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The rete testis of birds

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INTRODUCTION

The rete testis, especially that of mammals, has recently received much attention (Voglmayr, Waites & Setchell, 1966; Setchell, Voglmayr & Waites, 1969; Tuck, Setchell, Waites & Young, 1970). It has been shown to add to and modify the fluid entering the vasa efferentia from the testis. The rete testis of mammals contributes about 65 % of the total fluid entering the efferent ductules from the testis, and the composition of the fluid from the seminiferous tubules differs from that of the rete testis (Waites, 1977). The rete testis therefore plays an important role in the secretion of the fluid in which spermatozoa are suspended and transported to the epididymis. The structure of the rete testis of mammals has been elucidated by, among others, Roosen-Runge (1961), Bustos-Obregon & Holstein (1976), Dym (1976), Amann, Johnson & Pickett (1977), Roosen-Runge & Holstein (1978) and Osman (1978) in attempts to relate structural characteristics of the rete cell to the performance of this secretory function. However, the exact mode of function of the rete remains to be clearly understood.

Apart from studies on the domestic fowl by Tingari (1971, 1972) and on the turkey by Hess, Thurston & Biellier (1976) and Hess & Thurston (1977) in which histological and some ultrastructural studies were carried out and reported, little is known about the structure and content of the avian rete testis, although the histological appearances of the rete testis of the Japanese quail (Aire, 1979*a*) and guinea-fowl (Aire, Ayeni & Olowo-Okorun, 1979) have been reported. In these studies, structures similar to the straight tubules or tubuli seminiferi recti of mammals were seen. Judging from micro-stereological studies by Aire (1979*b*), the rete testis of birds (excluding the intra-testicular and intracapsular portions) appeared to constitute a significant volumetric proportion (13·3 % for the fowl, 9·9 % for the Japanese quail and 10·7 % for the guinea-fowl) of the epididymal region and it is tempting to assume an important functional role for the avian rete testis.

In the present paper a more detailed comparative study has been made by histological and electron microscopical (both scanning and transmission) preparations of the rete testis in the domestic fowl (*Gallus gallus domesticus*), the Japanese quail (*Coturnix coturnix japonica*), the guinea-fowl (*Numida meleagris galeata*) and the drake (*Anas platyrhynchos*).

MATERIALS AND METHODS

Adult, sexually active, male domestic fowl, Japanese quail, guinea-fowl and duck were used in this investigation. The birds were anaesthetised with chloroform or thiopentone sodium (May & Baker Ltd.) and prepared for vascular perfusion through the heart, in the case of the Japanese quail, or the dorsal aorta in the thoracic region

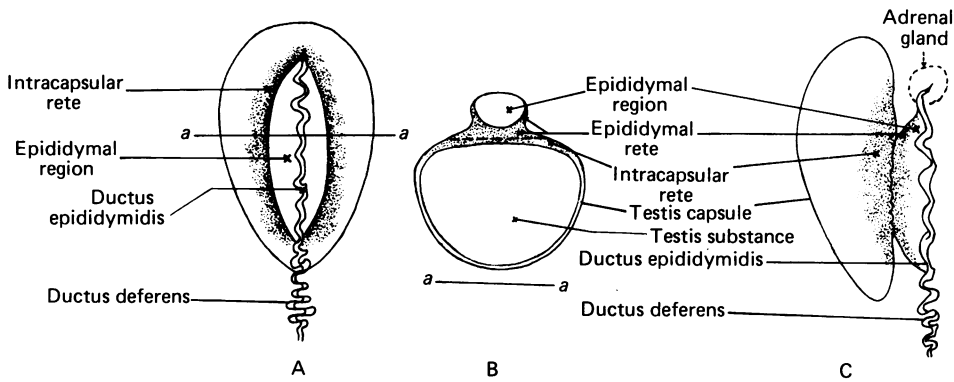


Fig. 1. Diagrams of the gross structure of the testis and epididymal region. (A) is an *en face* view of the dorsomedial aspect of the testis, showing the epididymal region and the area occupied by the intracapsular rete testis. (B) shows a transverse section of the testis as at *a–a* in (A). (C) is a lateral view of the testis and the attached epididymal region. Not drawn to scale.

in the other larger birds. The perfusate was 3 % glutaraldehyde buffered with 0·067 % cacodylate solution. Some of the tissues were subsequently processed and embedded in Epon for transmission electron microscopy. Semithin sections were cut and stained with toluidine blue and ultrathin sections were cut and stained with uranyl acetate and lead citrate. For scanning electron microscopy, tissues from the rete testis region of the drake were critical-point dried, mounted on stubs and sputter coated with gold-palladium.

Some tissues were also processed for light microscopy. The ultrastructure of the rete tissues was observed in a Hitachi HS-9 transmission electron microscope and a Jeol JSM 35 scanning electron microscope.

OBSERVATIONS

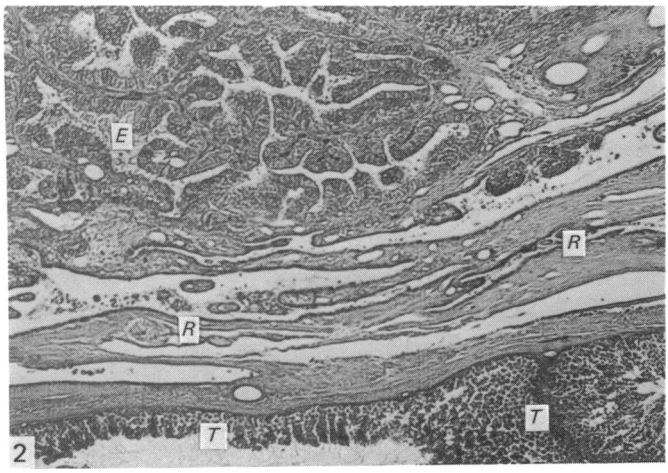
The rete testis of birds is located on the dorsomedial aspect of the testis, and links the seminiferous tubules to the rest of the epididymal region (Fig. 1). It consists of intratesticular, intracapsular (intratunical) and extratesticular parts (Fig. 2). A clean excision of the epididymal region from the testis left the intratesticular and intracapsular portions of the rete intact and separated from the extratesticular portion which formed an integral part of the epididymal region. The intracapsular rete radiated from the dorsomedial surface of the testis towards the epididymal region (Fig. 2), and the fluid content of this portion of the rete was high and easily observed by the naked eye. Apart from the attachment face, the extratesticular rete covered the immediate lateral, cranial and caudal aspects of the epididymal region (Fig. 2).

