

皱纹盘鲍肠粘膜上皮的结构和功能*

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摘 要 以透射电镜和扫描电镜观察、组织化学及酶活性测定等方法研究了皱纹盘鲍的肠和直肠。肠和直肠粘膜上皮由 5 种细胞组成。具微绒毛的柱状细胞呈现吸收细胞的超微结构特征, 纤毛柱状细胞参与运输食物颗粒和粪便, I 型腺细胞具蛋白酶、非特异性酯酶和脂酶活性, 以顶浆分泌形式分泌消化酶, II 型腺细胞分泌物可能与包裹粪便有关, 杯状细胞分泌酸性粘多糖。体外酶活性分析表明肠和直肠粘膜上皮分别只有 4 种和 3 种植物多糖酶。

关键词 皱纹盘鲍 肠 直肠 结构 功能 酶

皱纹盘鲍 (*Haliotis discus hannai* Ino) 隶属腹足纲、前鳃亚纲, 是我国北方沿海人工养殖的一种珍贵的经济贝类, 以褐藻、红藻等为食, 也可吞食小动物。与食性相适应, 其消化道甚长, 约相当于体长的 3 倍, 其中尤以迂曲的肠最长 (Dales, 1981)。刘传林等 (2000) 和崔龙波等 (2001) 分别对皱纹盘鲍齿舌和消化腺的结构与功能进行了研究。Boer 等 (1990) 和 Franchini 等 (1992) 分别对腹足类动物 *Lymnaea stagnalis* 和 *Planorbium corneum* 的肠的研究指出, 这两种动物的肠粘膜上皮均由多种不同类型的细胞组成, 肠不仅仅涉及机械消化的功能, 还参与内吞、吸收、分泌等活动, 其功能甚至比消化腺还复杂和重要。皱纹盘鲍肠和直肠粘膜上皮具有哪些特点, 在机体消化过程中发挥什么作用? 作者通过透射电镜和扫描电镜观察、组织化学及酶活性分析等方法以期解决上述问题, 为皱纹盘鲍的消化生理研究提供理论依据。

1 材料和方法

1.1 材料

36 只皱纹盘鲍于 1996 年 5 月取自烟台市芝罘区隆海海珍品养殖场, 鲍壳长 5.8~6.2cm, 壳宽 3.7~4.2cm, 雌、雄个体分别为 17 只和 19 只。解剖取出肠 (前、中、后段) 及直肠后进行研究。

1.2 方法

1.2.1 透射电镜观察 组织块用 2.5% 戊二醛和 1% 锇酸双固定、梯度酒精脱水、Epon812 环氧树脂

脂包埋, 切片厚 50~70 nm, 醋酸铀和柠檬酸铅双重染色。JEM-1200EXII 型透射电镜观察。

1.2.2 扫描电镜观察 将肠和直肠粘膜上的粘液冲洗干净后, 于 2.5% 戊二醛和 1% 锇酸双固定、梯度丙酮脱水、醋酸异戊酯置换、常规临界点干燥、离子镀膜。日立 S-570 型扫描电镜观察。

1.2.3 组织化学研究 依染色方法的不同, 组织块分别置于 10% 福尔马林液、Bouin 氏液、Zenker 氏液或 Carnoy 氏液固定、石蜡包埋、切片厚 5~8 μm 。进行以下染色: PAS 反应显示多糖、唾液消化后 PAS 反应显示糖原、Alcian 蓝-PAS 反应区分中性与酸性粘多糖、汞溴酚蓝法显示蛋白质、对二甲氨基苯甲醛-亚硝酸盐法显示色氨酸、Turnbull 氏蓝法显示铁、以及茜素红 S 法显示钙。

