CONTRACTILE CELLS WITHIN THE MAMMALIAN TESTIS: THEIR LOCATION, DEVELOPMENT AND POSSIBLE SIGNIFICANCE

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ABSTRACT

Contractile cells within the mammalian testis occur in two sites, the tunica albuginea of the testicular capsule and the peritubular tissue surrounding the seminiferous tubules. In many species, including rat, pig, and man, contractile cells in the tunica albuginea are concentrated at the posterior pole of the testis, in relation to the epididymis. In the rabbit, however, the tunica albuginea contains two distinct layers of smooth muscle and the isolated testicular capsule exhibits rhythmic movements. In most mammals, the peritubular tissue of the seminiferous tubules consists of four layers, two cellular and two noncellular, and contractile cells are confined to the internal cellular layer. Differentiation of the contractile cells, both in the testicular capsule and within the peritubular tissue, occurs in the immediate postnatal period and is complete prior to the onset of spermatogenic activity.

Movement of nonmotile spermatozoa out the testis may result from a number of factors, including ciliary action within the rete testis and efferent ductules, active secretion of fluid by the seminiferous epithelium, and activity of the contractile cells within the testis. Evidence is presented which supports the hypothesis that the contractile cells, both in the testicular capsule and in the peritubular tissue, aid in the movement of spermatozoa out of the testis, although the relative contributions of the contractile cells in these two sites may vary with the species.

1. INTRODUCTION

Spermatozoa, produced within the seminiferous tubules of the testis, initially are inactive and nonmotile. From the seminiferous tubules, they pass via straight tubules into the rete testis. This is a network of irregular tubules lying within the mediastinum testis, a mass of fibrous tissue located in the posterior wall of the

testis and continuous externally with the testicular capsule. The rete testis is drained by a number of efferent ductules, the epithelial lining of which is ciliated. These ductules run into a single ductus epididymidis. The passage of spermatozoa through this long ductus epididymidis is slow and, during their passage, the spermatozoa mature and commence to move vigorously. The ductus epididymidis is continuous with the ductus deferens that passes to the prostatic urethra and eventually to the exterior. The movement of spermatozoa out of the testis, therefore, is not due to mobility of the gametes themselves and may result from a number of factors, including ciliary action within the rete testis and the efferent ductules, active secretion of fluid by the seminiferous epithelium, and contractile activity of smooth muscle cells within the testicular capsule and within the lamina propria (peritubular tissue) of the seminiferous tubules.

Evidence that ciliary action can move nonmotile spermatozoa from the testis generally has been discounted. Leeson (1962), in examining the rete testis, determined that too few cilia were present to effect sperm transport. Winet (1977) later calculated that ciliary action within the efferent ductules was insufficient to propel the sperm suspension. Recently, it has been observed that transport of spermatozoa in the human is unaffected in cases of Kartagener's (ciliary immobility) syndrome (Afzelius, 1976). Secretion of fluid by the seminiferous tubules, however, does contribute to the transport of spermatozoa out of the testis, as evidenced by the fact that ligation of the efferent ductules in laboratory rodents retards sperm flow distal to the point of ligation (Toothill and Young, 1931) and results in marked increases in testicular fluid (Van Wagenen, 1924). Secretion of fluid therefore supplies the medium, and possibly a pressure gradient as well, to promote transportation of spermatozoa.

Another factor, less well-recognized, that is thought by many investigators to contribute effectively to the movement of spermatozoa out of the testis, is the presence of contractile cells within the testicular capsule and within the peritubular tissue surrounding seminiferous tubules. That these cells do increase the flow of spermatozoa out of the testis has been demonstrated directly by administering contractile agents and noting the resultant efflux of spermatozoa from the rete testis (Hafs et al., 1974; Voglmayr, 1975). The purpose of this article is to review the information that concerns the location of the contractile cells, their development, and possible significance.

