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The histochemistry and electronmicroscopy of Brunner's glands in the guinea-pig

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INTRODUCTION

The knowledge of the anatomy and physiology of Brunner's glands has recently been reviewed by Grossman (1958). They are believed to secrete an alkaline fluid containing mucin and no significant amounts of digestive enzyme have been associated with them. In all animals so far investigated, except rabbit, the secretory vesicles of the acinar cells are similar in histological appearance to the mucin droplets in the goblet cells of the intestines. These secretory vesicles vary greatly in their staining reactions in different animals (Florey & Harding, 1934; Jennings & Florey, 1956). Bensley (1903) could not identify a Golgi apparatus in the acinar cells but Florey & Harding (1933) figure this in a supranuclear position and suggest that the 'mucin is being elaborated in contact with the trophospongium'.

MATERIAL AND METHODS

Four adult guinea-pigs were used. For electronmicroscopy the tissue was obtained immediately after death from coal gas poisoning and fixed in chilled 1% buffered osmium tetroxide (Zetterqvist, 1956) for 2 hr., dehydrated in graded ethyl alcohols and then transferred into a mixture of equal volumes of absolute alcohol and propylene oxide for 1 hr., then into propylene oxide for ½ hr. and embedded in Araldite. Ultra-thin sections were cut on a Leitz ultramicrotome, picked up on uncoated copper grids and stained by either the Karnovsky method (1961) or 1% uranyl acetate for 1 hr. and dried in the dessicator. They were screened in the A.E.I. E.M.6 electron-microscope. Thick 1 μ sections, adjacent to the thin sections used for electronmicroscopy, were stained with Mallory's azan II-methylene blue mixture (Richardson, Jarett & Finke, 1960). These were compared with the sections stained with haematoxylin and eosin and the electron micrographs.

For histochemistry, eleven animals were killed by intraperitoneal nembutal and the tissues were taken from the duodenum proximal to the entry of the bile duct. For the demonstration of glycogen, tissue fixed in Lison's 'Gendre' fluid at $-20°$ C., was sectioned in paraffin wax and subjected to the periodic acid-Schiff technique before and after incubation with diastase. Sections of tissue fixed in Lillie's alcoholic lead nitrate were subjected to the periodic acid-Schiff technique or stained with 0·1% toluidine blue in 30% ethanol or with 0·1% alcian blue in 3% acetic acid, before and after each of the following procedures: mild acid hydrolysis (0·02 N sodium acetate/0·02 N hydrochloric acid) at pH 2·5 for 4 and 24 hr. at 60° C.; incubation with neuraminidase (*Vib. cholera* receptor-destroying enzyme—

Burroughs, Wellcome and Co.) for 4 and 24 hr. at 37° C.; incubation with testicular hyaluronidase (Benger's), 1 mg./ml., at pH 6·3 for 4 and 24 hr. at 37° C. in 0·2 M phosphate buffer; incubation with papain 200 mg. in 20 ml. of 0·02 M acetate buffer, pH 5·4, containing 6·4 mg. potassium cyanide and 33·4 mg. (0·005 M) ethylene diamine tetra acetic acid, for 2 hr. at 37° C. (Quintarelli, Tsuiki, Hashimoto & Pigman, 1961). These hydrolytic and extraction techniques were repeated on sections of tissue fixed in neutral buffered 10 % formalin. The methylene blue extinction test was carried out at a series of pH values ranging from 2·6 to 5·3, in solutions of the dye buffered with veronal acetate, on sections fixed in alcoholic lead nitrate and on others fixed in neutral formalin.

The methyl green/pyronin technique, before and after extraction with ribonuclease, and the Feulgen technique, were carried out on tissue fixed for 6 hr. in neutral formalin and embedded in paraffin wax; sections from the same block were stained with haematoxylin and eosin (Pearse, 1960).

For the detection of lipid, a block of tissue 5 × 5 mm. fixed in formal calcium (1 % calcium chloride in 10 % formalin) was carried through the stages of the acid haematein technique to the point where frozen sections were cut. The sections were then either coloured with alcoholic Sudan black B or treated with Nile blue sulphate (Cain, 1947) or subjected to the complete acid haematein technique (Baker, 1946). Pyridine extracted controls were stained in parallel. As an alternative procedure, controlled chromation, followed by coloration with Sudan black B or with 0·1 % haematoxylin, containing 0·05 % ferricyanide, pH 3·5 (Elftman, 1954), was carried out on frozen sections cut from fresh material with the cold microtome. Similar sections, without prior chromation, but fixed in formal calcium, were coloured with Sudan black B.

The distribution of two enzymes was investigated. Acid phosphatase was studied using Gomori's (1950) lead nitrate method on frozen sections of tissue fixed in cold (0–4° C.) formal-calcium for 24 hr. Incubation was carried out at pH 5·0 for 15, 30 and 60 min. at 37° C. and the following controls were used: (i) omission of substrate from the medium; (ii) inclusion of 0·01 M sodium fluoride in the medium. The Gomori calcium-cobalt method for alkaline phosphatase was applied to frozen sections of tissue fixed in 10 % formalin for 4 hr. at 0–4° C. Incubation times of ½, 1½, 5, 15 and 30 min. and 2 and 4 hr. were used. Controls were incubated in medium lacking the substrate.