新鲜组织块直接于恒冷冰冻切片机上切片, 切片厚 6~10 μm 。切片分别进行以下染色: Cunningham 氏明胶薄膜法显示蛋白酶、Gomori 氏吐温 (40 和 80) 法显示脂酶、酸性乙酸- α -萘酚-六偶氮对品红法显示非特异性酯酶、Gomori 氏硝酸铅法显示酸性磷酸酶、Gomori 氏钙钴法显示碱性磷酸酶、以及苏丹黑 B 法显示脂类。以上组织化学方法见 Pearse (1983)。

1.2.3 酶活性测定 5 只个体为一组, 平行测定三组。肠和直肠粘膜上皮经匀浆后, 进行以下 4 种多糖水解酶活性的测定: 用 3, 5-二硝基水杨酸显色法测定淀粉酶、纤维素酶和海藻多糖酶的活性 (Bernfeld, 1955), 以波长 232 nm 进行紫外光吸收

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测定褐藻酸酶活性 (Boyd *et al.*, 1977), 以牛血清蛋白为标准, 用考马斯亮蓝 G250 显色法测定蛋白质 (Bradford, 1976)。

2 结果

2.1 透射电镜观察

皱纹盘鲍的肠可均等地分为前、中、后三段。肠与直肠粘膜上皮由 5 种细胞组成: 具微绒毛的柱状细胞、纤毛柱状细胞、I 型腺细胞、II 型腺细胞和杯状细胞。

具微绒毛的柱状细胞: 是肠中、后段除肠沟外的主要组成细胞。细胞游离缘具密集的微绒毛 (图版 I: 1), 微绒毛长约 $2.0 \mu\text{m}$, 直径约 $0.1 \mu\text{m}$ 。游离端质膜常见内陷, 质膜下方有大量直径为 $0.05 \sim 0.1 \mu\text{m}$ 的胞饮泡 (图版 I: 2)。在细胞顶端, 有许多线粒体和少量的多泡小体 (图版 I: 1), 细胞之间通过桥粒等相互连接。在细胞中部, 见数量不等的内含电子致密物质的次级溶酶体, 高尔基体和内质网主要位于核的上方, 许多大小不一的脂滴主要见于细胞中部 (图版 I: 3)。肠后段的具微绒毛的柱状细胞其基物质膜内折形成指状突起、深入细胞内部, 指状突起之间含有大量的线粒体 (图版 I: 4)。在细胞基部与基底膜之间常见神经分布 (图版 I: 5)。

纤毛柱状细胞: 是肠前段、肠沟和直肠的主要组成细胞。细胞游离缘具密集的纤毛, 纤毛长约 $9 \mu\text{m}$, 直径约 $0.2 \mu\text{m}$ 。基体与纤毛小根清晰可见, 带横纹的纤毛小根深插入细胞内部, 大量的线粒体分布于纤毛小根之间 (图版 I: 6)。细胞游离缘还有稀疏的微绒毛。纤毛柱状细胞的其它结构与具微绒毛的柱状细胞相似。

I 型腺细胞: 在肠由前至后该细胞数量逐渐增多, 在直肠则少量存在。该细胞游离端狭窄, 游离缘有短的微绒毛。该细胞的显著特征是在细胞中部、特别是基部含有大量的分泌颗粒 (图版 I: 4, 7)。分泌颗粒表面有被膜, 小者直径约 $0.05 \mu\text{m}$, 大者约 $0.6 \mu\text{m}$ 。大多数分泌颗粒的内容物均质、电子密度致密, 少数颗粒由呈中等电子密度的细颗粒状物组成。在细胞基部, 数十个或数百个分泌颗粒再由膜包围而集中在一起, 挤压邻近细胞而使后者狭窄 (图版 I: 4, 7)。在细胞中部, 分泌颗粒多散在于细胞中。

II 型腺细胞: 主要分布于直肠, 肠沟也少量存在。该细胞的结构特征为细胞顶端和中部充盈大量

的分泌颗粒 (图版 I: 8)。仅有内质网和高尔基体等少量细胞器被挤压于细胞基部。具被膜的分泌颗粒较大, 平均直径 $1.1 \mu\text{m}$, 内容物呈细沙状, 电子密度致密。有的分泌颗粒破裂, 内容物溢出。细胞游离缘有微绒毛。可见游离面质膜破裂, 释放出分泌颗粒或其内容物 (图版 I: 8)。