2. CONTRACTILE CELLS WITHIN THE TESTICULAR CAPSULE

In the past, histological descriptions of the testicular capsule implied only that it was a membrane of dense fibrous tissue that served to contain the underlying parenchyma of seminiferous tubules. In all mammals examined to date, it has been shown to consist of three layers: the tunica vaginalis visceral, an outer thin serous layer; the tunica albuginea, which forms the substance of the entire capsule; and the tunica vasculosa, an innermost thin layer of loose, vascular areolar tissue. The outer tunica vaginalis visceral is a complete layer composed of mesothelial cells that are attenuated. It can be so thin that on occasion it may be beyond the resolution of the light microscope, which may explain why it has been considered to be an incomplete layer by some authors. It has been examined in detail by Leeson and Adamson (1962) who showed that in the rat, rabbit, and human, microvilli extend into the cavity of the tunica vaginalis and that cell inter-

faces between adjacent cells appear relatively free of interdigitations and desmosomes. The mesothelium lies upon a thin basement membrane that separates it from the underlying tunica albuginea. The innermost layer of the testicular capsule, the tunica vasculosa, consists of networks of blood vessels embedded within a delicate areolar connective tissue. It is associated closely with the seminiferous tubules and interstitial tissue of the testis that lie immediately beneath it and is adjacent to the testicular capsule. By some authors it is classified as part of the testicular parenchymal tissue, rather than as a component of the capsule (Davis et al., 1970).

The intermediate and most prominent layer of the testicular capsule is the tunica albuginea. Classically, it has been described as a dense, fibrous membrane composed of bundles of collagenous fibers and numerous fibroblasts. More recently, it has been shown to contain contractile cells in all mammalian species that have been examined for their presence. Included in this list are rat, dog, and cat (Leeson and Cookson, 1974), rabbit (Holstein, 1967; Holstein and Weiss, 1967; Leeson and Forman, 1981), horse, pig, and sheep (Chacon-Arellano and Woolley, 1980), and man (Holstein, 1967; Langford and Heller, 1973; Leeson and Cookson, 1974). The cells have been said by numerous authors to be of two types: true smooth muscle cells and contractile fibroblasts or myofibroblasts. The only possible functional difference between these cell types is the spontaneous, phasic contractility of true smooth muscle such as is found in the rabbit testicular capsule, as opposed to the solely tonic contraction of "myofibroblasts" in the rat testicular capsule. Although we acknowledge that minor anatomical distinctions may exist, we shall refer to all cells as being contractile or as smooth muscle.

In the rat, the tunica albuginea generally is dense, regular connective tissue with relatively few connective tissue cells (Leeson and Cookson, 1974). Also present are bundles of smooth muscle cells, particularly prominent at the posterior pole of the testis. The smooth muscle cells occur in small bundles and as single cells and exhibit occasional cell contacts or gap junctions. Bundles of small nerve fibers, mainly unmyelinated, also are present and occasionally are seen closely related to a smooth muscle cell. Bundles of contractile myofilaments within the cytoplasm of these cells insert into granular electron dense material (dense bodies) either within the bundles or attached to the cell membrane (attachment zones), as in smooth muscle cells elsewhere (Gorgas and Bock, 1974). In man, the arrangement appears similar to that in the rat, in that the smooth muscle cells generally are concentrated at the posterior pole of the testis (Holstein, 1967; Langford and Heller, 1973; Leeson and Cookson, 1974). Smooth muscle cells are more numerous in the capsules of dog and cat, although here, too, the number of smooth muscle cells at the anterior pole of the testis is few. Additionally, isolated skeletal muscle fibers are present in the capsules of rat and dog but it has been suggested by Leeson and Cookson (1974) that they may have resulted from abnormal or unusual development and differentiation of embryonic myoblasts.