OBSERVATIONS

Electronmicroscopy

The acini of Brunner's glands are bounded by an ill-defined granular basement membrane of about 20 mμ thickness and low electron density (Pl. 1, figs. 2 and 3). Outside this membrane and in contact with it there are the fine collagen fibres and connective tissue cells of the submucosa interspersed with finely granular material. The fibres range from 50 to 65 mμ in diameter; some show a periodicity of about 65 mμ. The basement membrane is separated from the plasma membrane of the acinar cells by a clear interval of 13 mμ which extends as a wedge between the bases of adjacent acinar cells. The acinar cells of Brunner's glands measure up to 10 and 7 μ in dimension.

The plasma membranes are 6–10 mμ in thickness. Basally they are relatively smooth with a few infoldings which run inwards for short distances into the cytoplasm and then turn or divide in a T-fashion to run parallel to the base (Pl. 1, fig. 2). A few small pinocytotic vesicles are present close to the basal part of the cell. The plasma membranes of adjacent cells are separated by an electron translucent interval of 13 mμ (Pl. 2, fig. 4). In this situation adjacent plasma membranes are, in places, wrinkled and dovetailed into one another with varying degrees of complexity. Desmosomes are present but infrequent; they display a thickening of the plasma membrane from the customary 7 mμ to about 20 mμ over a distance of about 100 mμ. In these situations the intercellular gap contains electron-dense material. In one section only has an intercellular canaliculus been observed; the gap between the cells is increased and a few microvilli are present. There are no microvilli at the apical surfaces of the acinar cells. Where secretion is being discharged into the lumen of the acinus the plasma membrane is ruptured (Pl. 2, fig. 6). A few pinocytotic vesicles are present in close association with the apposed surfaces of the acinar cells.

The nucleus of the acinar cell is oval in outline and basally placed. An occasional nucleolus is seen. Most of the supranuclear region of the cell is occupied by large oval or polyhedral secretion droplets about $1{\cdot}2 \times 0{\cdot}8\,\mu$ in dimension, and sometimes larger, with the long axis in the long axis of the cell (Pl. 1, fig.1; Pl. 2, fig. 6). These droplets are separated in most places by thin partitions of cytoplasm which are perforated in some situations. In places a membrane about 6 mμ thick can be identified around the secretion droplets. Internal to this each droplet possesses a fine reticular framework of fibrils of about 2 mμ in diameter, studded with more or less spherical dark granules of about 3 mμ in diameter (Pl. 2, fig. 6).

The cytoplasm of the cell is characterized by its high electron density which approaches that of the nucleoplasm. Between the secretion droplets, especially in the angular intervals between three or more droplets and along the margins of the cell, there are a few spherical dark granules, of an electron density slightly greater than the surrounding cytoplasm; these measure about $0{\cdot}5\,\mu$ in diameter. Their internal details are difficult to discern.

The ribosomes of the cell are angular in outline; they are scattered throughout the cytoplasm and arranged in rows, in loose clusters or in single rows around the mitochondria and secretion droplets (Pl. 1, fig. 3). They are of the order of 1·2 mμ in greatest dimension and, when in rows, are distributed at more or less regular intervals of 30 mμ between their centres. In the loose clusters they are more widely separated at about 50 mμ. Where the ribosomes are in more or less parallel rows, material slightly less electron dense than the surrounding cytoplasm separates them. In places this seems to be continuous with the contents of the secretion droplets. Nowhere are the ribosomes seen to be associated with parallel membranes of endoplasmic reticulum.

Numerous mitochondria, of an oval or sausage shape, some measuring as much as $1{\cdot}5 \times 0{\cdot}4\,\mu$, are present throughout each cell but more particularly at the base, close to the nucleus, and along the lateral margins flanking the secretion droplets. They possess widely spaced parallel cristae and a matrix which is more electron dense than the surrounding cytoplasm (Pl. 1, fig. 3; Pl. 2, fig. 4).

The Golgi complex is well developed and extensive (Pl. 2, fig. 5). It consists of irregular vacuoles of varying size, the contents sometimes resembling closely those of the secretion droplets of the cell, a few small vesicles, and small stacks of very fine smooth parallel membranes. The whole complex is situated supranuclearly and extends a considerable distance amongst the secretion droplets. The parallel membranes measure about 6 mμ in thickness and the distance between their centres varies from 15 to 20 mμ.

At the base of each cell, close to and to one side of the nucleus there is one (or rarely two) dense irregularly oval osmiophilic complex, sometimes as much as 2 μ in its greatest dimension (Pl. 1, fig. 1). This osmiophilic complex contains at one end a vesicle up to 1·0 μ in diameter bounded by a dense wall 8 mμ thick enclosing less dense homogeneous contents. Capping this vesicle is a heterogeneous mass consisting of one or more very dense oval bodies honeycombed with lighter circumscribed elliptical areas up to 50 mμ in longest dimension, resembling vacuoles, interspersed with short thick dense parallel membranes and homogeneous small, round, electron-dense bodies. The 'vacuoles' in the honeycombed masses contain a finely reticular material. The parallel membranes are about 13 mμ thick and 20 mμ between their centres. At one end a pair of membranes frequently terminates in one of the small dense bodies which in turn seems to grade through transitional forms to the larger honeycombed oval bodies (Pls. 1 and 2, figs. 2–5). This osmiophilic complex is close but not connected to the Golgi complex. Mitochondria lie in close contact with it and may occasionally be found amongst the osmiophilic components (Pl. 1, fig. 3; Pl. 2, fig. 4).

