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Ultrastructure of the epithelial cells in the epididymal region of the turkey (*Meleagris gallopavo*)

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INTRODUCTION

The epididymal region of the male chicken is functionally important in the transportation and maturation of spermatozoa, the secretion and resorption of fluids, and the removal of degenerating spermatozoa (Lake, 1957; Lake, 1962; Munro, 1938; Tingari, 1971; Tingari, 1973; Tingari & Lake, 1971; Tingari & Lake, 1972). In mammals, the epididymis has similar functions (Orgebin-Crist, 1969) and has the additonal function of sperm storage (Glover & Nicander, 1971).

Previous studies of the male turkey reproductive system have been concerned with general morphology (Hess, Thurston & Biellier, 1976). In view of the dynamic function of the ducts in the epididymal region, it is important that the ultrastructure of the ductal epithelia be determined. This report gives an account of the ultrastructure of the epithelial cell types found in the epididymal region of the turkey.

MATERIALS AND METHODS

Eight yearling Large White turkey breeder males were selected as producers of normal semen (using the criteria of Thurston *et al.* 1975). The turkeys were anaesthetized with sodium pentabarbital and killed by phlebotomy. A bilateral incision was made in the abdomen and the testes and associated ducts were exposed.

Glutaraldehyde (3 %) in Millonig's (1961) phosphate buffer (pH 7·35) was injected under the tunica albuginea of the testis in several locations (Dal Lago & Lucke, 1973), but not in the epididymal region, and fixative (22 °C) was poured over the testes and ducts. Within 5 minutes the testes were removed and the epididymal region was dissected into 1 mm^3 pieces and fixed for 1 hour at 4 °C. Following a buffer rinse, the tissue was post-fixed for 1 hour at 4 °C in 2 % osmium tetroxide phosphate buffered at pH 7·35. The samples were then rinsed with buffer, dehydrated in ethanol and embedded in Spurr's resin (Spurr, 1969).

Thin (1 μm) sections were cut, stained with toluidine blue, and examined with the light microscope for determining the orientation of the individual ducts in the epididymal region. Ultrathin sections cut from selected areas with a diamond knife were stained for 10 minutes with 1 % ethanolic uranyl acetate, for 2 minutes with lead citrate (Reynolds, 1963) and then examined with a Philips EM300 electron microscope.

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RESULTS

Hess *et al.* (1976) previously described the epididymal region of the turkey as consisting of the rete testis, the ductuli efferentes, narrow and wide connecting ductules, and the ductus epididymidis. The ultrastructure of the cell types found in these ducts is reported here as follows:

Rete testis

Squamous and low cuboidal cells (Fig. 1) formed the epithelium of the rete, which is a system of channels conveying spermatozoa from the seminiferous tubules to the ductuli efferentes. The lamina propria containing dense regular connective tissue and bundles of smooth muscle was separated from the epithelia by a prominent basal lamina.

Squamous cells

The squamous cells were more electron-dense than the cuboidal cells and were spread out in juxtaposition with a prominent basal lamina (Figs. 1, 2). Tight junctions and interdigitating plasmalemmas formed cohesive intercellular connexions. The nuclei were large and invaginated, and some had distinct nucleoli. Dense chromatin coalesced along the nuclear envelope, while the inner nucleoplasm was finely granular, sometimes containing small round vesicles. The cytoplasm contained large mitochondria, occasional extended cisternae of rough endoplasmic reticulum and sparse Golgi complexes (Fig. 2). A few membrane-bound, electron-dense bodies were also observed.

Cuboidal cells

The cuboidal cells appeared to have a greater ratio of cytoplasm to nucleus than the squamous cells, and their surfaces were smooth with few microvilli. Nuclei were usually round but sometimes folded (Fig. 1), and contained dense marginated chromatin and occasional large nucleoli (Fig. 1). Cytoplasmic organelles (Fig. 3) included arrays of Golgi cisternae containing many vesicles, abundant smooth endoplasmic reticulum, rough endoplasmic reticulum and a few small, electron-dense bodies. The mitochondria were smaller, but more numerous, than those of the squamous cells. The cuboidal cells were connected by gap junctions and junctional complexes, but had loosely aligned plasmalemmas.

Ductuli efferentes

The cells of the rete testis changed abruptly into ciliated and non-ciliated columnar cells in the ductuli efferentes (Fig. 4), with approximately two ciliated cells for every five non-ciliated cells. The non-ciliated cells of the ductuli efferentes and connecting

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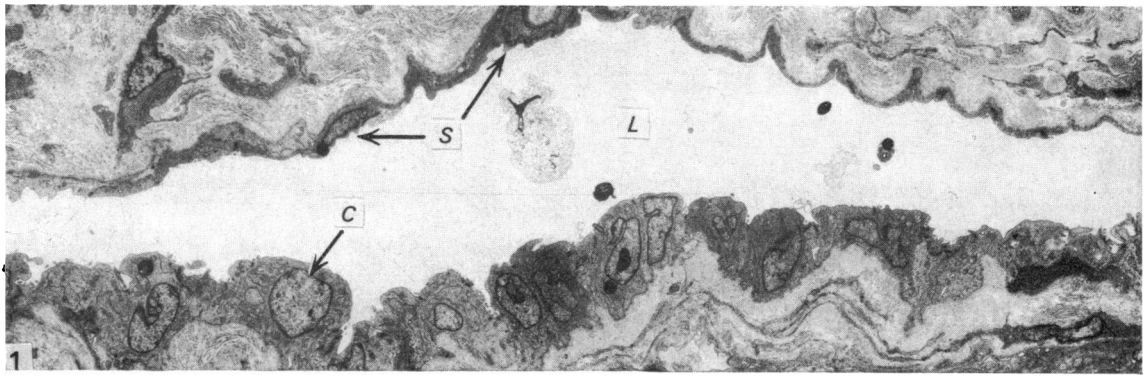
Fig. 1. Rete testis. The lumen (*L*) is lined by cuboidal (*C*) and squamous (*S*) cells. A thick layer of connective tissue is beneath the epithelium. × 2340.

Fig. 2. Squamous cell of the rete testis. This cell is short and elongate, contains few mitochondria (*M*) and rough endoplasmic reticulum (*Rer*). *Nu*, nucleus; *Jt*, intercellular junction; *Bl*, basal lamina. × 24000.