Fig. 2. Histological section showing part of the testis (*T*), rete testis (*R*) and epididymal region (*E*) of the domestic fowl. H. & E. × 80·6.

Fig. 3. Part of the testis of the guinea-fowl showing the 'tubulus rectus' (*T*), seminiferous tubules (*S*), rete testis (*R*) and testicular capsule (*C*). H. & E. × 128. (From Aire *et al.* 1979.)

Fig. 4. Part of the testis of the Japanese quail showing two seminiferous tubules opening (arrows) into a straight tubule. Note cuboidal epithelium of the tubule within the testicular capsule (*C*). Trichrome stain. × 320.

Fig. 5. Scanning electron micrograph of the rete testis of the drake. Lamellae (*L*) and folds (*F*) which break up rete channels are present. *P*, proximal efferent ductule; *C*, testicular capsule. × 240.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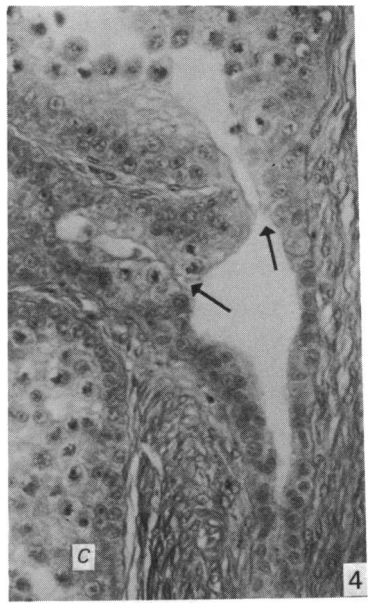
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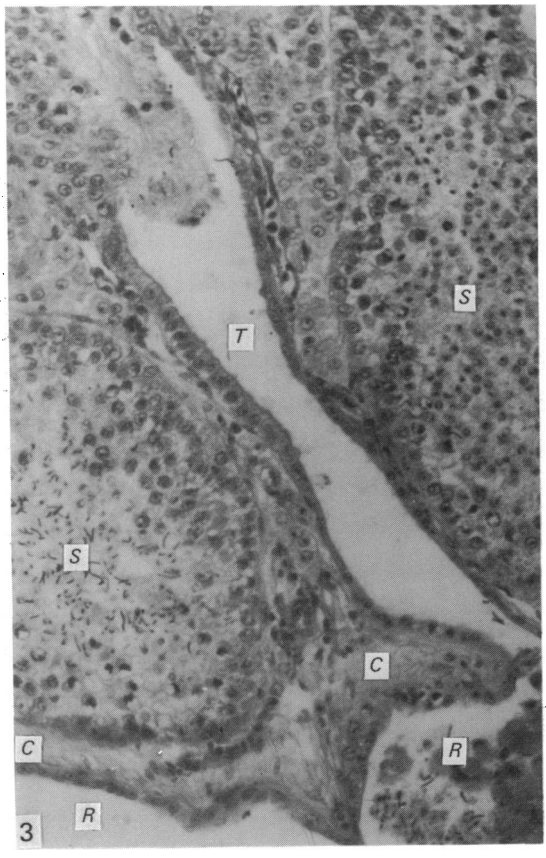
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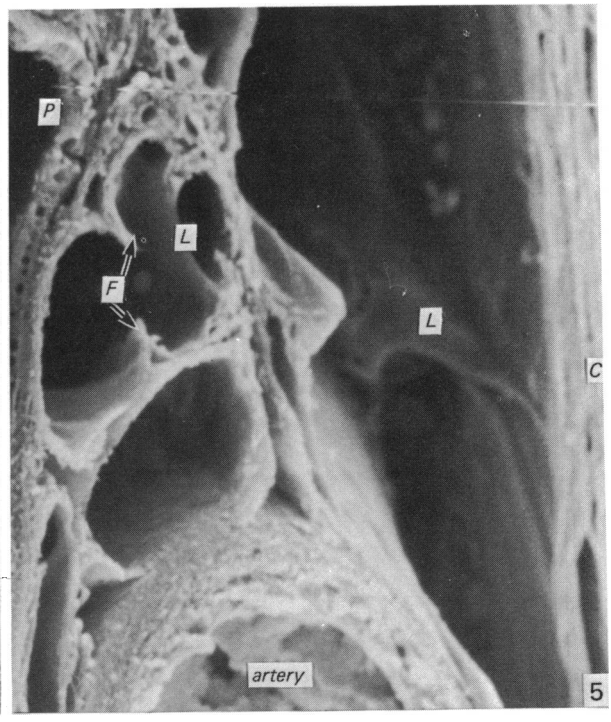
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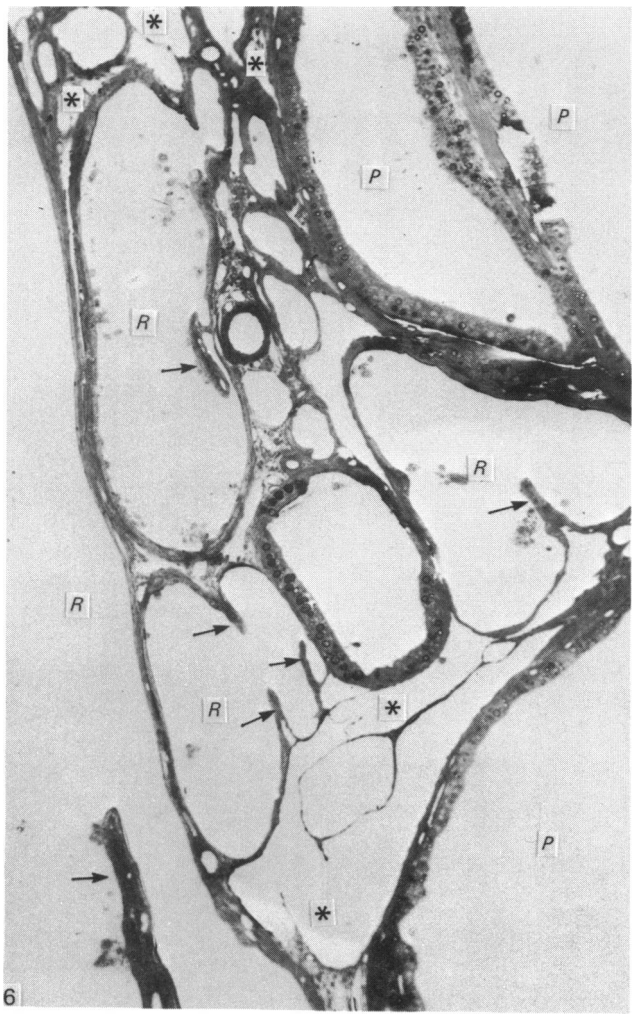