杯状细胞: 少量散在于肠, 直肠数量较多。细胞内充满大量的分泌颗粒 (图版 I: 6)。

2.2 扫描电镜观察

肠前段内壁形成几条不规则的纵行褶皱, 其上皮细胞为具纤毛的细胞, 但纤毛较稀疏 (图版 I: 9)。至肠中段, 纵行褶皱逐渐变小至消失, 仅剩两条纵行褶皱形成了肠沟, 其余部分的肠内壁则形成有规律的环形褶皱 (图版 I: 10)。肠沟的纵行褶皱的粘膜上皮主要为具纤毛的细胞, 在纤毛细胞之间散在表面具球形分泌物的细胞。肠沟以外的粘膜上皮一类是表面具密集微绒毛的细胞, 该细胞顶部较平整, 形态不规则, 直径大小不一, 平均约 $7.0 \mu\text{m}$ (图版 I: 11)。另一类细胞散布于具微绒毛的细胞之间, 细胞顶端直径明显小于具微绒毛的细胞, 细胞表面有短而稀疏的微绒毛, 许多细胞顶端细胞质向腔内凸出, 形成大小不等的球形分泌泡 (图版 I: 11)。当其内容物排出后, 细胞顶端则形成大小不等的孔洞。此类细胞为 I 型腺细胞。

直肠内壁形成 3~4 条粗大的纵行褶皱。直肠粘膜上皮主要为具纤毛的细胞, 纤毛密集。在纤毛细胞之间散在着顶端具大小不等的球形分泌物的细胞 (图版 I: 12), 它们是杯状细胞或 II 型腺细胞。

2.3 组织化学研究

PAS 反应: 杯状细胞的细胞质呈阳性, 具微绒毛的柱状细胞的微绒毛和 II 型腺细胞的分泌颗粒呈弱阳性。唾液消化后 PAS 反应: 粘膜上皮细胞均呈阴性, 不含糖原。Alcian 蓝-PAS 反应: 杯状细胞的细胞质呈蓝色。汞-溴酚蓝法: I 型腺细胞和 II 型腺细胞的分泌颗粒分别呈蓝色和深蓝色。对二甲氨基苯甲醛-亚硝酸盐法: II 型腺细胞的分泌颗粒呈深蓝色, 但 I 型腺细胞的分泌颗粒呈阴性。Turnbull 氏蓝法: 具微绒毛的柱状细胞和纤毛柱状细胞的顶端细胞质有细小的蓝色颗粒, 肠腔与直肠腔中也有蓝色内容物。茜素红 S 法: 粘膜上皮细胞均呈阴性。Cunnigham 氏明胶薄膜法: I 型腺细胞的顶端细胞质及游离缘呈透明空斑, 显示蛋白酶活性 (图版 I: 13)。Gomori 氏吐温法: I 型腺细胞的细胞质有少量棕黑色颗粒, 显示脂酶活性。酸性

乙酸- α -萘酯-六偶氮对品红法: I型腺细胞、具微绒毛的柱状细胞和纤毛柱状细胞的顶端细胞质呈红棕色,显示非特异性酯酶活性,但肠沟处的细胞酶活性较弱(图版 I: 14)。Gomori 氏硝酸铅法: 粘膜上皮细胞均呈阴性,不具酸性磷酸酶活性。Gomori 氏钙钴法: 具微绒毛的柱状细胞的游离端质膜呈黑色,显示碱性磷酸酶活性(图版 I: 15)。苏丹黑 B 法: 具微绒毛的柱状细胞和纤毛柱状细胞有黑色颗粒。