Fig. 3. Low cuboidal cell of the rete testis. There are numerous mitochondria (*M*) and cisternae of rough endoplasmic reticulum (*Rer*). A well developed Golgi complex (*G*) is also seen. *Nu*, nucleus; *Jt*, intercellular junction. × 20500.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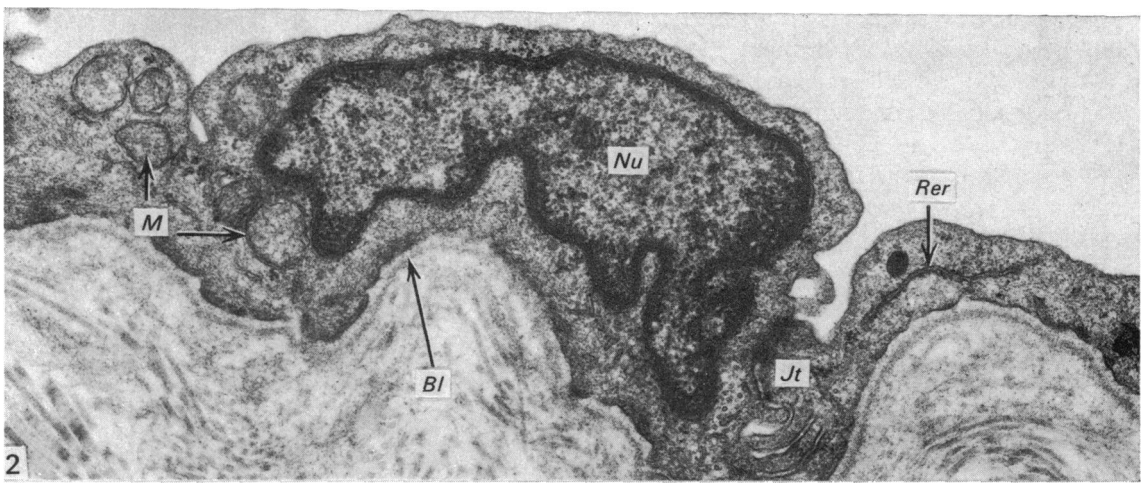
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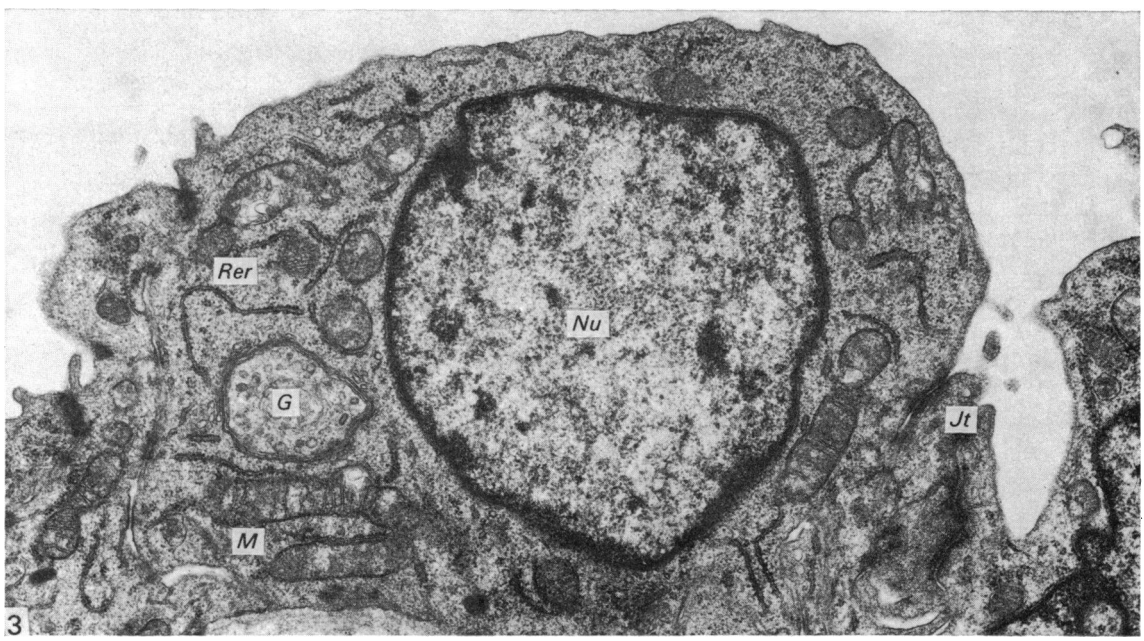
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ductules were similar to the Type I cells described by Tingari (1972) in the epididymal region of the chicken. Therefore, this cell type was classified as Type I in the turkey also. Occasional basal cells were present with an ultrastructure similar to those found elsewhere in the epididymal region. The basal cell is discussed with the epithelial cell types found in the ductus epididymidis.

Ciliated cells

Microvilli projected from the cell surfaces between numerous cilia (Fig. 5) which contained basal bodies and striated rootlets extending into the apical cytoplasm. The nuclei had prominent invaginations (Fig. 7), marginated chromatin and distinct nucleoli, and were often surrounded by bundles of cytoplasmic fibrils (Fig. 8). Mitochondria were closely packed in the apical cytoplasm (Fig. 5) and were associated with microtubules and rough endoplasmic reticulum, which was observed throughout the cytoplasm. Golgi complexes were located near the nuclei, and arranged as parallel arrays of membranes (Fig. 6). The apical cytoplasm contained occasional osmiophilic bodies and vacuoles were dispersed throughout the cell (Figs. 4, 6).

Non-ciliated Type I cells

The non-ciliated cells of the ductuli efferentes were more electron-dense than the ciliated cells (Fig. 4). Numerous microvilli projected from their surfaces into the ductal lumen (Fig. 11). Tight cell junctions held the loosely aligned plasmalemmas. The nuclei were round with large nucleoli (Fig. 9), and often contained nuclear vesicles (Fig. 10) which appeared in pairs or as single structures, with an amorphous central matrix surrounded by an osmiophilic ring. The vesicles were covered with a finely granular material.

Prominent Golgi complexes (Fig. 9), consisting of concentric membranes associated with dense bodies and lipid-like vesicles, were present near the nuclei. Numerous large mitochondria were found in the apical and basal cytoplasm (Figs. 11, 12) and were always associated with rough endoplasmic reticulum, dark osmiophilic bodies or lipid-like vesicles. A few concentric mitochondria surrounded lipid vesicles (Fig. 12) or Golgi–rough endoplasmic reticulum complexes (Fig. 13). Autophagic vesicles were identified at different sites within these cells, appearing to have fused with the plasmalemma (Fig. 14).