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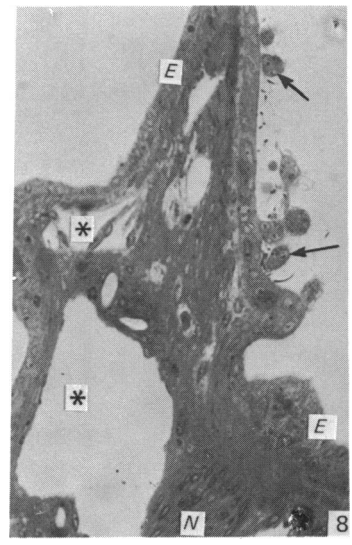

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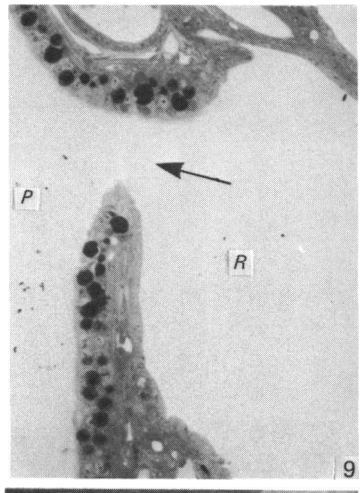

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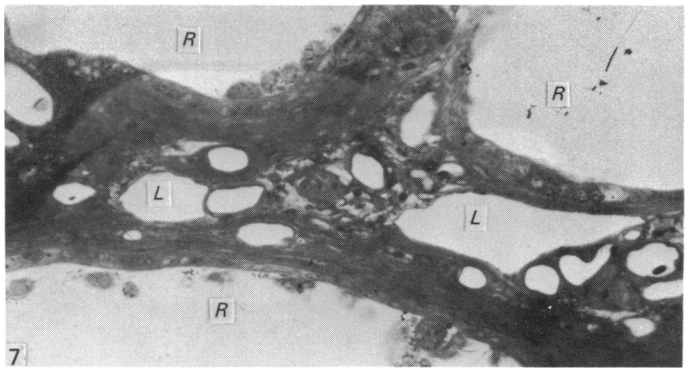

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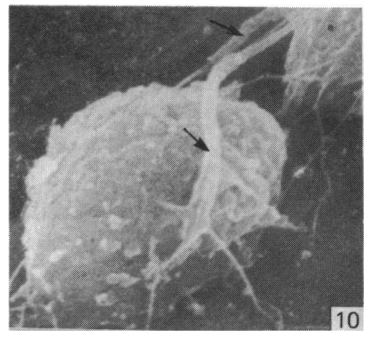
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The seminiferous tubules opened into the rete testis directly or into the 'straight tubules' (Aire, 1979*a*; Aire *et al.* 1979) which are similar in outline to the straight tubules or tubuli seminiferi recti of mammals. The 'straight tubules', which may be regarded as part of the intratesticular portion of the rete testis, were only occasionally seen (Fig. 3). One or more seminiferous tubules may be seen opening into them (Figs. 3, 4). The epithelial lining of the straight tubules consisted of simple high cuboidal or low columnar cells, which became low cuboidal or squamous as the tubule joined the rete testis proper.

The rete testis proper was made up of channels or spaces which were broken up into cavernous spaces or lacunae mainly by sheets or lamellae of connective tissue enclosed by rete epithelium (Fig. 5). Folds of tissue (Fig. 6) and occasionally strand-like or strut-like tissue overlaid by rete epithelium were also encountered. Except for the thinnest portions of the lamellae and the smallest struts of supporting or dividing tissues, the connective tissue of the rete was remarkably rich in blood and lymphatic vessels (Figs. 6, 7). Nerve bundles and mononuclear cells, especially plasma cells, were also commonly seen in the connective tissue (Fig. 8). The rete testis channels opened into the proximal efferent ductules caudally (Fig. 9).

The rete lacunae contained fluid and sparse cells which included spermatozoa, desquamated early germ cells and macrophages. The germinal cells were found within the lumina suspended in the fluid, while the macrophages were found mostly lying on the rete epithelium (Figs. 7, 8, 10). Macrophages were found in the rete testis of only the domestic fowl (*Gallus gallus domesticus*) and duck (*Anas platyrhynchos*).

SEM views of the surface of the epithelial lining of the rete showed that the cell outlines varied from elongated to regular polygons (Fig. 11). The cell margins were marked by a concentration of microvilli, while the central portions bore only a few (Fig. 11). A majority of the cells bore a single filamentous structure whose exact constitution was not clear (Fig. 11), although ultrastructural studies (*vide infra*) seemed to indicate that they might be cilia.

Transmission electron microscopy of the rete testis epithelium

The rete cells varied in height from high cuboidal in the rarely seen 'straight tubule' to simple squamous in the rete testis proper. Cuboidal epithelial cells also often lined the rete at recesses or at sharp turns within the rete testis channel, and at the junction between the rete testis and the proximal efferent ductule epithelium (Fig. 12). The epithelium, in most sections, showed overlapping of cells (Fig. 13); a thin process from one cell overlay one or more adjacent cells. A pseudostratification of the epithelium might thus occur. Not all cells, therefore, reached the lumen, and some

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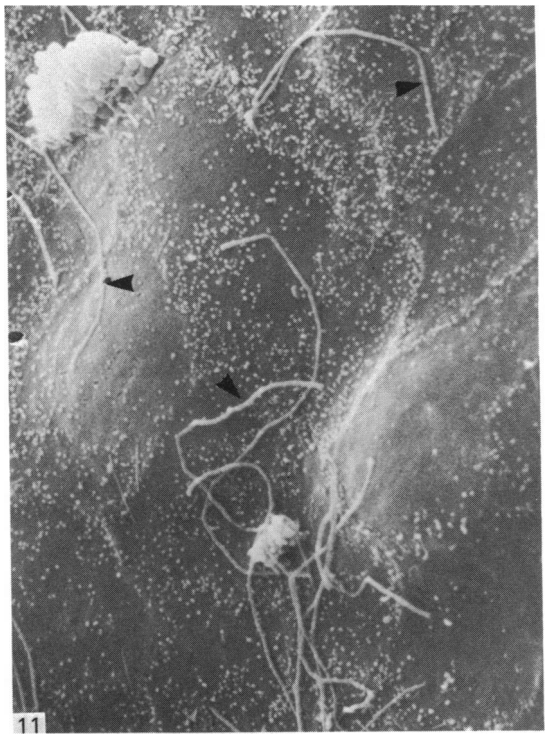
Fig. 6. Plastic section showing part of the epididymal region of the drake. *R*, rete testis channels; *P*, proximal efferent ductules; arrows, folds of rete epithelium; *, lymphatic vessels. Toluidine blue stain. × 100·8.

