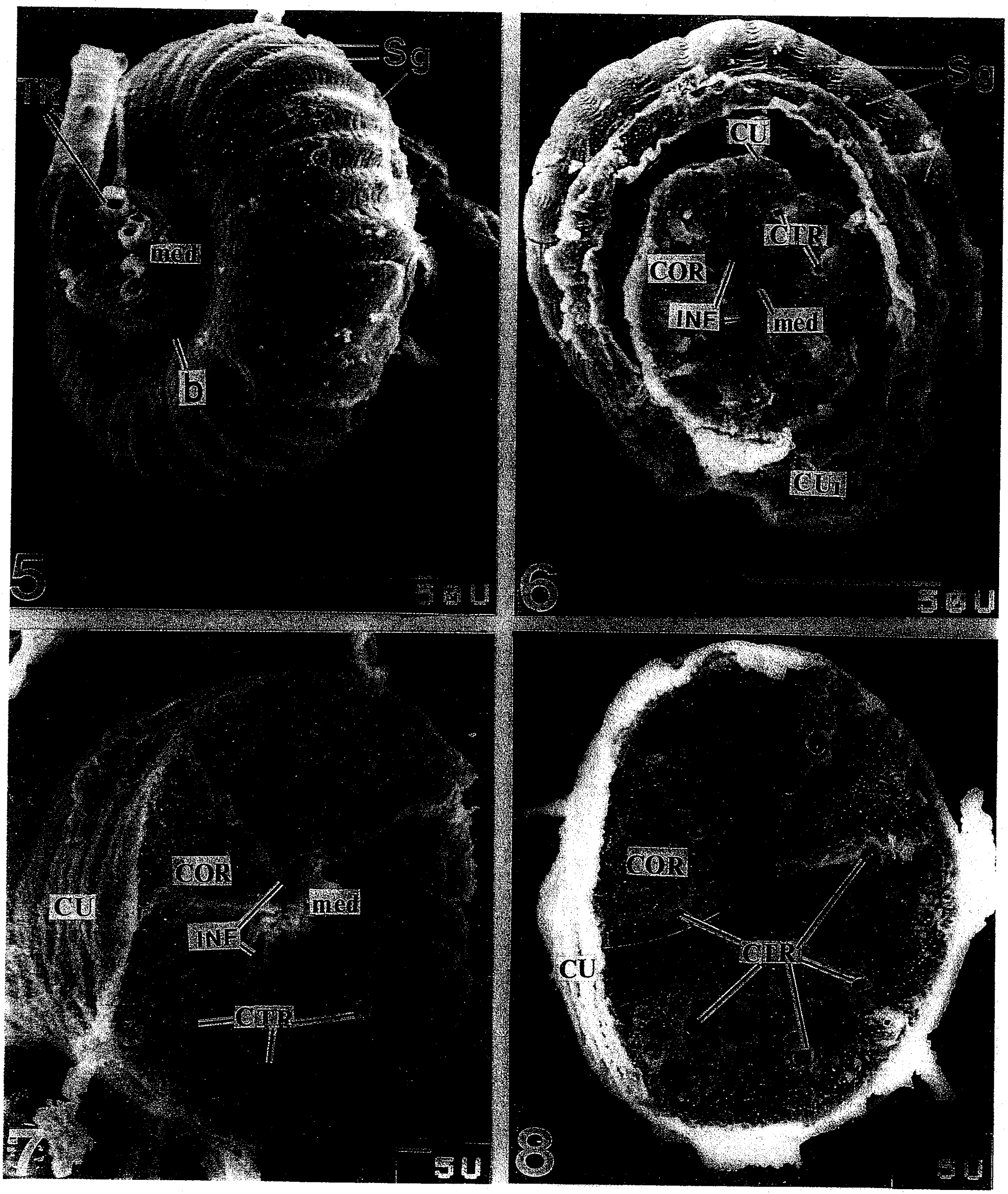
The micrographs of transverse fractures (Figs. 6 to 8) show that the cortex is covered with a layer of cuticle. The cortical epithelial cells (COR) appear in a columnar shape, with a radial arrangement from the center of the fracture (Figs. 6, 7). The medulla (med) is located in the center of the papilla. Between the cortical epithelial cells and the medulla, there is a vacuum space named the infundibulum (INF). The medulla and the infundibulum extend to the posterior tip (Fig. 8). The texture of the cortex in the posterior part appears more loose, with several vacuums present known as the intercellular sinuses (INSS). The cortical tracheae are easily found in pairs in the cortical epithelial cells (Figs. 6 to 8, CTR).