The apical cytoplasm, which often projected into the ductal lumen, contained an

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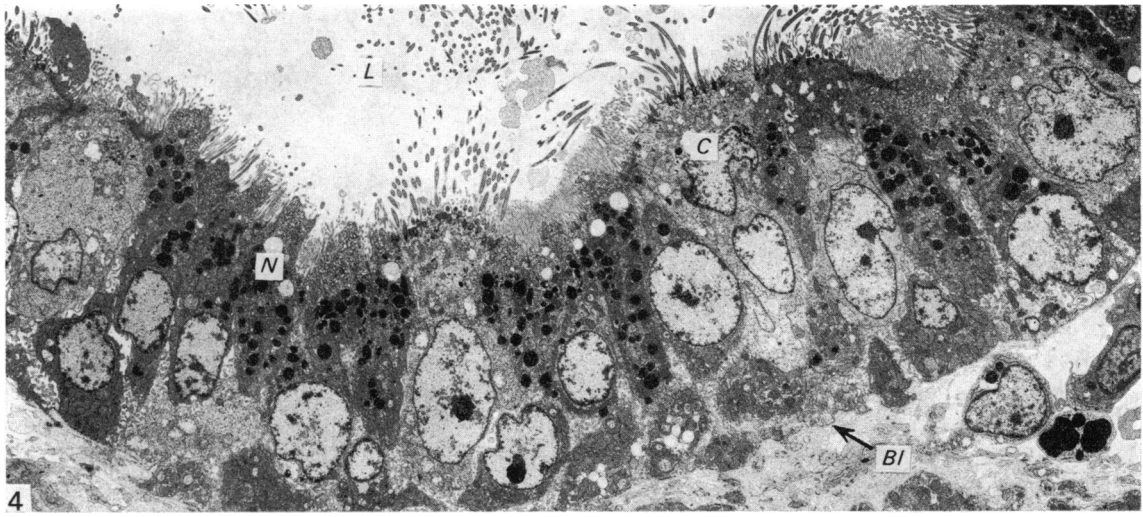
Fig. 4. Ductulus efferens. The pseudostratified epithelium consists of non-ciliated (*N*) cells with large electron-dense granules and ciliated (*C*) cells with cilia extending into the ductal lumen (*L*). *Bl*, basal lamina. ×2160.

Fig. 5. The ciliated cells of the ductulus efferens contain numerous mitochondria (*M*) in the apical cytoplasm. Cilia (*C*) with typical axonemal structures project into the lumen between microvilli. Rootlets (*R*) extend from the basal bodies (*B*) deep within the cytoplasm. *O*, osmiophilic body. ×16000

Fig. 6. The Golgi complex (*G*) of the ciliated cell is small and consists of closely packed cisternae near the nucleus (*Nu*). *V*, lipid vesicle. Ductulus efferens. ×9520.

Fig. 7. The nucleus (*Nu*) of the ciliated cell is highly folded, providing increased surface area. The nucleus was usually basal. *V*, lipid vesicle; *N*, nucleus of a non-ciliated cell. Ductulus efferens. ×38000.

Fig. 8. Ciliated cell of the ductulus efferens. Short strands of fibrillar bundles (*F*) are found near the nucleus (*Nu*). ×38000.



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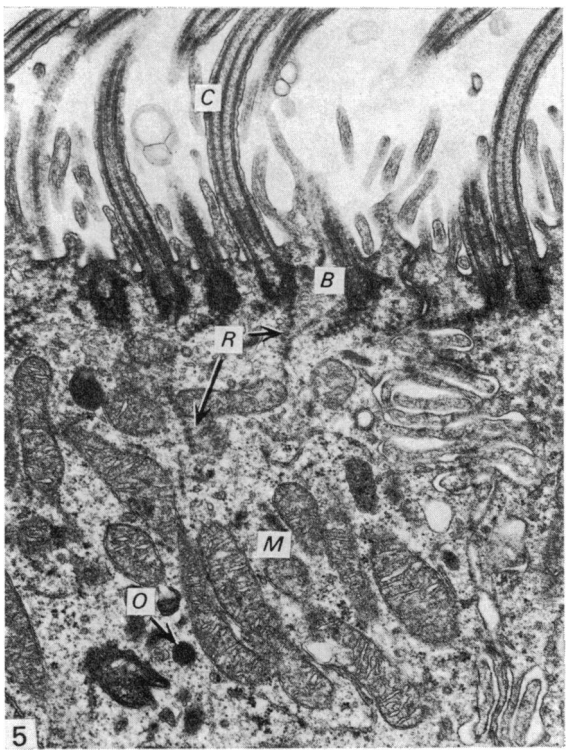

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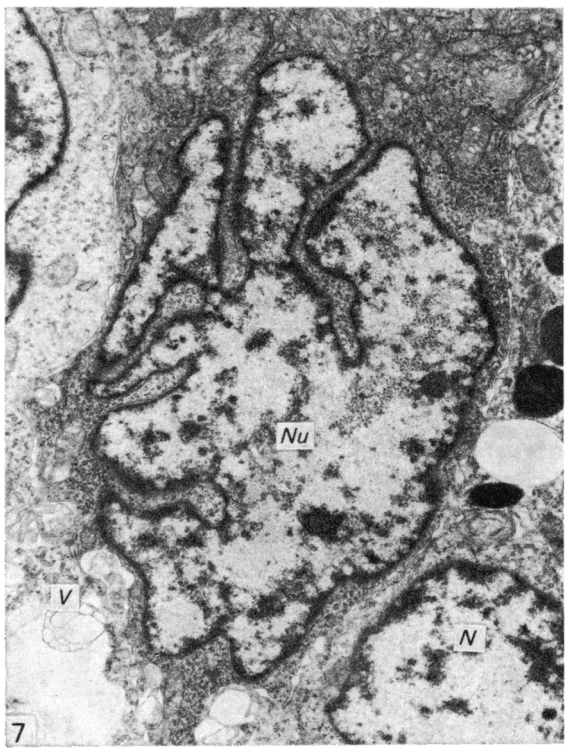

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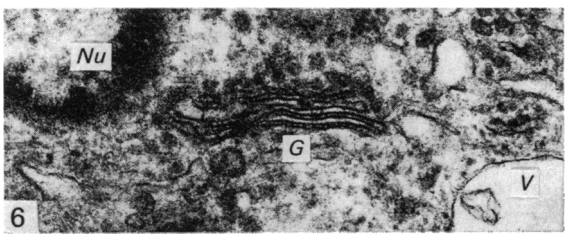

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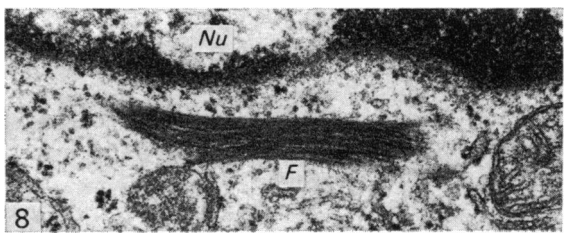

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abundance of small structures (Fig. 11) which resembled electron-dense rods or 'bar-bells'. Rounded portions of cytoplasm containing the rod structures and rough endoplasmic reticulum were seen in the ductal lumen, and appear to be derived from the Type I cells by apocrine secretion. While some cells projected considerable amounts of cytoplasm into the lumen (Fig. 16), others showed no blebbing (Fig. 15).