Fig. 7. Plastic section of rete testis tissue and channels of the drake. Note the highly vascular nature of the surrounding connective tissue. *R*, rete testis channels; *L*, lymphatic vessels. Toluidine blue. × 320.

Fig. 8. Plastic section of rete testis tissue of the drake showing a nerve bundle (*N*), macrophages (arrows), epithelium (*E*) and lymphatic vessels (*). Toluidine blue. × 280.

Fig. 9. Plastic section showing a rete channel (*R*) opening (arrow) into a proximal efferent ductule (*P*). Drake. Toluidine blue. × 320.

Fig. 10. Scanning electron micrograph of the rete testis of the drake showing two macrophages lying on the rete epithelium. Arrows indicate spermatozoa closely associated with the macrophages, probably in the process of being ingested by them. × 3000.



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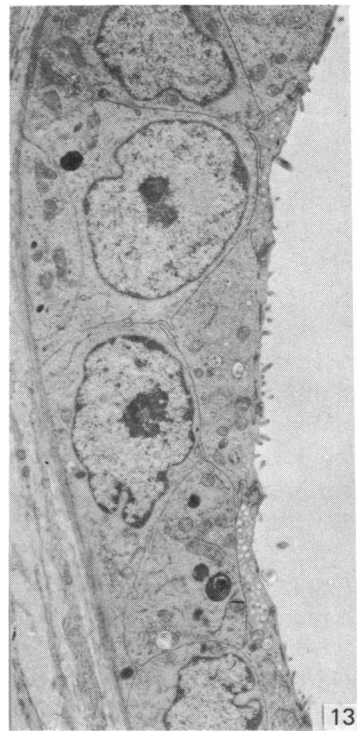

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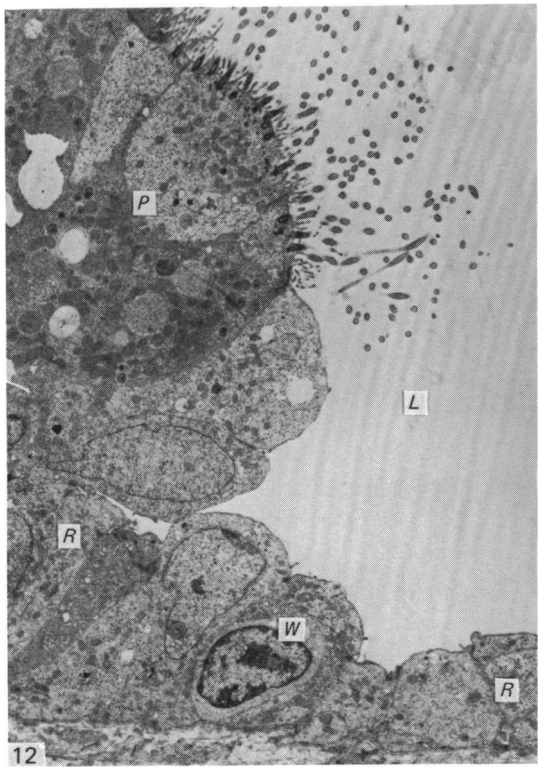

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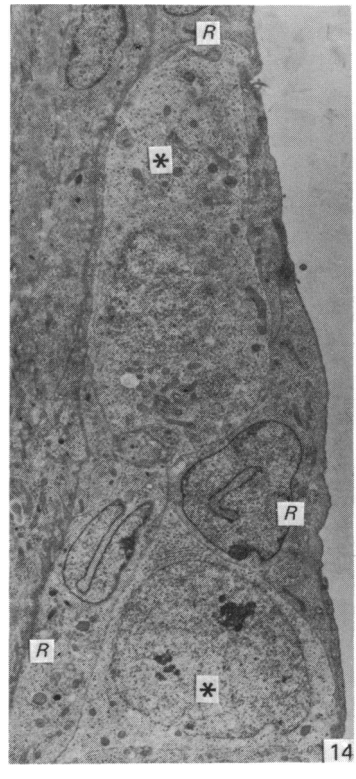

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appeared not to reach or lie on the basal lamina of the epithelium. With SEM, the parts of the rete which characteristically showed overlapping cells both in histological preparations and by TEM also showed highly elongated cell profiles. Areas where oval, polygonal cells occurred showed a true, simple squamous or cuboidal epithelium.

In good sections, a mixture of spermatogonia and rete cells at the beginning of the rete testis were sometimes seen (Fig. 14). In such transitional epithelia, the spermatogonia were normal structurally, and processes of the rete cells overlay them and thus prevented their reaching the rete lumen (Fig. 14). This transitional epithelium gradually changed to the typical rete epithelium caudally, as spermatogonia disappeared.

Caudally, as a rete testis lacuna opened into a proximal efferent ductule, the rete epithelium changed into high cuboidal or columnar type just before the typical epithelium of the proximal efferent ductule began (Fig. 12).

The apical or luminal border of the rete testis epithelial cell bore a few short microvilli which appeared to be straight or cylindrical in well fixed tissues (Fig. 15). Pleomorphic microvilli did not normally occur. In good sections, a centrally placed cilium might be seen arising from a basal body and projecting into the rete lumen (Fig. 16). Centrioles were also occasionally seen in the sub-apical cytoplasm (Fig. 16). Mitochondria occurred in moderate numbers, and were oval to elongated in shape. They occurred about equally both above and below the nucleus. The cristae were lamellar in shape. The Golgi complex was moderately developed and usually situated above or lateral to the nucleus. Sometimes it budded off small vesicles (Fig. 17). A number of vacuoles and numerous microvesicles (Fig. 16) might be seen in the sub-apical portion of the cytoplasm. In a few cells, the cytoplasm just below the apical plasma membrane contained large numbers of vacuoles filled with flocculent material (Fig. 18). A few multivesicular bodies and dense bodies also occurred in the cytoplasm (Figs. 15, 18).