In contrast to the rat, dog, cat, and human, the rabbit tunica albuginea contains two distinct layers of smooth muscle, a superficial layer of longitudinally oriented cells that runs parallel to the long axis of the testis and a deeper layer of circularly arranged cells that is oriented along the circumference of the testis (Davis et al., 1970; Leeson and Forman, 1981). The two layers of muscle are separated by a band of collagenous fibers and the deeper layers of the tunica

albuginea contain heavy concentrations of collagenous fibers and numerous fibroblasts. Ther peripheral cytoplasm of the smooth muscle cells is occupied almost exclusively by myofilaments, with dense bodies present both within the cytoplasm and at the cell membrane. Occasional micropinocytotic vesicles or caveolae occur in relation to the cell membrane. Other organelles are sparse and are located principally in a paranuclear position. Each cell is surrounded by a complete basal lamina, except at the sites of close contact between neighboring cells.

Other species in which smooth muscle has been found in the testicular capsule include the horse, pig, and ram (Chacon-Arellano and Wooley, 1980). In the horse, numerous muscle cells, oriented parallel to the long axis of the testis, occur on the posterior surface and in places form a continuous layer just beneath the tunica vaginalis. Deeper layers of the tunica albuginea contain only a few isolated muscle cells. On the medial, lateral, and anterior surfaces, the muscle cells are less consistently longitudinal in orientation and less closely grouped. The smooth muscle of the tunia albuginea appears to be continuous with the internal cremaster muscle, which is well-developed in the horse and runs parallel to the vessels of the spermatic cord. The tunica albuginea of the pig is much less muscular than that of the horse. The smooth muscle cells generally are branched and are concentrated on the posterior surface of the testis in relation to the epididymis. In the ram, the muscle component is least well-developed and the cells, either branched or myofibroblastic in nature, are located in the deeper layers of the capsule.

To date, the only reports to appear concerning the development of muscle elements within the testicular capsule are those of Leeson (1975) and Leeson and Forman (1981) who followed the postnatal development of the rat and rabbit testicular capsules, respectively. In the rat, fully differentiated smooth muscle cells within the capsule can be identified from the thirtieth postnatal day but from birth to 24 days smooth muscle cells are not identifiable by light microscopy. On elctron microscopy, myocytes, differentiating cells showing the presence of cytoplasmic myofilaments, attachment plaques, and micropinocytotic vesicles, are present at birth and undergo rapid differentiation to morphological maturity at 30 days. As Leeson has pointed out, it is at 30 days postnatal that the testis in the rat achieves a scrotal position, although sexual maturity does not occur until about 60 days postnatal. In the rabbit, smooth muscle cells within the tunica albuginea are not identifiable at birth by light microscopy but by electron microscopy myocytes in early stages of differentiation are seen. It is not until 42 to 49 days postnatal that smooth muscle cells can be identified by light microscopy. Differentiation of smooth muscle cells within the capsule is completed by 128 days postnatal, which corresponds approximately to the onset of spermatogenesis. At this time, the muscle is arranged in two organized layers, a superficial layer of longitudinally oriented cells and a deeper layer of circularly arranged cells.

From a functional point of view, it has been demonstrated that those testes in which contractile cells can be observed microscopically also contract either rhythmically or after pharmacological stimulation if maintained in a suitable medium. The isolated rabbit testicular capsule shows rhythmic movement, with a frequency of two or three beats a minute, and there is some evidence to suggest that acidic lipids with prostaglandin-like characteristics are major determinants of the contractility (Hargrove et al., 1973). In contrast to the rhythmic

movements of rabbit testis, the rat testicular capsule in vitro and in vivo does not contract rhythmically. However, tonic contractions do occur after treatment with acetylcholine, norephinephrine, or other agonists (Davis et al., 1970). In addition to the rat and rabbit, dog, cat, and human testicular capsules also contract (Hargrove et al., 1977). Cat testes in vitro, like those of the rabbit, contract rhythmically, but at a lower amplitude. At present, it is not known whether or not the smooth muscle cells receive any innervation. Most autonomic efferent nerve fibers that pass from the internal spermatic plexus into the tunica albuginea are thought to accompany and supply blood vessels (Risley and Skrepetos, 1964). However, it is possible that these sympathetic fibers also may innervate the smooth muscle cells of the capsule. It has been shown that the rabbit testicular capsule, either in vivo or isolated and placed in saline, exhibits rhythmic movements which continue in vivo in the presence of adrenergic and cholinergic blocking agents (Hargrove and Ellis, 1976). Additionally, surgical or pharmacological sympathectomy results not in a decrease but in an increase in the number of spermatozoa found in the epididymis of the rabbit (Hodson, 1965).