Connecting ductules

The pseudostratified columnar epithelium of the connecting ductules was smoothly contoured. Individual cells did not always appear next to the basal lamina and were loosely arranged with many intercellular spaces (Fig. 17). The cell types included ciliated and non-ciliated Type I columnar cells and basal cells with ciliated cells greatest in number and non-ciliated cells recognized by their cytoplasmic protrusions into the ductule lumen. The ratio of ciliated to non-ciliated cells was approximately 2:1. The ultrastructure of the rare basal cells was similar to that described for the basal cells of the ductus epididymidis.

Ciliated cells

The ultrastructure of these cells was similar to the ciliated cells of the ductuli efferentes, except that they were shorter, appeared to contain fewer mitochondria (Fig. 18), and bundles of microfibrils did not surround the nuclei. Nuclei with prominent infoldings were found in the apical and basal cytoplasm.

Non-ciliated Type I cells

These cells were similar to those found in the ductuli efferentes, except for the following characteristics: Golgi complexes were not as elaborate, mitochondria (Fig. 19) were generally elongated and were not arranged concentrically around Golgi or lipid vesicles and the apical cytoplasm contained fewer large electron-dense bodies and small rod-shaped and 'bar-bell' structures.

Fig. 9. Nucleus (*Nu*) of a non-ciliated Type I cell in the ductulus efferens. A well developed Golgi complex (*G*) consists of parallel array of membranes around a vesicle (*V*). *N*, nucleolus. ×12500.

Fig. 10. Vesicular structures often found in the nucleus of Type 1 cells. Ductulus efferens. ×33750.

Fig. 11. Non-ciliated Type I cell of the ductulus efferens. Numerous rod-shaped and 'bar-bell' structures (*R*) are seen in the bleb which extends into the lumen. In the apical cytoplasm are mitochondria (*M*) closely associated with rough endoplasmic reticulum (*Rer*). Large osmiophilic bodies (*O*) and smaller dense bodies (*Db*) are found in the apex of this cell type. ×19000.

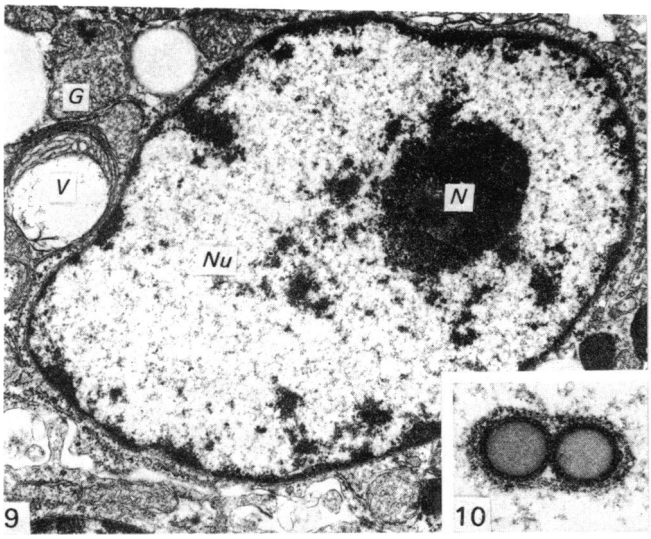
Fig. 12. Basal portion of a Type I cell of the ductulus efferens. Numerous mitochondria (*M*) are packed near the basal lamina (*Bl*). Lipid vesicles (*V*) are seen along with dilated portions of smooth endoplasmic reticulum (*Ser*). ×10080.

Fig. 13. Mitochondrion (*M*) from a Type I cell. The mitochondria are arranged in concentric formation around rough endoplasmic reticulum (*Rer*). Ductulus efferens. ×32000.

Fig. 14. Large autophagic vesicles (*A*) containing finely granular material and dense bodies (*Db*) are seen in the apical cytoplasm of a non-ciliated Type I cell. One vesicle appears to have fused with the surface membrane (arrow). Ductulus efferens. ×15640.

Fig. 15. Apical cytoplasm of Type I cell which is not blebbing into the lumen. Ductulus efferens. *R*, rod-shaped structures; *M*, mitochondria. ×8900.

Fig. 16. The apical cytoplasm of this Type I cell is seen projecting into the lumen. The bleb (*B*) does not contain the rod-shaped structures (*R*). ×8960.



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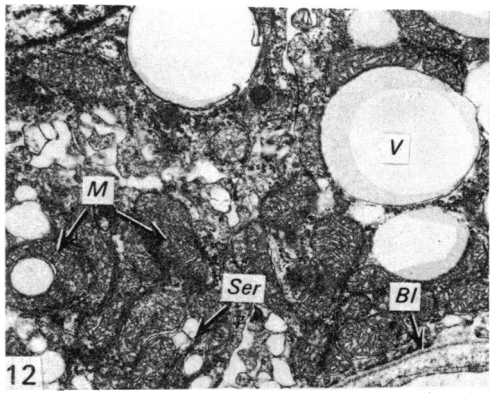

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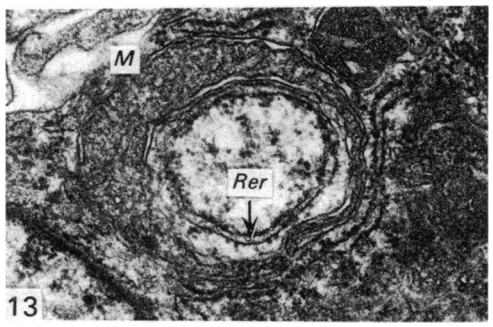