Histochemistry

The periodic acid-Schiff reaction (Pl. 3, fig. 7) stains the contents of the cells a bright pink and there is no alteration of the staining character in the diastase-treated controls. Hence, the presence of glycogen in the cells has not been demonstrated. With toluidine blue (Pl. 3, fig. 8) the secretion droplets stain purplish red and with alcian blue (Pl. 3, figs. 9 and 10) they take on a deep blue colour. The γ-metachromasia with toluidine blue survives dehydration and embedding in balsam. Mild acid hydrolysis for 4 hr., extraction with neuraminidase and with hyaluronidase are without effect on the staining with the periodic acid-Schiff technique, toluidine blue and alcian blue. However, after incubation with papain, and, less completely, after acid hydrolysis for 24 hr., the cells are no longer stained by these three techniques. Extinction of staining of the cell secretion with methylene blue occurs at pH 2·6.

The methyl green/pyronin technique colours the nucleus green, the cytoplasm of the acinar cell giving a moderately intense pyronin positive reaction of reticular pattern, which is abolished almost completely by extraction with ribonuclease. No constant juxta-nuclear concentration of pyronin-positive material is observed. With the Feulgen reaction, the nuclei are coloured pink to purplish and no extra-nuclear Feulgen positive material is detected.

In sections cut from the block-fixed and post-chromed material and coloured with Sudan black B (Pl. 4, fig. 11) lipid granules are seen scattered throughout the cell, including some lipid material in or near the lumen of the acinus. After treatment with Nile blue sulphate, no pink staining is observed and the blue-coloured (acidic)

lipid present corresponds to the sudanophilic granules observed. When stained with acid haematein (Pl. 4, fig. 12), small blue-black granules of phospholipid are seen in the cell and also in the acinar lumen. By all three methods a complex, with dimensions similar to those seen in electron micrographs, i.e. 1–2 μ diameter, is stained; in some cells it may be seen to consist of a vesicle capped by a crescent-shaped mass. This complex is invariably close to the nucleus, being para- rather than supra-nuclear in position. Both this complex and the other lipid material are extractable by pyridine.

Similar results are obtained using fresh frozen sections treated by the Elftman method. The lipid, colouring with Sudan black and also staining with haematoxylin, consists of granules scattered throughout the cell, including the 1–2 μ diameter mass next to the nucleus, with some intra-luminal material.

Using fresh frozen sections fixed in formal calcium but not chromated, coloration with Sudan black apparently reveals less lipid in the cell. No intra-luminal lipid is observed, and the granules scattered throughout the cytoplasm are finer. However, the paranuclear lipid mass is clearly stained and is more frequently present than in the block fixed material.

Acid phosphatase (Pl. 4, fig. 13) is present in the Brunner's gland cell and is seen as punctate loci of activity scattered throughout the cytoplasm; the enzyme activity reaches its maximum after 30 min. incubation, at which time the nuclei are still unstained. In only a few cells does there appear to be a juxtanuclear concentration of activity. Control sections are negative. No alkaline phosphatase activity (Pl. 4, fig. 14) can be detected in the cells even after 4 hr. incubation, although a strongly positive reaction occurs in the brush borders of the duodenal villi after only 5 min. incubation. A reaction is also noted in the connective tissue between the acini of the glands.

DISCUSSION

Most of our knowledge of the secretions of Brunner's glands is derived from the work of Florey and his colleagues (for a full review see Grossman, 1958). The most characteristic components are mucins and a high concentration of bicarbonates giving the freshly collected fluid a pH of 8·0–8·2. Proteolytic and lipolytic enzymes have been detected; these show species differences and, where tests have been positive, their amounts have been so small as to cast doubt on their significance. A mucinase is also present in duodenal juice (Hartiala & Grossman, 1952); this has been presumed to be derived from Brunner's glands. Meulengracht (1939) associates the antianaemic factor (intrinsic factor of Castle) with what has been termed the 'pyloric gland organ' which includes Brunner's glands, but has been unable to detect any significant change in Brunner's glands in pernicious anaemia.

As regards mucin secretion, the results of the histochemical tests applied in this investigation do not conflict with those of previous workers. There are marked, and as yet unexplained, species differences in the histochemical reactions of the mucins. There is also a marked species difference in the uptake of ingested radioactive sulphur-containing inorganic sulphates (Jennings & Florey, 1956); Brunner's glands in the guinea-pig are noteworthy for their considerable uptake of sulphate as compared with those of the cat, rat and mouse. The present histochemical findings,

such as the low methylene blue extinction and the persistent metachromasia with toluidine blue further suggest that the secretion contains a sulphated mucopolysaccharide. Although the procedures employing mild acid hydrolysis and extraction with neuraminidase are known to demonstrate the presence of sialic acid in the salivary gland mucin (Quintarelli *et al.* 1961), it would appear that both this compound and also hyaluronic acid are either absent, or present only in low concentration, in Brunner's gland mucin. The latter alternative seems more probable in view of the fact that Werner (1953) finds sialic acid present in small amounts in epithelial secretions. Grossman (1958) suggests that a difference in the chemical composition of the secretion must exist as between species and suggests that, in some, the glands are mucoid secreting and in others mucin secreting. In the present inadequate state of our knowlege of the mucopolysaccharides this statement seems almost meaningless.