2.4 酶活性测定

三组 15 只个体肠与直肠粘膜上皮的淀粉酶、纤维素酶及海藻多糖酶平均比活力分别为 253 ± 95 (15) 与 115 ± 31 (15)、 145 ± 65 (15) 与 101 ± 48 (15)、以及 85 ± 5 (15) 与 0, 单位为 $1 \mu\text{g}$ 葡萄糖/min/mg 蛋白质; 褐藻酸酶的平均比活力分别为 0.79 ± 0.23 (15) 与 0.31 ± 0.06 (15), 单位为 1.0 光密度/hr/mg 蛋白质。

3 讨论

研究表明: 皱纹盘鲍的肠和直肠不只是食物和粪便通过的管道, 还具有更为复杂的功能。肠与直肠粘膜上皮由 5 种细胞组成, 它们分别发挥着各自不同的作用。具微绒毛的柱状细胞游离面具密集而长的微绒毛, 质膜内陷和细胞游离端出现大量的胞饮泡, 细胞中部出现表明进行物质降解的次级溶酶体, 细胞内含有贮存物质(脂滴), 这些都是吸收细胞的超微结构特征(Boer *et al.*, 1990; Bush, 1988; Franchini *et al.*, 1992)。组化研究亦表明, 具微绒毛的柱状细胞的游离端质膜显示碱性磷酸酶活性, 而碱性磷酸酶与物质的跨膜转运有关(Franchini *et al.*, 1992)。因此, 具微绒毛的柱状细胞具有从肠腔吸收养分的作用。此外, 肠后段具微绒毛的柱状细胞的基部质膜形成内褶, 内褶之间有许多线粒体, 这是水和离子转运细胞的形态

学特征(Boer *et al.*, 1990; Payne *et al.*, 1989), 表明肠后段的具微绒毛的柱状细胞还可以从肠腔中吸收水和离子。

I型腺细胞的结构特征是细胞内含有大量的分泌颗粒, 组化研究表明具有蛋白酶、非特异性酯酶和脂酶活性, 体外酶活性分析检测到肠和直肠上皮细胞具有四种和三种植物多糖酶活性, 扫描电镜下观察到 I型腺细胞的顶端细胞质凸出, 表明 I型腺细胞可能以顶浆分泌的形式分泌消化酶, 从而在肠和直肠腔内进行细胞外消化。

II型腺细胞亦含有大量的分泌颗粒。普通组织学检查很难分辨出 I型和 II型腺细胞分泌颗粒的差异, 二者均嗜酸性, 只是前者主要位于细胞的中基部、后者主要位于细胞的中上部(崔龙波等, 1995)。本研究表明 I型和 II型腺细胞的分泌颗粒在大小、性质上均有不同。II型腺细胞的分泌颗粒含色氨酸, 但 II型腺细胞不具蛋白酶、非特异性酯酶和脂酶活性。II型腺细胞与帽贝 *Patella vulgata* 肠棒状腺细胞的结构相似, 其蛋白性分泌物可能起凝固剂作用而加固粪团(Bush, 1988)。

纤毛柱状细胞亦具有像具微绒毛的柱状细胞类似的超微结构和组化性质, 表面亦具有一定的吸收作用(Boer *et al.*, 1990)。但纤毛柱状细胞的主要结构特征是具有纤毛及纤毛小根之间含有大量的线粒体, 并且该细胞主要分布于肠沟及直肠, 故纤毛柱状细胞的主要功能是依靠纤毛的摆动运送食物颗粒和粪便。

杯状细胞大量存在于其它腹足类动物如脉红螺(侯林等, 1991)、*Lymnaea stagnalis* (Boer *et al.*, 1990) 和 *Planorbarius corneus* (Franchini *et al.*, 1992) 等的肠道中。组化研究表明皱纹盘鲍肠和直肠的杯状细胞分泌酸性粘多糖, 故杯状细胞通过其分泌物而起润滑作用, 使食物和粪便的运送更为容易, 同时还起到粘合粪便的作用。