Long profiles of the cisternae of rough endoplasmic reticulum occurred throughout the cytoplasm, and they were generally moderately distended with a flocculent material in the cisternal cavity (Fig. 19). The ground substance of the cell also contained abundant polyribosomes or ribosomal rosettes. Lipid droplets were not uncommonly present in the cytoplasm (Fig. 17). Microfilaments were commonly seen around the nucleus which was characteristically irregular in outline (Fig. 20). The nucleus occupied more than half the volume of the cell, especially in the squamous type, and it showed scattered margination of chromatin (Fig. 15). Only one nucleolus, consisting of the pars amorpha and nucleolonema, occurred centrally within the

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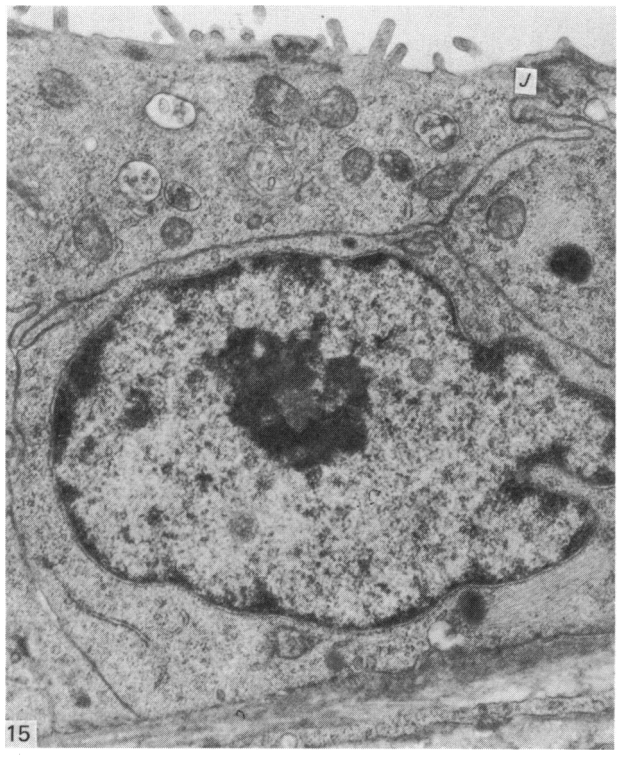
Fig. 11. Scanning electron micrograph of the surface of the rete testis epithelium of the drake. Note the presence of microvilli, especially along the cell borders. Also note the presence of filamentous structures (arrowheads) arising from the cell surfaces. × 3600.

Fig. 12. A transmission electron micrograph of the junction between the rete testis epithelium (*R*) and the proximal efferent ductular epithelium (*P*). Note the cuboidal or columnar type epithelium at the boundary between the two epithelia. Note also the presence of a lymphocyte (*W*) in the rete epithelium. *L*, lumen of ductule. × 3000.

Fig. 13. Survey transmission electron micrograph of drake rete testis. Note overlapping of cells, and irregular nuclei with one nucleolus. × 4500.

Fig. 14. Transmission electron micrograph of the transitional zone between the rete testis epithelium and the seminiferous epithelium. The spermatogonia (*) are prevented from reaching the rete testis lumen by rete cells (*R*). Domestic fowl. × 3000.



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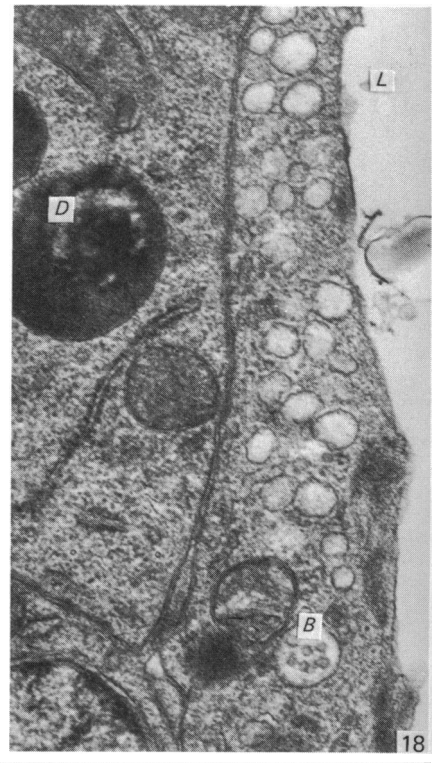

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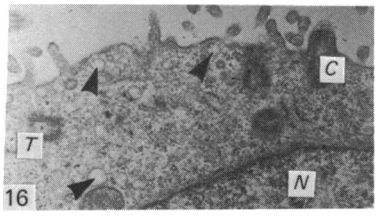

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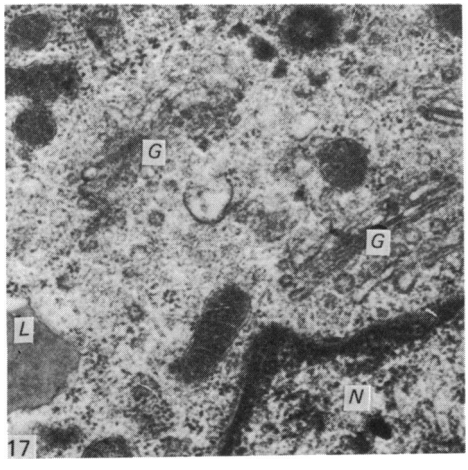

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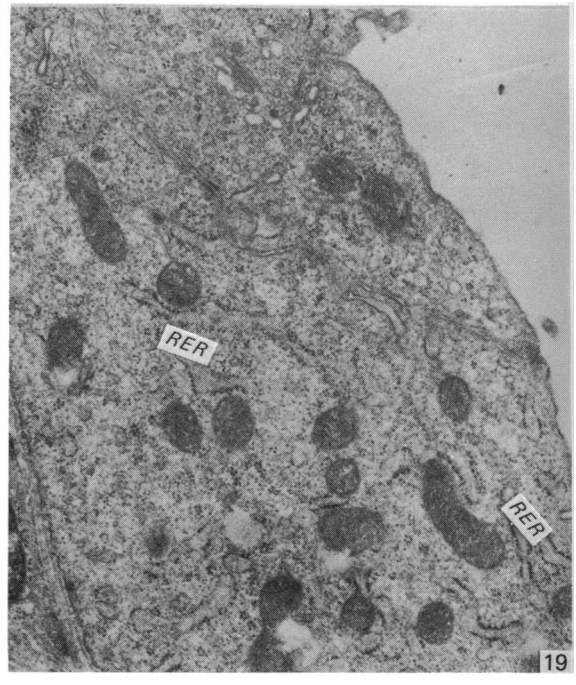

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nucleus. Junctional complexes attached adjacent cells at their apical ends, sometimes where they overlapped, as, for example, in Figures 15 and 21. The lateral plasma membranes of adjacent cells sometimes formed extensive and complex interdigitations (Figs. 21, 22). The basal plasmalemma lay on a basal lamina which might be regular or irregular in some sections (Fig. 23).