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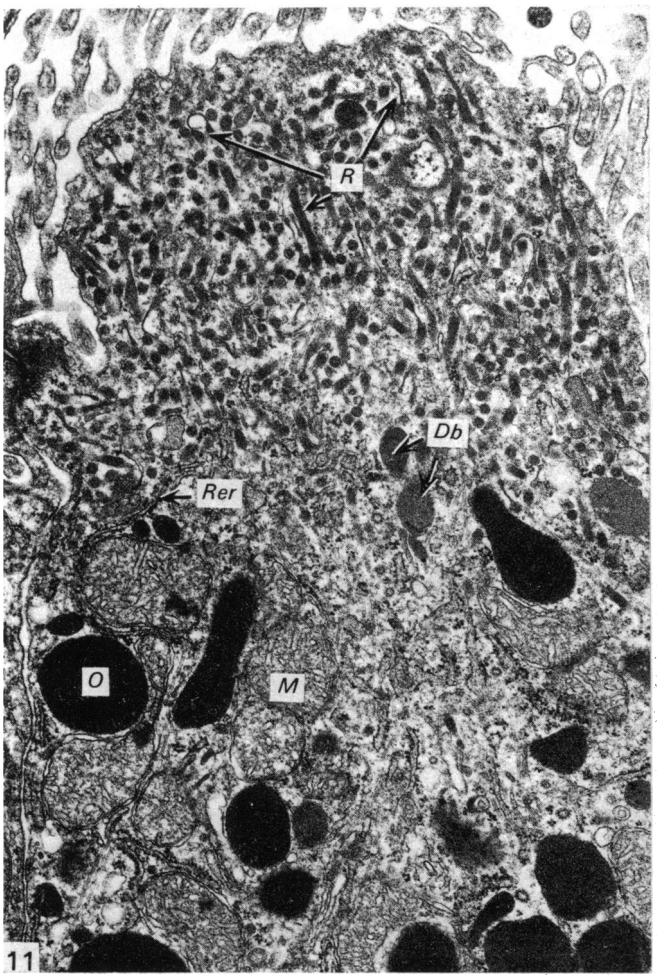

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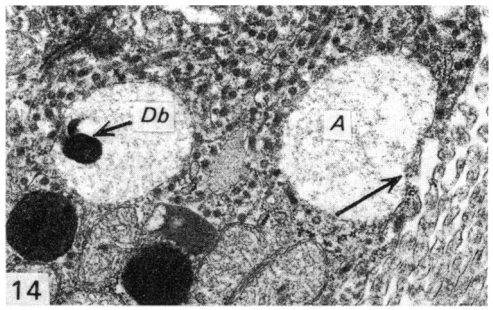

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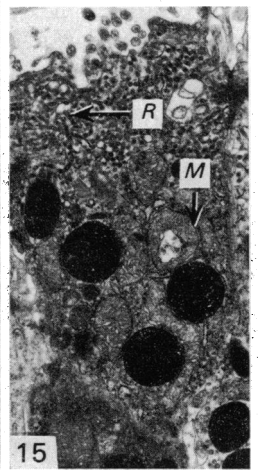

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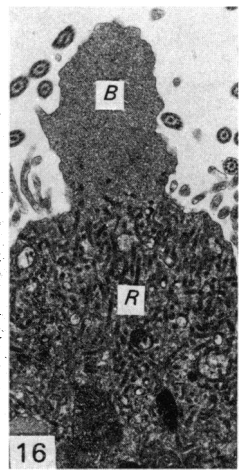

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Ductus epididymidis

A thick, pseudostratified columnar epithelium lined the ductus epididymidis (Fig. 20) which began abruptly at the end of the connecting ductules. The epithelium consisted of non-ciliated columnar cells and basal cells. Although the non-ciliated cells found here were quite different from the corresponding cells in the chicken (Tingari, 1972), for convenience of classification we have used the term Type II to represent the non-ciliated columnar cells in the ductus epididymidis of the turkey.

Non-ciliated Type II cells

The relatively smooth surface of these cells occasionally extends into the lumen of the duct. Cell junctional complexes and the lateral plasmalemmas produced tight cohesion. The round nuclei contained distinct nucleoli (Fig. 21), with condensed chromatin along the nuclear envelope. Golgi complexes were difficult to distinguish (Fig. 22), but the rough endoplasmic reticulum was well developed, exhibiting long cisternae with associated ribosomes (Figs. 20, 23), while numerous mitochondria and free ribosomes were scattered throughout the cytoplasm. Lipid-like vesicles, approximately 1–2 μm in diameter (Fig. 21), were abundant and gave the epithelium of the ductus epididymidis a characteristic electron-lucent appearance (Fig. 20).

Basal cells

This cell type was small and had a greater electron density than the surrounding cells (Fig. 24). Its profile was irregular, being low cuboidal or triangular (Fig. 24). Large, irregular shaped nuclei occupied most of the cytoplasm and contained condensed chromatin and occasional nucleoli. The Golgi complexes were small and difficult to distinguish; however, some rough endoplasmic reticulum was recognized, as well as a few mitochondria (Fig. 25). Small lipid-like vesicles and electron-dense granules were occasionally observed.

DISCUSSION

Our previous report (Hess *et al.* 1976) indicated few gross anatomical differences between the turkey and chicken epididymal region. In this report, several ultrastructural differences have been listed.

Tingari (1972) described the ultrastructure of five epithelial cell types in the epididymal region of the chicken: (1) low cuboidal, (2, 3) non-ciliated Type I and Type II, (4) ciliated and (5) basal. The epididymal region of the turkey contained six cell types: (1) squamous and (2) low cuboidal cells of the rete testis; (3) non-ciliated

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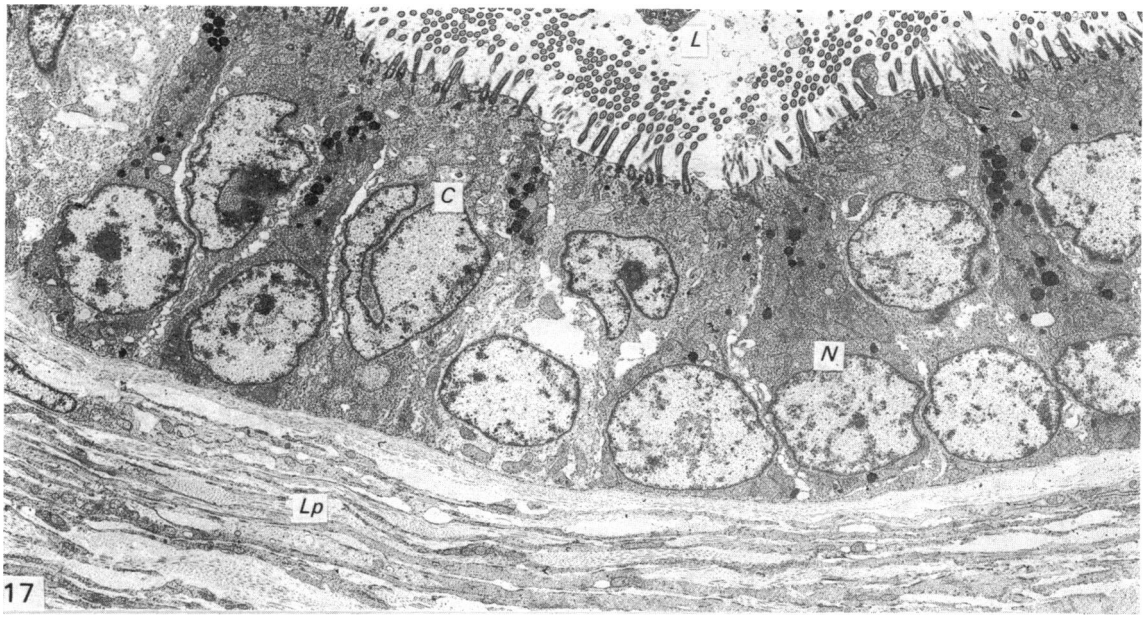
Fig. 17. Narrow connecting ductule. The lateral plasmalemma of the ciliated (*C*) and non-ciliated (*N*) cells is loosely organized, producing intercellular spaces. The non-ciliated Type I cells contain a few large, electron-dense bodies in their apical cytoplasm. *L*, lumen; *Lp*, lamina propria. × 3600.