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外 文 摘 要 (Abstract)

STRUCTURE AND FUNCTION OF MUCOUS EPITHELIUM OF THE INTESTINE IN *HALIOTIS DISCUS HANNAI* *

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Disk abalone (*Haliotis discus hannai* Ino) is one of the important marine cultivated species in North China. Brown algae and red algae are the chief foods of disk abalone. They can also swallow small animals. Adopting to their food habit, they have a very long digestive tract. It's about 3 times longer than their bodies. In previous years, studies on the digestion of disk abalone were mostly concentrated to the roles of the digestive glands and those of the digestive tract has been neglected. In this paper the intestine and the rectum of *Haliotis discus hannai* Ino were studied with TEM and SEM observations, histochemical methods and tests for some enzymatic activities. The intestine can be evenly divided into anterior, middle and posterior. The epithelia of the intestine and the rectum are composed of 5 types of cells: (1) The cells with microvilli were the main cell type in the mid and prointestine. Their free borders were closely aggregated of microvilli. They were 2.0 μm long and 0.1 μm in diameter. Under the cell membrane there were many pinocytic vesicles. On the top of the cell there were a lot of mitochondria and multivesicular bodies. In the middle of the cell some secondary lysosomes and many lipid drops of different size were found. In the postintestine at the basal part of the cells, the cell membrane went inward, deeply into the cell to form some finger-like protrusions. Among them, there were many mitochondria. Some nerves could be seen between the cell membrane and the basal membrane. (2) Ciliated cells' structures were similar to those of the microvilli cells. Instead of microvilli, the free border of the cell was aggregated of cilia. The basal bodies and the ciliary rootlets could be seen clearly. There were a lot of mitochondria among the rootlets. Ciliated cell was the main cell type in the prointestine, typhlosoles of intestine groove and rectum. (3) Gland cells I were distributed in the intestine. Its amount increased from the beginning to the end. There was only a small amount in rectum. The cells were narrow at top and there were some short microvilli on the free border. The striking character of these cells was that a large amount of secreting granules surrounded by membrane dispersed in the cells. At the basal part of the cells, tens or hundreds of granules were surrounded together

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by membrane again to form bulks which squeezed the neighbor cells and made them narrow in shape. Histochemical studies showed that the granules contained proteinase, nonspecific esterase and lipase, and there were 4 and 3 kinds of polysaccharide enzymes in intestine and rectum respectively. On the apices of many cells, there were swellings containing enzymatic secretion. (4) Gland cells II were mainly distributed in the rectum and typhlosoles. The top and the middle part of the cells were full of secretory granules. The diameter of the granule was about $1.1 \mu\text{m}$. The content looked like sand and dense in electron density. The results of the analyses of proteinase, nonspecific esterase and lipase were negative. (5) The goblet cells were distributed mainly in rectum. The histochemical test showed that the goblet cells secreted mucopolysaccharide, and a large amount of mucoprotein filled in the cells. The results showed that the intestine and the rectum of the *Haliotis discus hannai* Ino were not only tracts for passing food and feces, they also played important roles in digestion. The cells with microvilli exhibited the ultrastructure feature of absorptive cells. They can absorb nutrition and water from the lumen of the intestine. The activity of the alkaline phosphatase at the top region of the cells showed that transportation through cell membrane were carrying on. The gland cells I may secrete digestive enzymes by the apocrine, so extracellular digestion could take place in the lumen. The secretion of the gland cells II may be used to consolidate feces. The vibration of the ciliated cells can facilitate the movement of the food and feces. The mucopolysaccharide secreted by the goblet cells can lubricate the lumen and cement feces.