Another cell commonly seen in the rete testis epithelium is the lymphocyte (Fig. 12). These cells possessed a lighter cytoplasm than the surrounding epithelial cells, and their nuclei were less irregular in outline and very much more heterochromatic than those of the epithelial cells. No junctional complexes between them and adjacent epithelial cells were seen. It was only in the drake that macrophages (similar structurally to those found in the lumen of the rete) (Fig. 24) were seen within the rete epithelium (Fig. 25). No macrophage was seen actually breaking through the basal lamina nor breaking through the rete epithelial cells to gain entry into the rete lumen. But such intraepithelial macrophages did displace rete cells laterally and dorsally.

The rete epithelium lay on a connective tissue stroma consisting of dense aggregations of collagen fibres running in a disorganised fashion, and myofibroblast cells running parallel to the basal lamina of the epithelium (Figs. 26, 27).

DISCUSSION

It has been established that the rete testis of the domestic fowl develops from mesenchymal rete blastema interposed between the testis and mesonephros (Budras & Sauer, 1975), and therefore has an embryological origin, which differs from that of the seminiferous tubule. In most mammals (Roosen-Runge, 1961; Kormano, 1977) the rete is subdivided into intratesticular, intratunical and extratesticular portions. Similar observations in birds have been made by Budras & Sauer (1975) and Aire *et al.* (1979). The intratesticular portion is rarely observed, and consists mainly of the so-called 'straight tubules' or 'tubuli recti' (Aire *et al.* 1979). The latter have been seen only in the domestic fowl (Gray, 1937), the Japanese quail (Aire, 1979*a*) and guinea-fowl (Aire *et al.* 1979). The 'tubulus rectus' and the rete testis are organised in a similar fashion (Osman, 1978), and it is now thought that the 'tubulus rectus', in fact, constitutes part of the rete testis (Amann *et al.* 1977; Kormano, 1977; Roosen-Runge & Holstein, 1978).

In birds, most of the seminiferous tubules terminate by opening into the rete directly; only occasionally do one or more seminiferous tubules open into a 'tubulus rectus' which then empties into the rete testis proper (Aire *et al.* 1979). A transitional

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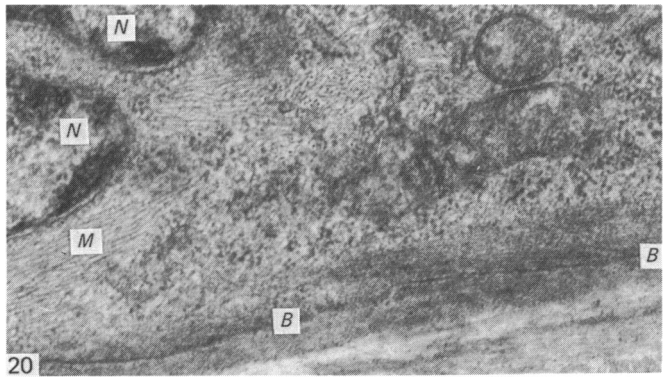
Fig. 15. Portions of rete epithelial cells of the drake. The microvilli are short and regular in shape. Multivesicular bodies also occur commonly in the cytoplasm. The nucleus is irregular and heterochromatic, and the nucleolus shows two distinct portions of pars amorpha and nucleolonema. *J*, apical junctional complex. × 15000.

Fig. 16. Apical portion of rete cell of the Japanese quail. A cilium (*C*) is seen arising from a basal body in the sub-apical cytoplasm. A centriole (*T*) is also seen. Note the presence of numerous microvesicles (arrowheads) in the cytoplasm. *N*, nucleus. × 17500.

Fig. 17. A portion of the rete cell of the Japanese quail showing moderately developed Golgi complexes (*G*). *L*, lipid droplet; *N*, nucleus. × 25600.

Fig. 18. Several vacuoles, similar to the multivesicular body (*B*), occur in the cytoplasm of a rete cell of the drake. *L*, lumen of the rete lacuna; *D*, dense body. × 30000.

Fig. 19. Portions of rete cells of the drake showing numerous profiles of rough endoplasmic reticulum (*RER*) in the cytoplasm. × 15000.



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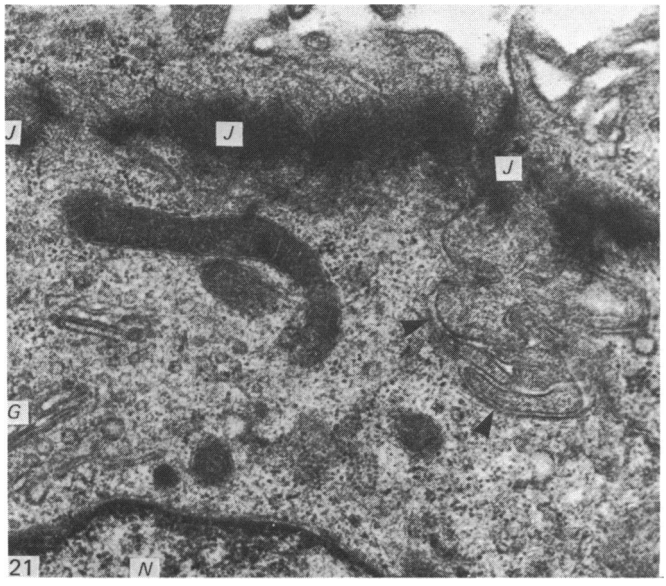