Fig. 5. A micrograph of the rectal papillar base, which is covered by a membraneous structure and distinguished by many segments (Sg). The center of the base is the top of the medulla (med), where several tracheae (TR) enter.

Fig. 6. A transverse fracture of the anterior part of the rectal papilla. There are several pairs of cortical tracheae (CTR) located at the cortical epithelium (COR). The medulla (med) is in the center of the fracture. Between the cortical epithelium (COR) and the medulla (med) is the infundibulum (INF). The rectal papilla is sheathed by a layer of cuticle (CU).

Fig. 7. A transverse fracture of the middle part of the rectal papilla, similar to the anterior part shown in Figure 6.

Fig. 8. A transverse fracture of the posterior part of the rectal papilla shows no medulla nor infundibulum. Several intercellular sinuses (INSS) are found in this part.


Sg
TR
med
b
5
50U
Sg
CU
CTR
COR
INF
med
CU1
6
50U
COR
CU
med
INF
CTR
7
5U
COR
CU
CTR
8
5U

From the longitudinally fractured sections (Figs. 9, 10), the the cortical epithelial cells (COR) of the base are columnar in shape and the medulla (med) and the tracheae (TR) combined together appear as a hat structure topping the medulla itself. From the hat structure, a tubular-shape section of the medulla (med) extends down through about two thirds of the tip of the papilla (Fig. 10, med). The medulla is obviously located in the cavity of the infundibulum (INF). The many spine-like structures (Figs. 9 to 11, b) protruding from the medulla are the trabeculae, connecting it to the cortex.

The cortical cells of the tips are typically columnar in shape, as shown in the micrographs of longitudinally fractured specimens (Fig. 10, COR). The cortex is covered by a sheath of cuticle (Fig. 10, Cu). The edges of the cells next to the infundibulum have a distinctive membrane called the basement membrane (Fig. 11, BM). The cortical tracheae (Fig. 9, CTR) extend through two sides of the cortex within the intercellular space (INS). There are large intercellular sinuses at the posterior part of the tip (Fig. 10, INSS). In the higher magnification micrograph (Fig. 11), one can see cellular substances in the cells, and the intercellular space between cells. When the papilla is enlarged, the cortical epithelial cells of the tip are mixed up together and cannot be distinguished from each other, the basement membrane of the cell and the infundibulum have disappeared, and the medulla appears to be lying on the cortex. Also, the medulla becomes much more slender that of the normal papilla (Fig. 11).