The findings in this investigation have several features in common with those of Moe (1960) in the cat. The basement membrane, foldings of the plasma membrane, the desmosomes and Golgi complex are similar in both animals. In the cat, however, a 'great number' of the acinar cells possess microvilli at their luminal surfaces. As in the guinea-pig, the ribosomes in the cat are arranged irregularly, in clusters or in rows; the latter, however, are components of α-cytomembranes which are said to be distributed irregularly through the cytoplasm. Judging from the electron micrographs the secretory droplets (Moe's large granules) are neither as numerous nor as closely packed in the cat and the cytoplasmic matrix is less electron dense. It is interesting that there also appears to be a species difference in the cell content of alkaline phosphatase. Moe (1952) finds that in the cat there is intense activity of the enzyme, whereas in this study Brunner's glands are consistently negative, confirming the results of Bourne (1943); the guinea-pig in this respect resembles the rabbit (Martin & Jacoby, 1949).

Bensley (1903) has been unable to observe a Golgi complex in Brunner's glands; Tschassownikow (1926) and Florey & Harding (1933) have identified this in a supra-nuclear position and the latter investigators suggest that the mucin of the glands is elaborated in contact with it, although in their autoradiographic study Jennings & Florey (1956) find that radioactive sulphate is first incorporated over the main mass of mucin of the cytoplasm, rather than in a concentrated supra-nuclear zone, as in the goblet cells. The electron microscopic studies confirm these observations. The Golgi complex is extensive and the larger vesicles in it contain material resembling that in the secreting droplets, which presumably contain mucin or a precursor of mucin. Acid phosphatase activity is said to be associated with Golgi membranes. However, there appears to be no evidence of a supra-nuclear localization of the enzyme activity in these cells, but rather a random scattering throughout the cytoplasm. It is possible that the activity here is associated with the dark spherical granules $0{\cdot}5\mu$ in diameter between the secretion droplets.

The ribosome content of the acinar cells indicates active protein synthesis. The close association of ribosomes with the secretion droplets is interesting, for whilst some part, possibly the mucopolysaccharide component of the secretion, may be derived from the Golgi complex, another moiety, namely the protein component, may be derived from the activity of the ribosomes. The continuity of the material

between parallel rows of ribosomes with the droplets and the encirclement of the latter, partially or completely, by ribosomes suggest a close functional association. The similar relation of ribosomes with mitochondria is difficult to explain in this particular situation.

The osmiophilic, phospholipid containing complex present in each cell raises questions as to its nature and function. It is considered to be a cytoplasmic organelle, always seen in close proximity to the nucleus. Although perhaps superficially resembling a nucleolus, this complex invariably lies outside the nuclear membrane and may be seen along with a nucleolus in the same field. It is believed that the constant basal and paranuclear position of the body in the cytoplasm is of functional significance. The question then arises as to whether the complex is degenerative or indeed functional. The possibility exists that it is concerned with the degeneration or replacement of some part of the cell and it is true that in certain pathological or abnormal conditions such structures have been seen. For example, dense bodies displaying similar polymorphism have been observed in the coagulating gland epithelium of the castrated rat (Brandes, Györkey & Groth, 1962) where they are associated with the involution of the cell. These authors trace a connexion between such bodies and lysosomes, based on their acid phosphatase activity. There might well be a similar association with the lysosomes in Brunner's glands and such an association would not necessarily imply an involutionary process of the gland cell. Nevertheless, the lack of evidence of acid phosphatase activity in the gland cell corresponding either in area or position to that of the osmiophilic complex does not support a similar relationship of the complex with the lysosomes, although at the same time not rendering it impossible. Moreover the constant occurrence of the complex in apparently normal cells in healthy young animals makes a degenerative role unlikely.

In appearance the paranuclear body closely resembles the lipochondria described by Kurosumi, Iijima & Kitamura (1958) and Iijima (1959) in the normal eccrine sweat gland. Ellis (1962) illustrates similar lipid bodies in eccrine sweat glands but does not give them any specific designation. Though none of these investigators state specifically whether these lipid bodies are a constant and characteristic feature of every cell in these glands and whether they are single or multiple, one is led to assume that they are multiple and a constant feature of both the dark and clear cells. Iijima associates their formation with the Golgi vesicles or granules and traces their breakdown. A similar association with the Golgi complex could not be traced in Brunner's glands. In this tissue, far from their ultimate dissolution, it would appear that densely osmiophilic parallel membranes produce uniformly dense osmiophilic bodies which in turn become honeycombed with vacuoles or converted into membrane-bound vesicles with less electron-dense contents. The honeycombed appearance of some of the lipid bodies has been attributed by Ellis to saturated lipid or other substance which is removed in preparation of the sections. A similar appearance is seen with light microscopy in large fat globules undergoing depletion as in wasting. It might indeed be indicative of physiological rather than post-mortem removal of fat. The constant occurrence and orientation of this phospholipid complex both in the histochemical and electron microscopic preparations suggest a definite function and, as this has not been described in other mucin-secreting

cells, it is tempting to associate it with bicarbonate secretion which constitutes the other characteristic component of the secretion of Brunner's glands. Incidentally, the eccrine sweat gland is concerned with the excretion of a salt. A step towards the elucidation of this structure might result from its study in so-called 'empty' glands, which have discharged their secretion after stimulation of the duodenal mucosa, and in different species.

Without attaching any special significance to them, Moe (1960) describes a few large rounded grains of high electron density and up to 1–2 μ diameter in most acinar cells. These are homologized with the osmiophilic grains described by Tschassownikow (1926) with light microscopy and some of them are said to have a core of low density. Though not identical in their morphology there appears to be little doubt that these grains correspond to our osmiophilic complexes.