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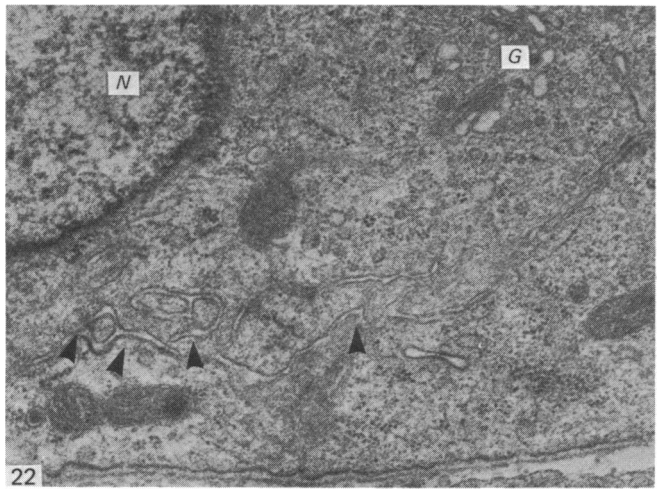

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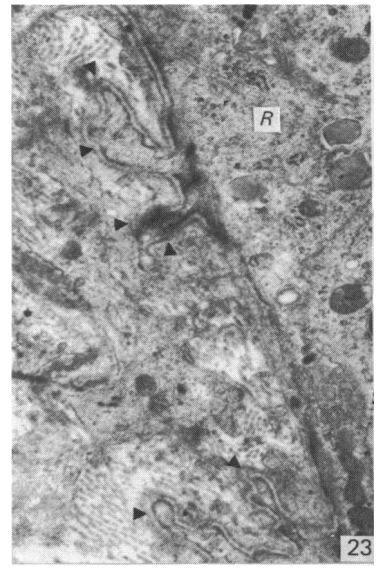

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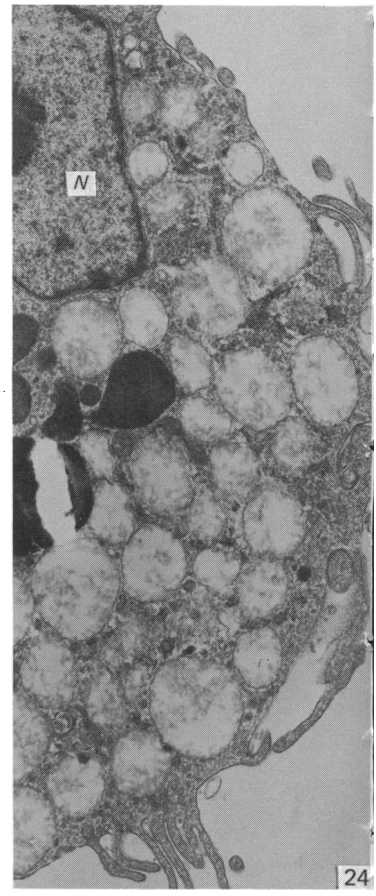

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epithelium, consisting of spermatogonia and rete testis cells, occurs at the proximal end of the 'tubulus rectus' or just caudal to the direct entry of the seminiferous tubule into the rete testis. The rete cells in this zone are similar in composition to rete cells found elsewhere.

The labyrinthine nature of the rete testis of birds is caused by broad longitudinal or vertical plates or lamellae of connective tissues enclosed in rete epithelium. A few thin strands of tissue may be seen traversing the lumen of the rete.

In man (Roosen-Runge & Holstein, 1978) and horse (Amann *et al.* 1977) the partitioning and/or supporting tissue consists mainly of strands or struts of tissue which are similar, grossly, to the chordae tendineae of the heart. Roosen-Runge & Holstein (1978) therefore called those structures of the rete 'chordae retis'. Because these structures include myoid cells it is not unlikely that their contraction and relaxation may act to move fluid and spermatozoa away from the rete testis into the efferent ductules.

Scanning electron microscope views of the surface epithelium of the rete reveal filamentous structures, which project singly from the cell surfaces into the rete lumen. Such 'filaments' have also been seen projecting singly from the rete cells of the horse (Amann *et al.* 1977) and man (Roosen-Runge & Holstein, 1978). Those of man have been identified as cilia, but not those of the horse and drake. However, a proportion of the rete testis cells of some birds, in good sections, shows a cilium arising from a basal body in the sub-apical cytoplasm and projecting into the rete testis lumen. The role of these sparse cilia is unknown. They may, beating individually, create a sluggish movement of the fluid content of the rete, thus allowing for its mixing and contact with the epithelium.

Ultrastructurally, the rete cells are similar in all the birds investigated. The height of the cells varied from high cuboidal to squamous. Tingari (1972) also made similar observations in the fowl. The height of the cell seemed to be largely determined by the location and, hence, the sectioning plane. However, the cells that marked the border between the epithelium of the rete testis and that of the proximal efferent ductule, as well as the cells of the so-called straight tubules, were distinctly cuboidal. Overlapping of the rete cells was rather the rule than the exception. Bustos-Obregon & Holstein (1976) recognised two cell types in the rete epithelium of man; squamous and prismatic cells. The former are darker than the latter which are also columnar. Cells of a height similar to those described for birds have also been reported for the rat (Leeson, 1962), rat, cat, rabbit, goat, boar, ram and bull (Osman, 1978).

On the basis of the organelle content of the rete cells in birds, the present author agrees with observations made by Tingari (1972) for the fowl, and concludes that these cells in birds are more active than those described for mammals (Ladman &

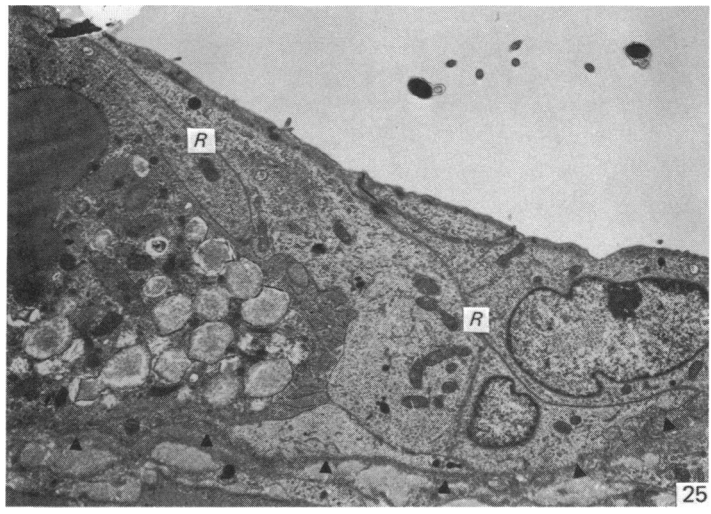
Fig. 20. Basal portion of the rete cell of the drake. *M*, microfilaments; *N*, nucleus; *B*, basal lamina. × 30000.