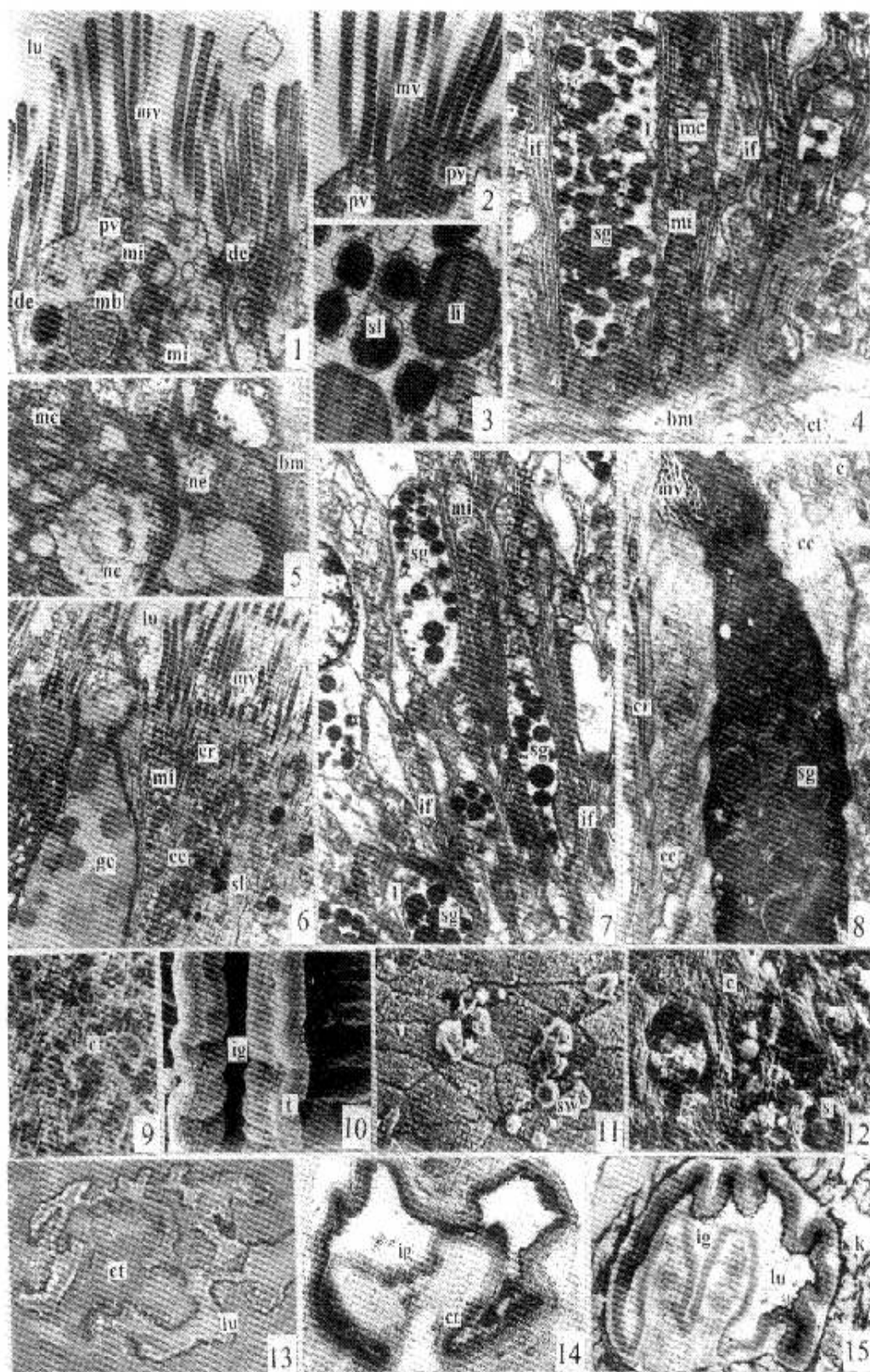
Key words *Haliotis discus hannai* Ino, Intestine, Rectum, Structure, Function, Enzyme