Fig. 18. This ciliated cell from a narrow connecting ductule contains fewer mitochondria (*M*), dense bodies and other cytoplasmic organelles than the ciliated cell of the ductuli efferentes. *C*, cilia; *Nu*, nucleus. × 14000.

Fig. 19. Non-ciliated Type I cell of a narrow connecting ductule. The nucleus (*Nu*) is typically located in the basal cytoplasm. Large mitochondria (*M*) are found throughout the cell, less densely packed than in the Type I cell of the ductuli efferentes. A few rod-shaped structures (*R*) are found in the cell apex. *Rer*, rough endoplasmic reticulum. × 8960.



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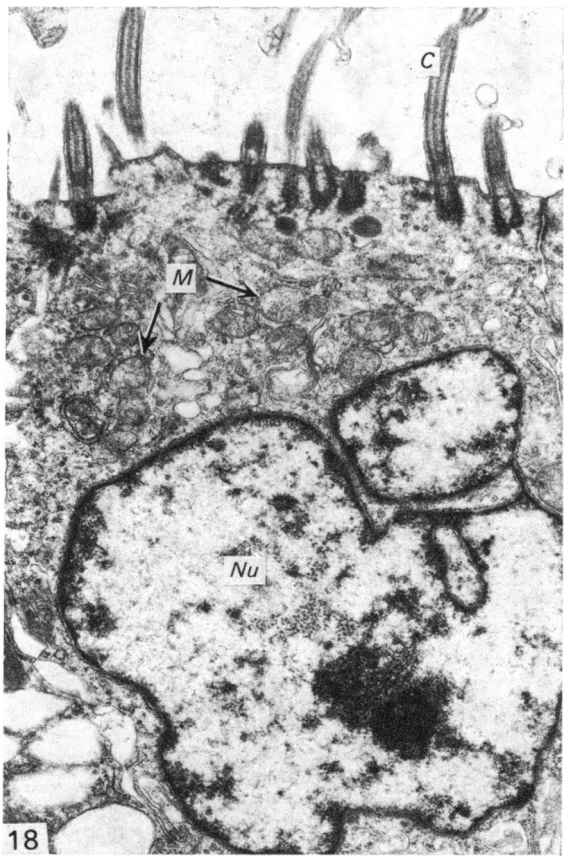

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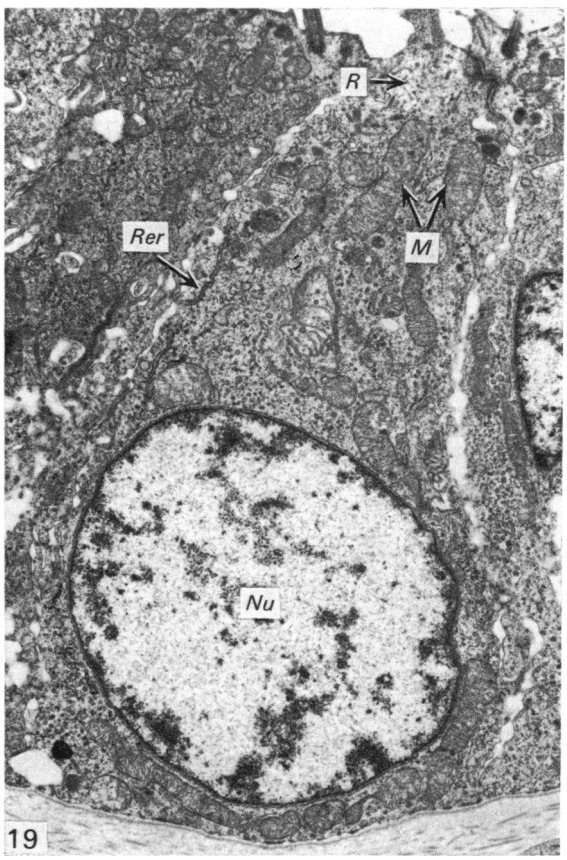

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Type I and (4) ciliated cells of the ductuli efferentes and connecting ductules; (5) non-ciliated Type II cells of the ductus epididymidis; and (6) basal cells, occasionally found in all the ducts except the rete.

Squamous and low cuboidal cells

Tingari (1972) classified all rete epithelial cells of the chicken as cuboidal, although some were more electron-dense than others. Squamous and low cuboidal cells were identified in the turkey rete, the squamous cells being more electron-dense than the cuboidal cells.

The cuboidal cells contained numerous mitochondria and rough endoplasmic reticulum and well developed Golgi complexes, similar to the cuboidal cells of the chicken. However, the squamous cells of the turkey contained only occasional rough endoplasmic cisternae and much less prominent Golgi structures, suggesting a definite difference in functional status. The cuboidal cells possibly are involved in secretion of proteinaceous fluids (Farquhar, 1969), as was suggested by Tingari (1972) for this cell type in the chicken.

Tingari (1972) observed phagocytosed spermatozoa within the rete epithelial cells of the chicken, but this was not observed in the turkey rete testis.

Non-ciliated Type I cells

Type I cells were found in the ductuli efferentes and narrow and wide connecting ductules of the turkey, but are apparently absent from the connecting ductules of the chicken (Tingari, 1972). These cells had ultrastructural characteristics of secretory cells, i.e. numerous electron-dense bodies, mitochondria, rough and smooth endoplasmic reticula and well developed Golgi complexes. The rough endoplasmic reticulum was more abundant than in Type I cells of the chicken (Tingari, 1972).