DISCUSSION AND CONCLUSION

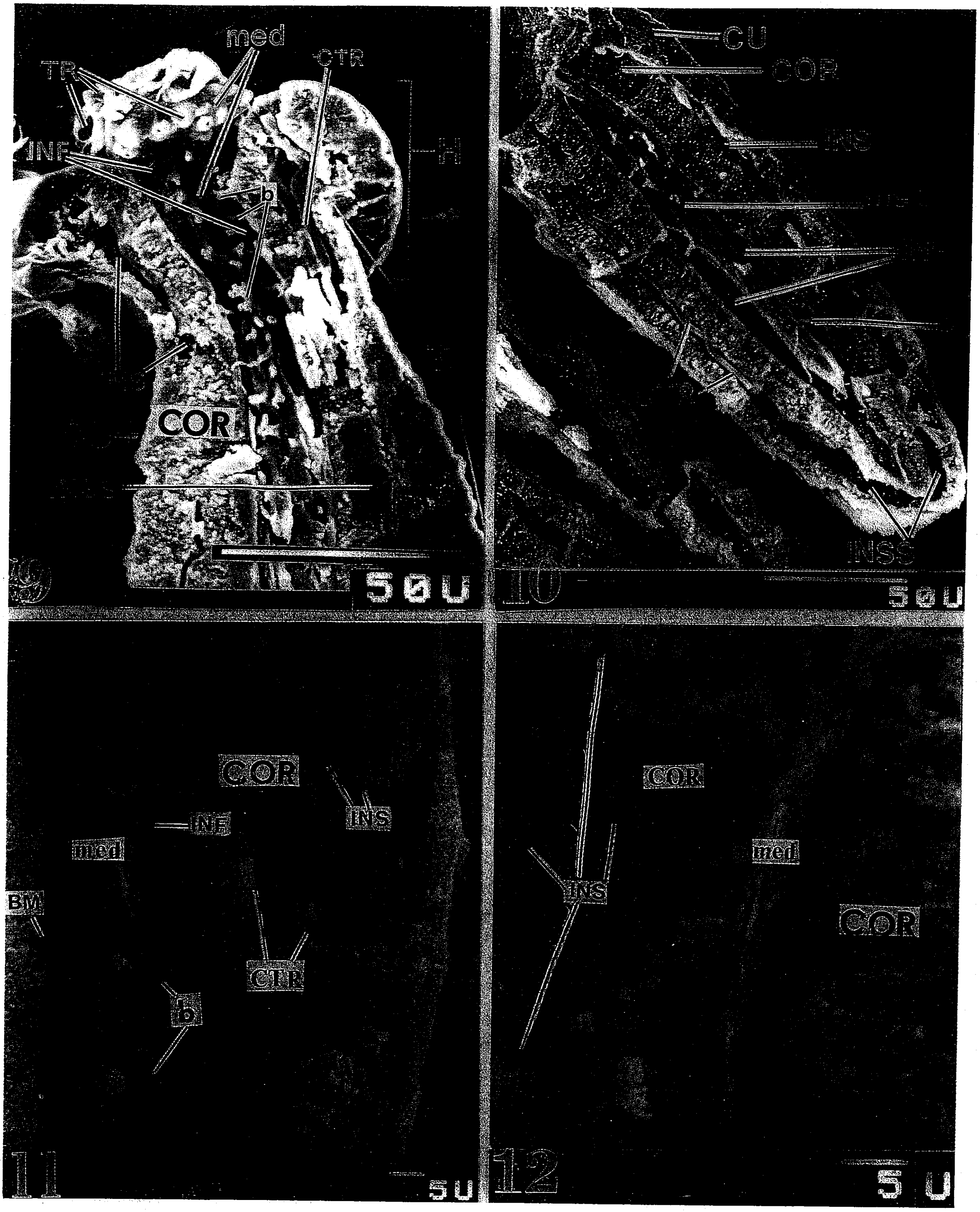
The rectal papillae of insects play an active role in transport of ions and water from the rectum (Smith, 1968; Berridge, 1967, 1970). Wigglesworth (1932) first recognized that the special structures (rectal pads, rectal papillae, etc.) associated with the rectum are responsible for absorbing ions and water. Earlier authors suggested were several alternative functions for this organ, such as respiration (Deegener, 1913); endocrine secretion (Martiis, 1924); absorption of organic food materials (Berless, 1909;

Fig. 9. A longitudinal fracture of the rectal papilla is comprised of two parts: The base, (B); and the tip, (T). The internal structure can be separated into the cortical epithelium (COR) and the medulla (med). Between these structures, there is a cavity of the infundibulum (INF). Many bridge-like structures of the trabeculae (b) connect the medulla and the plasmic basement membrane of epithelium. The intercellular spaces (INS) are located in the cortical epithelium.

Fig. 10. The micrograph shows the whole longitudinal fracture of the tip of the rectal papilla. The medulla (med) appears rod-like in shape, extending through to about one-third of the tip. There are intercellular sinuses (INSS) in the posterior part of the tip. b, trabecula; CU, cuticle; COR, cortical epithelium; INF, Infundibulum; INS, intercellular space.

Fig. 11. A high magnification micrograph of a part of the tip shows the structure of the cortex (COR) and the medulla (med), and the relationship of the trabecula (b) between the cortex and the medulla.

Fig. 12. A high magnification micrograph shows the structure of the posterior part of the tip while the rectal papilla is enlarged. The medulla (med) has become slender, lying on the cortex (COR). The infundibulum almost disappears. The cortical epithelial cells are disordered and interspersed with intercellular space (INS).