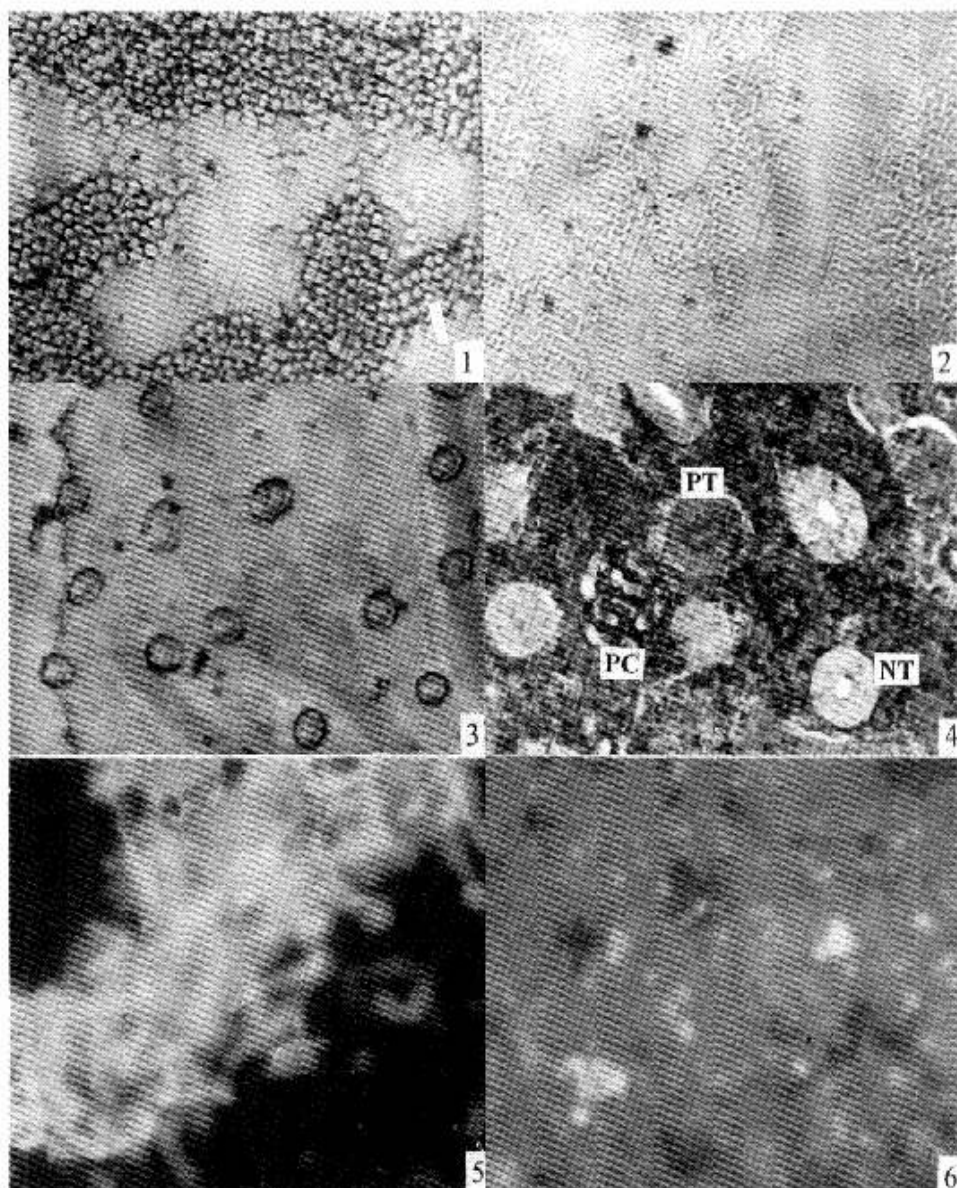
图 版 说 明 (Explanation of Plate)

图 版 I (Plate I)