The Type I cells in the turkey contained abundant mitochondria with a concentric arrangement around lipid vesicles and rough endoplasmic reticulum. Such associations indicate that these cells manufacture proteins, possibly albumen, which is found in turkey seminal plasma (Thurston, 1976). Lin & Chang (1975) have shown that albumen appears to be synthesized by bound polysomes and released directly into the cytoplasm. The release of protein into the lumen could be accomplished by

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Fig. 20. Ductus epididymidis. The non-ciliated Type II cells are tightly organized without intercellular spaces. They contain long cisternae of rough endoplasmic reticulum (*Rer*), small mitochondria (*M*), and numerous lipid vesicles *V*. *Nu*, nucleus; *Bl*, basal lamina; *L*, lumen; *B*, basal cell. ×2640.

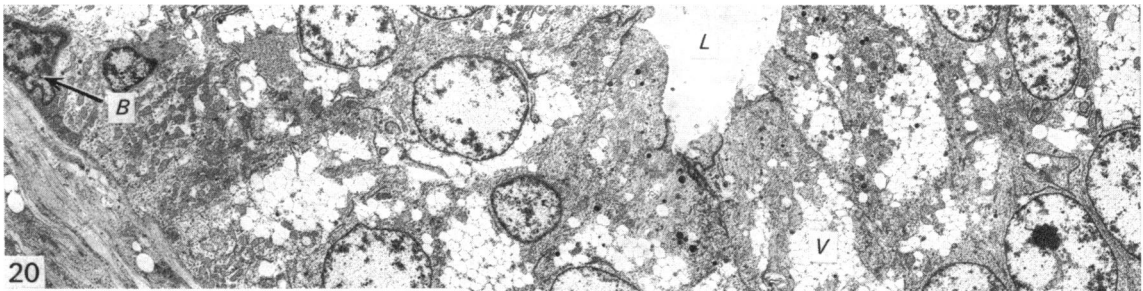
Fig. 21. Type II cell from the ductus epididymidis. The nucleus (*Nu*) is round and contains a distinct nucleolus. Most lipid vesicles (*V*) appear to be membrane-bound. *M*, mitochondria. ×8250.

Fig. 22. Type II cell from the ductus epididymidis. A small Golgi complex (*G*) lies close to the nucleus (*Nu*). ×16000.

Fig. 23. Type II cell from the ductus epididymidis. The rough endoplasmic reticulum (*Rer*) was arranged in parallel strands. ×32800.

Fig. 24. Basal cell from the ductus epididymidis. The nucleus (*Nu*) occupies most of the cytoplasm. The cell contains few cytoplasmic organelles and rests directly on the basal lamina (*Bl*). ×14500.

Fig. 25. Higher magnification of basal cell cytoplasm showing the nucleus (*Nu*), mitochondria (*M*), and nexus junctions (*Jt*). ×30400.



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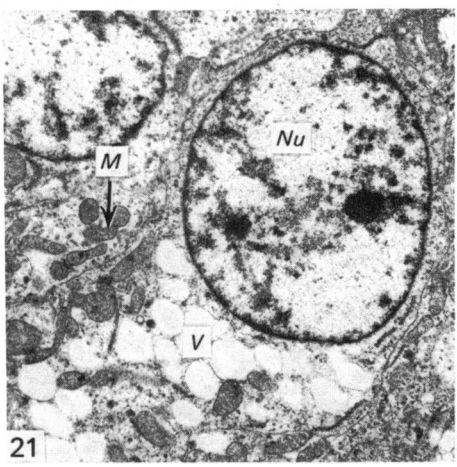

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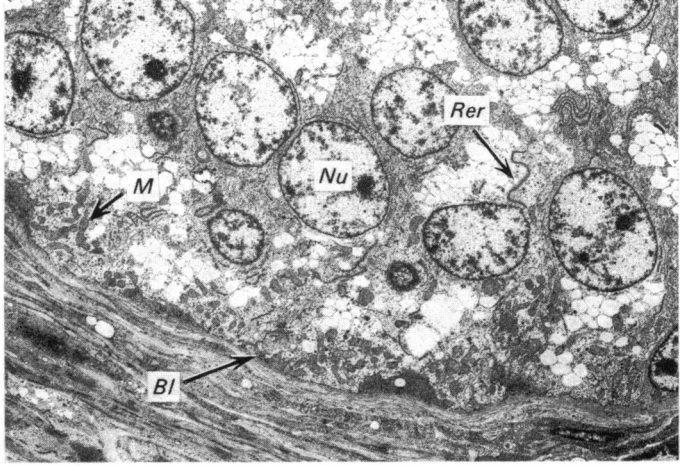

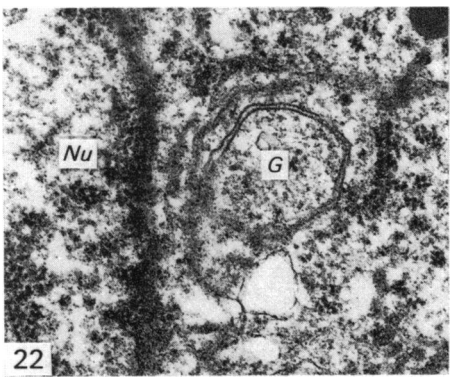

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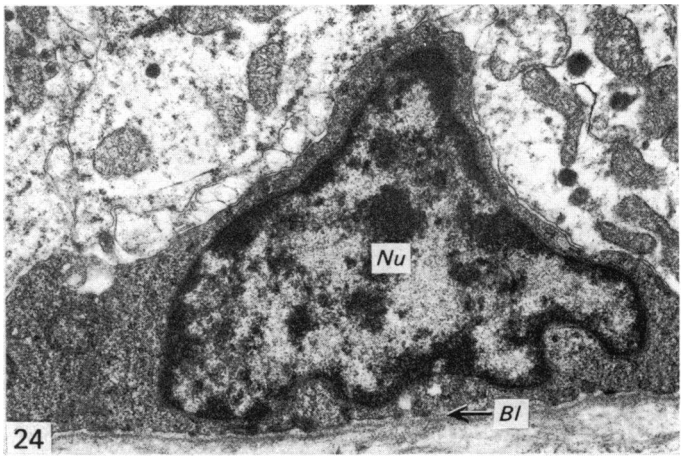

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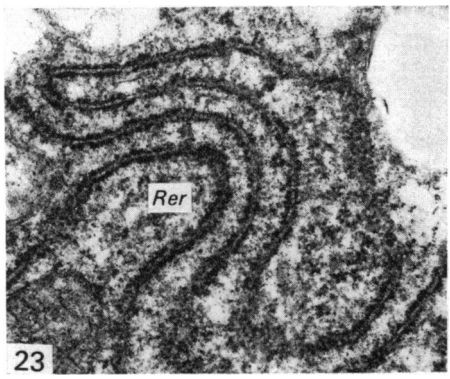