TR
med
CTR
INF
H
b
COR
50U
CU
COR
INS
INSS
10
50U
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INF
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BM
CTR
b
11
5U
COR
INS
med
COR
12
5U

Borri, 1925); excretion (Lowne, 1895; Hewitt, 1914); secretion (Petrunkewitsh, 1899; Trappman, 1923; Abbott, 1926); or simply mechanical support of the rectum. While some of these alleged functions have already been refuted by subsequent physiological work (Graham-Smith, 1934; Wigglesworth, 1965), secretion of ions rather than absorption has been suggested by Schmidt-Nielson (1965). Gupta and Berridge (1966b) pointed out that the rectal papillae of the blowfly, *Calliphora erythrocephala*, may use apical membranes of the epithelial cells for three functions: (a) secretion of hydrogen ions; (b) functioning as an ion exchange pump; (c) serving as an energy expending ion and/or water transport system. Berridge and Gupta (1967, 1968), in their investigation on the rectal papillae of the adult blowflies, then elucidated the possible mechanism of reabsorption of water and ions from the rectal lumen to the haemolymph and the transportation of ATPase. Hopkins (1967) observed the epithelial transport of water and inorganic ions in the rectal papillae of *Aedes aegypti*. Flower and Walker (1979) reported that water and ions can penetrate the cuticle of the rectal papillae of *Musca domestica*, and the lateral plasmic membrane of its epithelial cells are generally considered to be the main site of active transport.

Although there is no significant difference between the lengths of rectal papillae of male flies at various ages, the widths of papillae of immature and sexually mature male flies show substantial differences. The posterior part of the rectal papillae in the mature male *D. dorsalis* is enlarged (Fig. 3), with the production of the sex pheromone giving the rectum a balloon shape (Lee *et al.*, 1986; Lee and Chang, 1986). Implied is that the size changes of rectal papillae are strongly related to whether the male fly has reached sexual maturity. De Marzo *et al.* (1978) studied the anatomy, histology and physiology of the rectum and the rectal papillae in *Dacus oleao*, and proved a hypothesis in which the production and storage of the sex pheromone in the gland is associated with the rectum. The same evidence was reported by Schultz and Boush (1971) and Economopoulus *et al.* (1971) with the same fly. The latter authors additionally found that the rectum enlarges like a balloon when the male *D. oleae* produces the sex pheromone. However, De Marzo *et al.* (1978) did not relate sex pheromone production to enlargement of either the rectum or the rectal papillae in *D. oleae* fly, as the present observations infer for *D. dorsalis*. The physiological function of the rectal papillae enlargement and its relationship to the production of the sex pheromone requires further study.

D. dorsalis rectal papillae have a similar general organization to those of *D. oleae* (De Marzo *et al.*, 1978) and the blowfly (Gupta and Berridge, 1966a). The external structure of *D. dorsalis* rectal papillae strongly recalls in some aspects that reported in *Ceratitis capitate* by Dallai *et al.* (1987), who also used scanning electron microscopy. The surface of the papillae shows many folds running sinuously along the major axis (Figs. 4a and b). However, there are denticulations of numerous shapes at different levels of *C. capitate* rectal papillae, which never occur in those of *D. dorsalis*.

The internal organization of *D. dorsalis* rectal papillae is very similar to those of several Dipterans: *Calliphora erythrocephala* (Gupta and Berridge, 1966a); *Drosophila melanogaster* (Wessing and Eichelberg, 1973); *Dacus oleae* (De Marzo *et al.*, 1970) and *Ceratitis capitata* (Dallai *et al.*, 1985). All of them are comprised of a cortical epithelial cell layer and a medulla. Between them there is a round and deep cavity of infundibular space. The cell layer includes one or more regions of intercellular space towards the tip of papilla, in part forming the intercellular sinus. Both the intercellular sinus connect to the cavity of the infundibulum.