SUMMARY

1. Brunner's glands have been studied in the guinea-pig by electronmicroscopy and histochemistry.

2. The acinar cells lie on a basement membrane and are closely interlocked laterally; a few desmosomes are present. The luminal border of the cell is devoid of microvilli.

3. The apical part of the cell is packed with secretion droplets, the nucleus is situated basally and there is an extensive Golgi apparatus in the supra-nuclear region. Mitochondria, smooth membranes and rows or rosettes of ribosomes are scattered throughout the cell. Rows of ribosomes often partially encircle the secretion droplets and mitochondria. A dense osmiophilic complex resembling a lipochondrion is present in each cell, in the paranuclear position.

4. The secretion droplets are PAS positive, diastase resistant, alcianophilic. They display a γ-metachromasia which resists mild acid hydrolysis for up to 4 hr. and the action of neuraminidase. The cytoplasm is rich in ribonucleic acid.

5. With Sudan black B, Nile blue sulphate and acid haematein scattered lipid granules are found throughout the acinar cell. With all three methods there is, in the paranuclear position, a constant lipid body of dimensions corresponding to the osmiophilic complex seen in the electronmicrographs.

6. Acid phosphatase but not alkaline phosphatase is present; it is randomly distributed.

7. The significance of these findings and in particular of the osmiophilic complex is discussed.

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EXPLANATION OF PLATES

PLATE 1

All the figures in plates 1 and 2 are electronmicrographs.

The scale marker represents 1μ.

Fig. 1. Part of the wall of an acinus of Brunner's gland. Karnovsky method. $\times$ 8500.

Fig. 2. Basal region of an acinar cell showing basement membrane, secretion droplets and two osmiophilic complexes. Karnovsky method. $\times$ 25,000.

Fig. 3. High power view of one of the osmiophilic complexes seen in Fig. 2. Karnovsky method. $\times$ 67,000.

PLATE 2

Fig. 4. Basal regions of two adjacent acinar cells showing the plasma membranes, osmiophilic complexes, ribosomes and secretion droplets. $\times$ 25,000.

Fig. 5. Basal part of an acinar cell showing one of the osmiophilic complexes. Stained with uranyl acetate. $\times$ 25,000.

Fig. 6. Luminal part of an acinar cell showing the discharge of a secretion droplet. Ribosomes and parallel smooth membranes are also seen. Karnovsky method. $\times$ 25,000.

PLATE 3

Fig. 7. Crypts of Lieberkuhn and submucosa. Note the intense staining of the Brunner's glands; the mucin in the lumen of the crypts is also positive. PAS reaction. $\times$ 480.

Fig. 8. Persistent metachromasia in the cytoplasm of Brunner's glands. These are not so completely stained as with PAS. Toluidine blue. $\times$ 480.

Fig. 9. Positive staining of the mucin of Brunner's glands. The dark staining of the cytoplasm of the crypt cells is due to basophilia demonstrated with haemalum. Alcian blue and haemalum. $\times$ 480.

Fig. 10. Absence of staining of cytoplasm of Brunner's glands after extraction with papain. Alcian blue and haemalum. $\times$ 480.

PLATE 4

Fig. 11. Brunner's glands. Note basal paranuclear lipid masses approximately 1–2μ diameter. Sudan black B. $\times$ 1200.

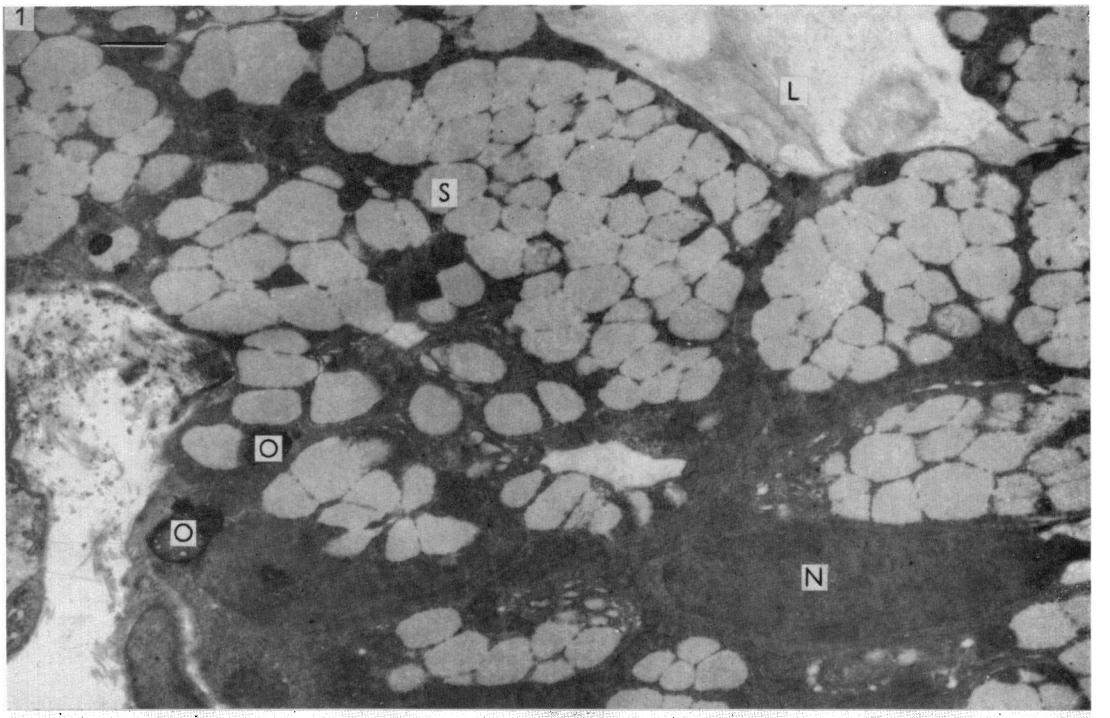
Fig. 12. Basal phospholipid masses in Brunner's glands. Compare distribution of lipid as seen here and in Fig. 11, with the osmiophilic complex in Pl. 1, Fig. 1. Acid haematein. $\times$ 770.