1. 具微绒毛的柱状细胞游离端 (Apex of the columnar cells with microvilli) $\times 15\ 000$
2. 具微绒毛的柱状细胞游离端 (Apices of the columnar cell with microvilli) $\times 12\ 000$
3. 具微绒毛的柱状细胞中部 (Middle region of the columnar cell with microvilli) $\times 8\ 000$
4. 肠后段粘膜上皮基部 (Basal region of epithelial cells in the postintestine) $\times 6\ 000$
5. 具微绒毛的柱状细胞基部 (Basal region of the columnar cells with microvilli) $\times 6\ 000$
6. 直肠粘膜上皮游离端 (Apex of the epithelial cells in the rectum) $\times 3\ 500$
7. 肠后段粘膜上皮基部 (Basal region of epithelial cells in the postintestine) $\times 6\ 000$
8. 直肠粘膜上皮游离端 (Apex of the epithelial cells in the rectum) $\times 6\ 000$
9. 肠前段 (Prointestine) $\times 1\ 000$
10. 肠中段 (Midintestine) $\times 40$
11. 肠后段 (Postintestine) $\times 1\ 200$
12. 直肠 (Rectum) $\times 700$
13. 肠中段横切面 (Cross section of the midintestine) $\times 10$
14. 肠后段横切面 (Cross section of the postintestine) $\times 25$
15. 肠后段横切面 (Cross section of the postintestine) $\times 25$

bm: 基底膜 (Basement membrane) c: 纤毛 (Cilia) cc: 纤毛柱状细胞 (Ciliated columnar cell) cr: 纤毛小根 (Ciliary rootlet) ct: 结缔组织 (Connective tissue) dc: 桥粒 (Desmosome) gb: 高尔基体 (Golgi body) gc: 杯状细胞 (Goblet-cell) ig: 肠沟 (Intestinal groove) If: 内褶 (Infolding) k: 肾脏 (Kidney) li: 脂滴 (Lipid) lu: 腔 (Lumen) mlb: 多泡小体 (Multivesicular body) mc: 具微绒毛的柱状细胞 (Columnar cell with microvilli) mi: 线粒体 (Mitochondrion) mv: 微绒毛 (Microvilli) n: 细胞核 (Nucleus) ne: 神经 (Nerve) pv: 胞饮泡 (Pinocytic vesicle) s: 分泌物 (Secretion) sg: 分泌颗粒 (Secretory granule) sl: 次级溶酶体 (Secondary lysosome) sw: 细胞顶端凸出 (Swelling of cell apices) t: 肠沟纵行褶皱 (Typhlosole) I: I型腺细胞 (Gland cell I) II: II型腺细胞 (Gland cell II)





1. 中华鳖胸腺印片, 示 ABC 法显示的 ConA 阳性标记的胸腺细胞 (Thymic imprint of *T. sinensis*, showing the positive thymocytes bound to ConA by ABC method) $\times 100$
2. 中华鳖胸腺印片, 示 ABC 法显示的 PWM 阴性标记的胸腺细胞 (Thymic imprint of *T. sinensis*, showing the negative thymocytes bound to PWM by ABC method) $\times 100$
3. 草鱼胸腺印片, 示 ABC 法显示的 ConA 阳性标记的胸腺细胞 (Thymic imprint of *C. idellus*, showing the positive thymocytes bound to ConA by ABC method) $\times 100$
4. 草鱼肾脏, 示 ABC 法显示的 PHA 阳性标记的肾小球 (PC) 和阳、阴性标记兼有的肾小管 (PT, NT) (Kidney of *C. idellus*, showing positive renal corpuscle (PC) and positive / negative renal tubules (PT/NT) bound in PHA by ABC method) $\times 200$
5. 中华鳖胸腺冰冻切片, 示 ConA 荧光标记的细胞群 (Thymic section of *T. sinensis*, showing the thymocytes bound to FITC-ConA) $\times 100$
6. 草鱼头肾冰冻切片, 示 ConA 荧光标记的细胞 (Head kidney section of *C. idellus*, showing the lymphocytes bound to FITC-ConA) $\times 100$