The medulla, which lies inside the rectal papilla, is composed of connective tissue cells, neurosecretory axons and tracheae. All of them are embedded within an extracellular matrix of collagen and mucopolysaccharide (Berridge, 1970). In the present observations using the scanning electron microscope, the medulla appears as a rod-shaped structure with many trabeculae, connecting to the cortical epithelial cells similar to that of the blowfly. The trabeculae provide the channels for the "flow" of collagen-like fibrils produced by the medulla (Gupta and Berridge, 1966a). Graham-Smith (1934) believed that the trabeculae were "Perforated with very fine canals, named transinfundibular canals", which allow a flow of nutritive fluid from the medullary cavity into the subcellular cavity of the cortical epithelial cells.

In the blowfly rectal papillae, there is an infundibular valve located at the opening of the infundibular space to the haemocoel. This valve is made up of a thin sheet of medullary cells enclosed within connective tissue and shown as a completely transparent contents from the transmission electron microscopic investigation (Gupta and Berridge, 1966a). In *D. dorsalis* rectal papillae, instead of the valve, several trabeculae connect the medulla and the basement membrane of the cortex at the opening of the infundibular space. The fine structure of those trabeculae will be investigated in a further report of transmission electron microscopic studies.

The cortical tracheal branches of the blowfly diverge from the main tracheal trunk in the medulla. The tracheal branches enter the cortical epithelium in pairs (Gupta and Berridge, 1966a). However, referring to the present study for *D. dorsalis*, there are several tracheal trunks entering the cortex through the top of the medulla, sometimes bifurcating from one tracheal trunk before extending into the medulla (Fig. 5, TR). In the cortex, the branched cortical tracheae always appear as a pair in the epithelium.

Based on morphological studies, the structure of *D. dorsalis* rectal papillae is quite similar to those of the blowfly. From a physiological point of view, the rectal papillae of both flies include an extensive system of intercellular spaces, with intercellular sinuses in the apical regions. The intercellular spaces and intercellular sinuses are enclosed by the lateral plasmic membranes of the epithelial cells. The contents of the intercellular sinuses are presumably evacuated only through the infundibular space into the haemolymph. In the blowfly rectal papillae, those contents flowing from the infundibular space into the haemolymph are controlled by the infundibular valve (Gupta and Berridge, 1966a). In *D. dorsalis*, however, they flow directly from the opening of the infundibular space into the haemolymph uncontrolled by any valve. Berridge and Gupta (1967) suggested that the contents were controlled entirely by osmotic activity of the epithelial cells of the rectal papillae. The epithelial cells absorb water and ions from the rectal lumen by "pumping ions", such as potassium, into the intercellular spaces. From comparisons of the rectal papillae in both insects, it can be postulated that the function of the rectal papillae of *D. dorsalis* is the transportation of water and ions from the rectal lumen to the haemolymph via absorption of cortical epithelial cells into the intercellular space, the intercellular sinus and finally to the infundibulum.

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利用掃描電子顯微鏡研究東方果實蠅雄性成蟲直腸突起之形態

李文蓉　程建中　林美容

東方果實蠅 (*Dacus dorsalis* Hendel) 具有四個直腸突起 (Rectal papillae)，每個直腸突起呈圓錐狀，其外部形態可分爲兩部：頂部呈圓圈狀於直腸前端突出於體腔稱基部 (Base)，其他末端呈圓錐狀插入直腸腔內部份稱爲端部(Tip)。基部由一層基膜 (Basement membrane) 包著，端部外層爲角膜 (Cuticle)。直腸突起之大小與成蟲羽化後日齡關係不顯著，其長爲 0.58 至 0.64 mm，寬爲 0.16 至 0.22 mm 間。當雄蠅性成熟而分泌費洛蒙時，直腸突起呈膨脹之現象，與初羽化者有明顯之差別。直腸突起的內部結構分皮層 (Cortex)和髓部 (Medulla) 兩者間有漏斗溝 (Infundibular space)相隔，並有許多橫條 (Trabeculum) 連絡。皮層上皮細胞 (Cortical epithelium) 間有細胞間隙 (Intercellular spaces)。氣管從髓部頂部插入分至皮層，成對的排列於細胞間隙內。直腸突起末端三分之一處，欠髓部和漏斗溝，完全爲皮層，但有許多大型的細胞間竇 (Intercellular sinuses)。東方果實蠅直腸突起可能具水分及離子運輸之生理功能。