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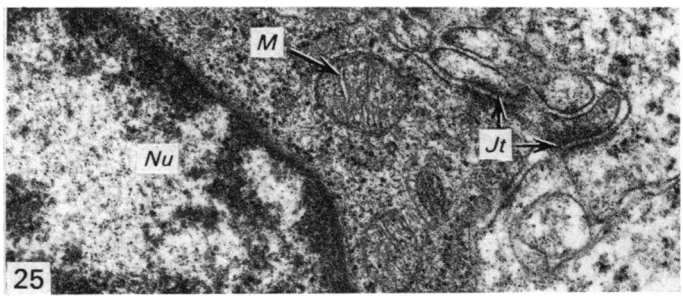

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apocrine secretion, which may account for the cytoplasmic blebs observed projecting from the Type I cells of the ductuli efferentes (Hess *et al.* 1976). Such features have been regarded as artifacts of fixation (Nicander, 1965; Hoffer, Hamilton & Fawcett, 1973). However, the observation of membrane-bound portions of cytoplasm in the lumina of the ductuli efferentes and connecting ductules, and the ultrastructural evidence of blebbing, indicate genuine apocrine secretion.

The rod and 'bar-bell' shaped structures located in the apical cytoplasm of the Type I cells were similar to those reported in the chicken (Tingari, 1972). Their function is unknown, although they resemble the lysosomes described by Saito & Ogawa (1974). The large electron-dense secretory-like granules found in the Type I cells may also be a type of lysosome (Hoffer *et al.* 1973), a conclusion which requires verification by staining for acid phosphatase activity.

Tingari (1972) associated 'worm-like' structures in the apical cytoplasm of the chicken Type I cells with absorption of ductal fluids. The turkey Type I cells contain numerous small rod-shaped bodies and other lysosome-like structures, and also have rather loosely organized lateral plasmalemmas. Such features are characteristics of absorbing epithelia (Strauss, 1964; Staley *et al.* 1972). Morphological evidence shows that the spermatozoa are highly compacted after leaving the connecting ductules (Hess *et al.* 1976). The Type I cells, then, may be absorptive as well as secretory.

Non-ciliated Type II cells

The Type II cells of the chicken are thought to have a secretory function similar to cells of exocrine glands (Tingari, 1972) which contain well developed Golgi with piled cisternae, vacuoles of smooth endoplasmic reticulum, much rough endoplasmic reticulum and dense membrane-bound bodies. In contrast, Type II cells in the turkey do not resemble secretory cells of exocrine glands, but do contain long cisternae of rough endoplasmic reticulum, and numerous lipid vesicles which may be associated with steroid secretion (Tingari, 1973).

Tingari (1972) also reported ultrastructural evidence of absorption in the Type II cells of the chicken. This cell type in the turkey contained few structural features indicative of absorption. Occasionally, small infoldings of the apical cytoplasm resembling pinocytotic vesicles were seen, but very few lysosomes were identified as one would have expected in cells highly active in absorption. Further, the close-knit organization of their lateral plasmalemmas in the ductuli efferentes and connecting ductules are not in accord with an absorptive role.

Resorption of spermatozoa by the Type II cells of the chicken was reported by Tingari (1972), who concluded that digestion of spermatozoa was the function of the lysosomes. As indicated above, the equivalent cell type in the turkey showed no evidence of spermatozoa resorption.

Ciliated cells

Ciliated cells were found in the ductuli efferentes and narrow and wide connecting ductules of the turkey. However, they rarely occurred in the wide connecting ductules of the chicken (Tingari, 1972). It may be that the wide connecting ductules of the chicken are transitional ducts, since they also contain Type II non-ciliated cells which are found predominantly in the ductus epididymidis (Tingari, 1972). In the turkey, the epithelium of wide connecting ductules is the same as that of narrow ductules, containing Type I non-ciliated and ciliated cells. The ciliated epithelium of

the wide ductules abruptly changes to a non-ciliated epithelium in the ductus epididymidis (Hess *et al.* 1976).

The cells of the ductuli efferentes and connecting ductules of the turkey were ultrastructurally similar to those described in the chicken (Tingari, 1972), and presumably serve to transport spermatozoa. Fibrillar bundles surrounding the nuclei were also found in the ciliated cells, and apart from a possible role in cell contraction (Tingari, 1972), their function is unknown.

The ciliated cells did not contain phagocytosed spermatozoa, unlike the rete, Type II and ciliated cells of the chicken (Tingari, 1972). However, evidence of phagocytic activity has been found in these cell types in turkeys producing abnormal yellow-coloured semen (Hess & Thurston, 1976) like that produced in chickens after ligation of the ductus deferens (Tingari & Lake, 1972).

The large vacuoles seen in the cytoplasm were similar to those described by Tingari (1972), who speculated that the ciliated cells function in fluid resorption. This is supported by the increase in vacuoles following ligation of the ductus deferens of the chicken (Tingari & Lake, 1972). Evidence of pinocytosis was not found in the ciliated cells of the turkey. However, lysosomal-like bodies were present, and could be conceived in the breakdown of resorbed materials.

Basal cells

Tingari (1972) reported fibrillar bundles around the nuclei of basal cells in the ductus deferens of the chicken; however, such fibres were not observed in the turkey epididymal region. The basal cells of the ductus deferens may be more contractile than those in the epididymal region.

SUMMARY

The epithelial cells in the epididymal region of the turkey were classified ultrastructurally by electron microscopy. Six cell types were described: squamous and low cuboidal cells of the rete testis, non-ciliated Type I and ciliated cells of the ductuli efferentes and connecting ductules, non-ciliated Type II cells of the ductus epididymidis, and basal cells occasionally found in all the ducts except the rete.

The squamous cells were more electron-dense and contained fewer organelles than the cuboidal cells. The Type I cells secreted blebs of material into the ductal lumen and contained numerous mitochondria, extensive rough and smooth endoplasmic reticulum and well developed Golgi complexes, indicating active apocrine secretion. The Type I cells also contained large zymogen-like granules and numerous rod-shaped bodies which were considered to be lysosomes associated with an absorptive function. The Type II cells had small Golgi complexes and numerous lipid vesicles. Ciliated cells presumably concerned in the transport of spermatozoa contained numerous mitochondria in the apical cytoplasm, lobulated nuclei and perinuclear fibrillar bundles. Lysosomal-like bodies and large cytoplasmic vacuoles indicated an absorptive function. The basal cells were smaller and more electron-dense than other cell types, and rested directly on the basal lamina.

This study has shown that the epithelial cells of the ductuli efferentes appear to be the most active cells of the turkey epididymal region. They apparently function in the transportation of spermatozoa, resorption of luminal fluids, and the secretion of proteinaceous material.

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