Fig. 13. Acid phosphatase reaction. Particulate activity in the cytoplasm of Brunner's glands. Gomori lead sulphide method. $\times$ 480.

Fig. 14. Alkaline phosphatase reaction. No activity in the Brunner's gland cells. Note the reaction in the connective tissue between the acini and also in the luminal borders of the villi. Gomori calcium-cobalt method. $\times$ 75.

LIST OF ABBREVIATIONS

BG Brunner's glands
BM Basement membrane
DS Discharging secretion droplet
G Golgi apparatus
I Infolded plasma membrane
L Acinar lumen
LC Crypts of Lieberkuhn
LM Lipid mass
M Mitochondria
N Nucleus
O Osmiophilic complex
PM Plasma membrane
PS Parallel smooth membranes
R Ribosomes
S Secretion droplet
V Villi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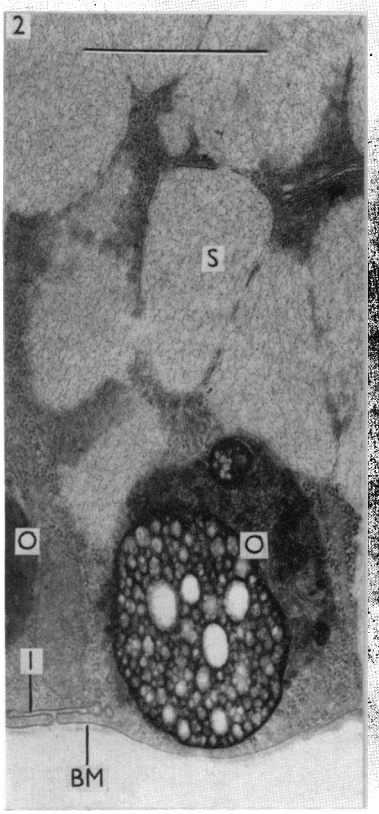
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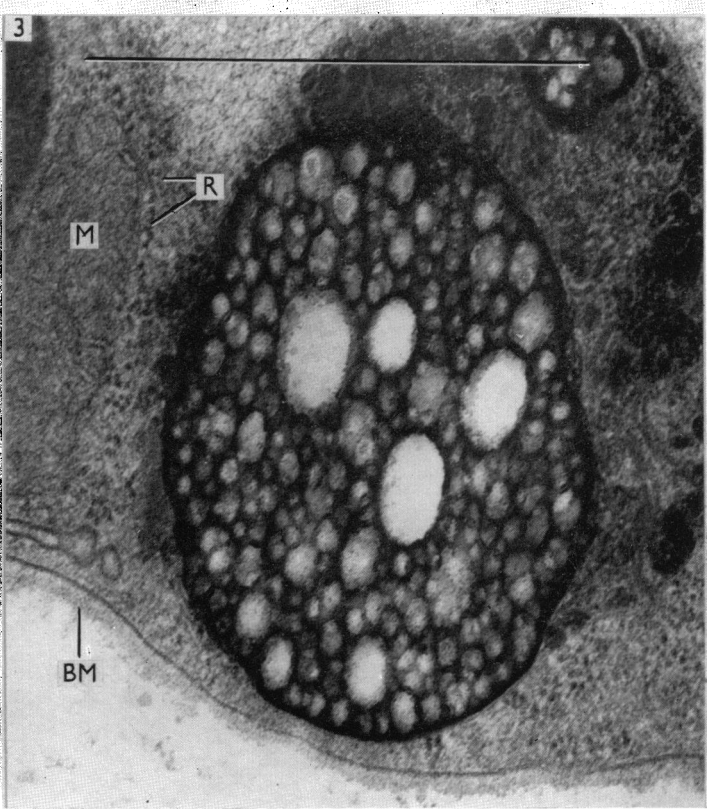
3
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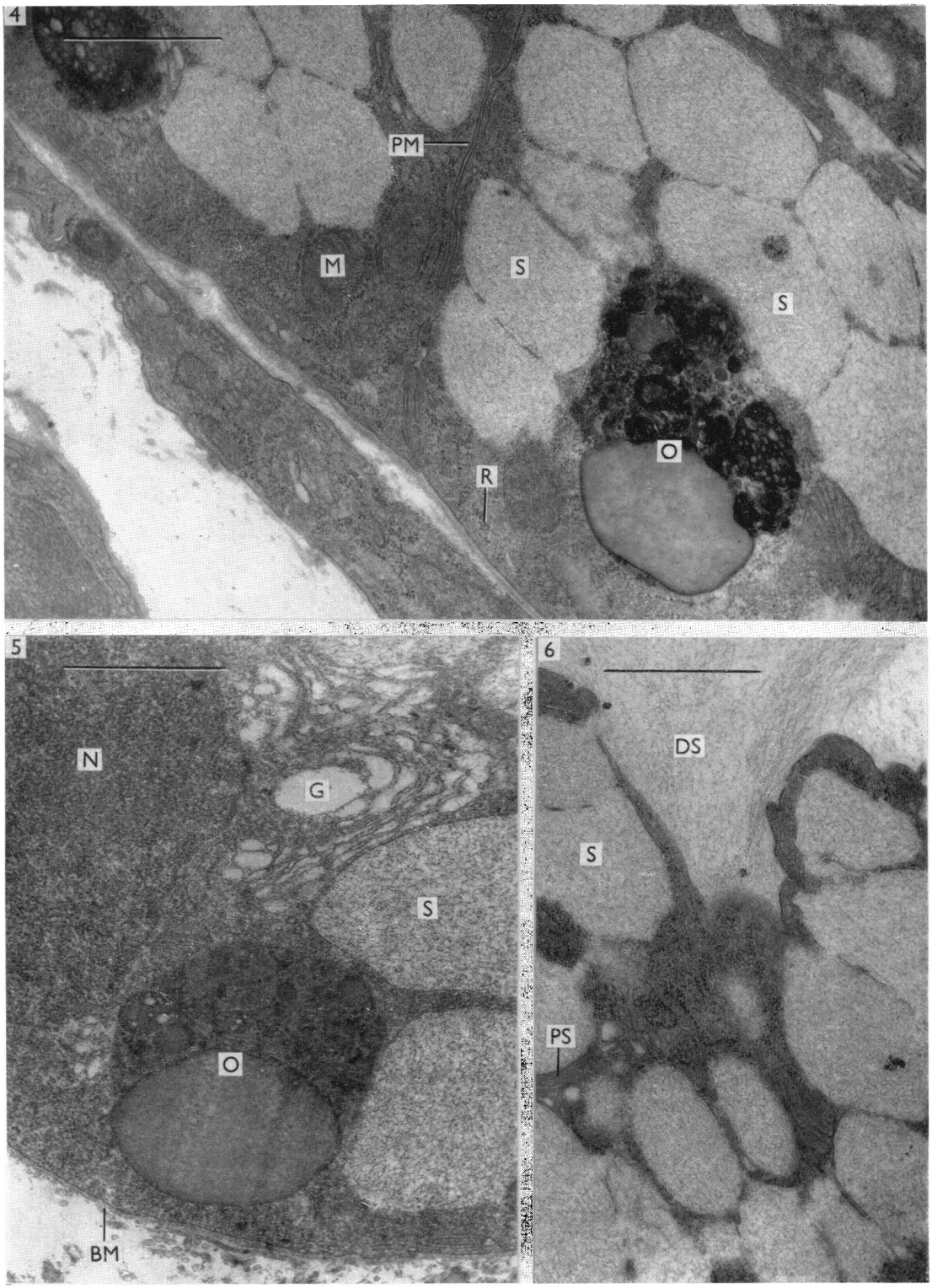
4
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M
S
S
O
R
5
N
G
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6