Fig. 21. Junctional complexes (*J*) may occur extensively and remarkably because of overlapping of cells in the rete testis epithelium. *G*, Golgi complex; *N*, nucleus; arrowheads indicate extensive and complex interdigitations of the lateral plasma membrane. Japanese quail. × 25600.

Fig. 22. Arrowheads show complex interdigitation of adjacent plasma membranes of rete cells. *G*, Golgi complex; *N*, nucleus. Domestic fowl. × 20000.

Fig. 23. Basal portion of a rete cell (*R*) lying on an irregular formation (arrowheads) of the basal lamina. Domestic fowl. × 11520.

Fig. 24. Part of a macrophage found in the lumen of the rete testis of the drake. Note the numerous vacuoles with flocculent material in their lumina. *N*, nucleus. × 10000.



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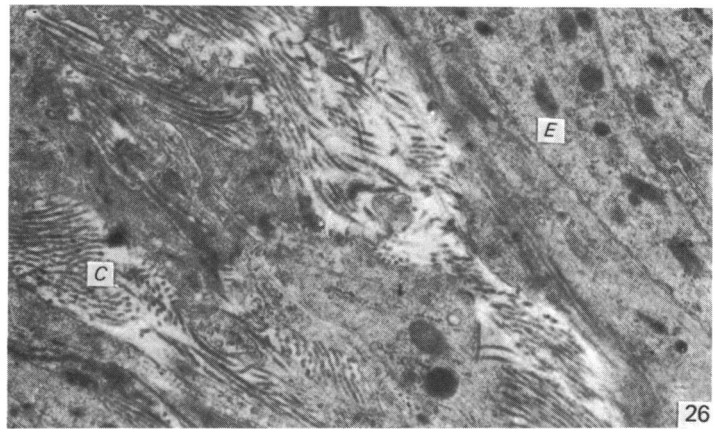

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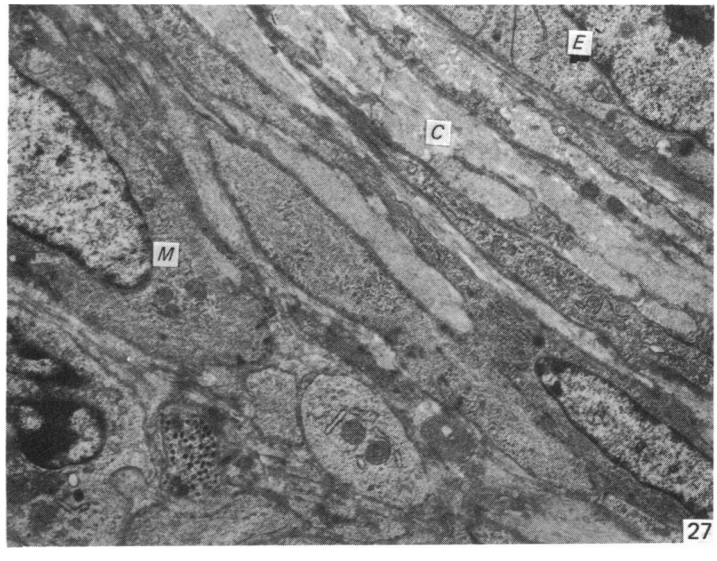

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Young, 1958; Leeson, 1962; Bustos-Obregon & Holstein, 1976; Dym, 1976; Osman, 1978). Nevertheless, the ultrastructural features of the rete cells in birds do not provide evidence of a secretory role on those cells. Rete testis fluid of birds has, to the knowledge of the author, not been analysed in order to determine whether or not its content is similar to the fluid secreted by the seminiferous tubules. The significance of the remarkable vascularity of the connective tissue in the rete region of birds is not yet known. The rete epithelium is known to be responsible for producing about 65 % of the total fluid found in this part of the tract (Waites, 1977). Whether this contribution is by a secretory process or by a passive transportation process is unclear. Osman (1978) speculates on the involvement of the rete epithelium in transfer of substances and fluid from the blood vessels into the rete channels, or *vice versa*, but the presence of several microvesicles in the sub-apical cytoplasm of the rete cells in birds (this study) and mammals (Osman, 1978) also suggests some active secretory process. This process may, however, be of limited importance only.

Unlike mammals (Dym, 1976), birds have an extensive lymphatic supply of the rete testis connective tissue. The significance of this also is not clear, but it may be connected with reverse transfer of substance from the rete channels into the vascular system.

Previous reports have shown the presence of macrophages in the rete testis channels (Aire & Malmqvist, 1979*a*), and of lymphocytes in the excurrent ducts of the testis, including the rete, in the domestic fowl (Aire & Malmqvist, 1979*b*). In the present study, macrophages were seen abundantly in the rete testis channels of the cock and drake. In the latter, macrophages were seen in the connective tissue of the rete system, and such cells were even seen insinuating themselves between rete cells in an apparent attempt to gain entry into the rete lumen where a large number of them were seen lying on the epithelium. Both the intraepithelial lymphocytes and macrophages have been discussed more fully in the papers referred to above.

SUMMARY

The rete testis in the domestic fowl (*Gallus gallus domesticus*), Japanese quail (*Coturnix coturnix japonica*), guinea-fowl (*Numida meleagris galeata*) and drake (*Anas platyrhynchos*) was studied histologically and with both the scanning and transmission electron microscopes. All the birds have rete epithelial cells varying between squamous and high cuboidal. A cilium-like structure projects from the luminal portion of most cells into the rete lumen, and the outline of the cells varies from polygonal to elongate. Sparse, stubby microvilli were concentrated on the cell borders. Ultrastructural features suggest only moderate secretory and absorptive activities in the cells. The rete testis of birds is amply supplied with blood as well as lymphatic vessels and nerves. Intraepithelial lymphocytes form part of the rete epithelium, and macrophages are present in large numbers in the rete lumen of the domestic fowl and drake and, to a lesser degree, also in the rete epithelium of the drake.

Fig. 25. Rete testis epithelium of the drake showing a macrophage (on the left) within the epithelium. *R*, rete epithelial cells. Arrowheads show the basal lamina of the epithelium. The nucleus of the macrophage is not included within the limits of this micrograph. × 4000.

Fig. 26. The connective tissue on which the rete testis epithelium (*E*) lies consists largely of bundles of collagen (*C*). Domestic fowl. × 7680.

Fig. 27. Myofibroblasts (*M*) also occur in the connective tissue surrounding the rete testis epithelium (*E*). *C*, collagen. × 7500.

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