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S
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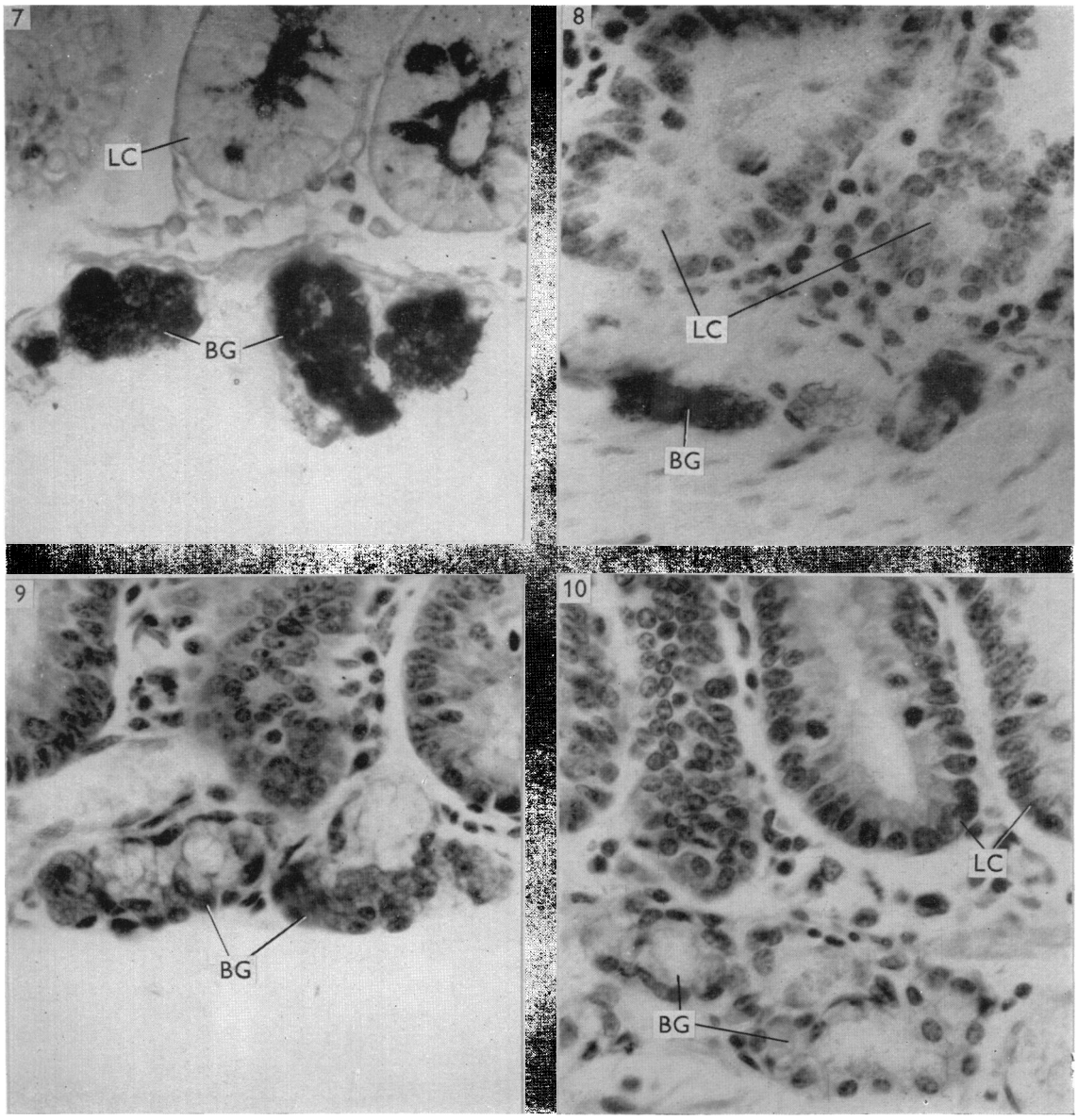
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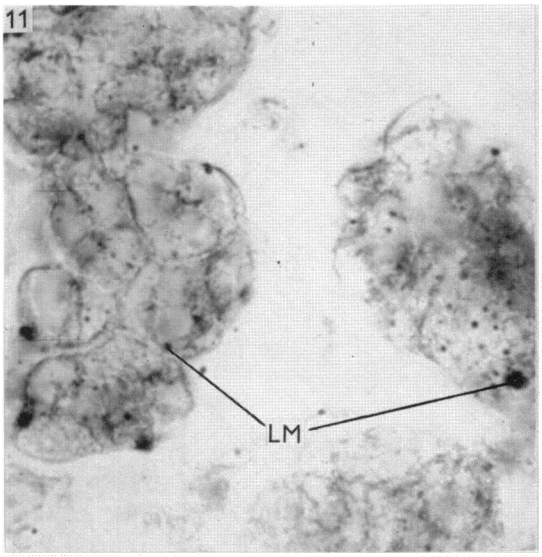
LC
BG
8
LC
BG
9
BG
10
LC
BG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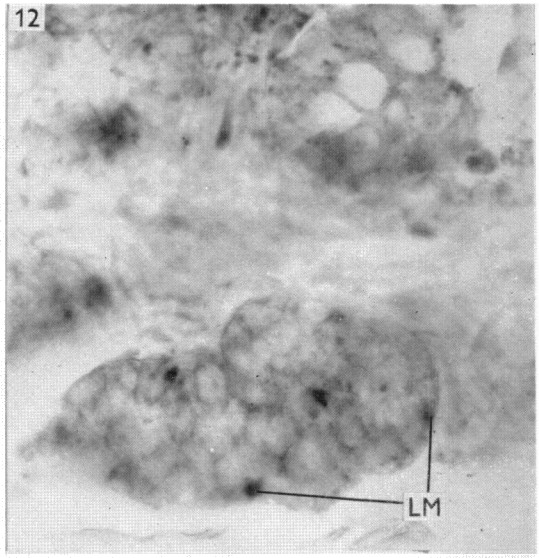
12
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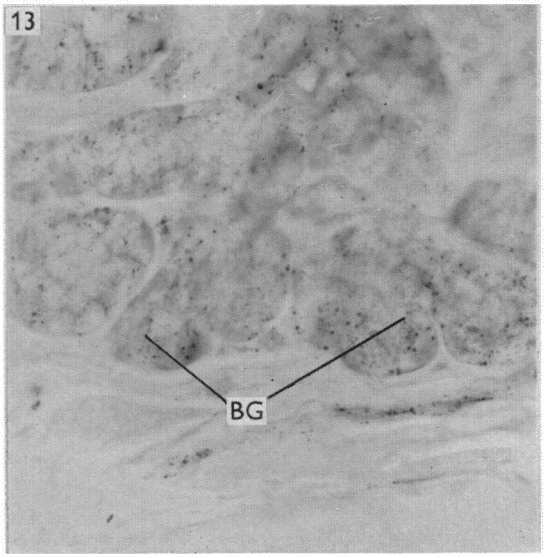
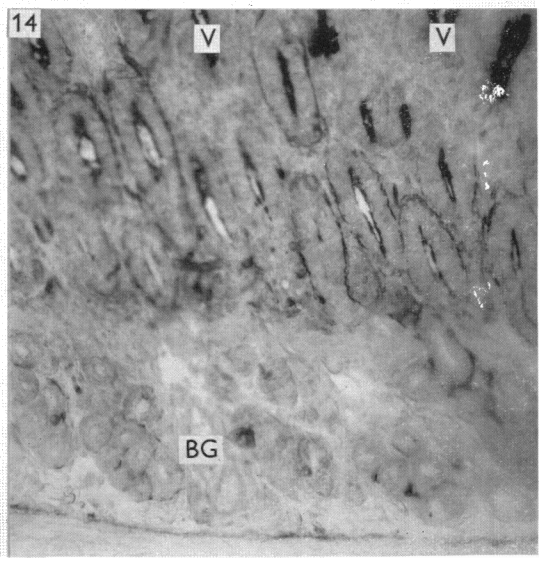

13
BG


14
V
V
BG