Also of interest from a functional point of view is that rabbit testes are capable of contracting in vitro as early as one month postpartum, but with an amplitude much reduced in comparison with the values for the adult. The autorhythmic contractions and the contractile responses to prostaglandins are qualitatively like those of testes from mature animals (Ellis et al., 1972). Yet, the developmental study of Leeson and Forman (1981) has indicated that smooth muscle cells within the testicular capsule still are immature at one month postpartum and do not achieve structural maturity until 18 weeks postpartum. However, the myocytes present at one month postpartum do contain within their cytoplasm numerous myofilaments, often associated with attachment plaques and probably are capable of contraction.

Following numerous physiological and pharmacological studies, Davis and Langford (1970) concluded that contraction of the testicular capsule resulted in a pumping action capable of transporting nonmotile spermatozoa from the testis in the ductus epididymidis. More recently, however, Setchell (1978) has suggested that contractions of the capsule, rather than assisting in movement of spermatozoa out the the testis, may be involved in maintenance within the testis of the correct pressure to regulate the movement of fluid between the capillaries and the interstitium.

3. CONTRACTILE CELLS OF THE PERITUBULAR TISSUE

In the mammalian testis, the seminiferous tubules are surrounded by a peritubular or boundary tissue (lamina propria) that separates them from the intertubular tissue. In all mammals that have been examined to date, this tissue contains cells that resemble smooth muscle. Although the arrangement of the peritubular tissue varies to some degree with the species, generally it can be subdivided into four layers:

a) *Internal Noncellular Layer.* Essentially this is the space between the most peripheral cells of the seminiferous epithelium and the internal cellular layer. Immediately in relation to the epithelium is a basal lamina rich in glycoproteins (Clermont, 1958; Schmidt, 1964), external

to which is an intercellular space containing a network of collagenous fibers.

b) *Internal Cellular Layer.* This layer is composed of flattened cells that exhibit many of the characteristics of smooth muscle, including the presence of intracytoplasmic filaments, attachment plaques, and micropinocytotic vesicles or caveolae. Commonly, cells composing this layer are connected to each other by desmosomes.

c) *External Noncellular Layer.* This is very similar to the internal noncellular layer and also contains glycoproteins and collagenous fibers.

d) *External Cellular Layer.* Cells of this layer are attenuated and contain few organelles. They lack intracytoplasmic filaments and by most investigators are considered to be fibroblasts.

This alternating structure of noncellular and cellular layers is found in most mammalian species, with contractile cells confined to the internal cellular layer unlike avian species such as the fowl where contractile cells occupy the external cellular layer and fibroblasts comprise the internal cellular layer (Rothwell and Tingari, 1973).

In mammals, Burgos et al. (1970) have distinguished three types of arrangements in the peritubular tissue, based on the distribution and topography of the cellular and noncellular layers. Type A is characterized by a single layer of myoid cells between the internal and external noncellular layers. This type is found in the rat (Clermont, 1958; Leeson and Leeson, 1963), mouse (Ross, 1967), and hamster (McCord, 1970). In type B, myoid cells are present in two to four layers and are intermingled with a peripheral network of collagenous fibers and fibroblasts. The guinea pig and chinchilla (Fawcett et al., 1969) possess type B peritubular tissue. Type C is characterized by multiple layers of myoid cells and by the presence of infoldings of the internal noncellular layer and its subdivision into an inner homogeneous component and outer layer containing collagenous fibers. This type is found in man (Ross and Long, 1966), cat (Burgos et al., 1970), ram (Bustos-Obregon and Courot, 1974), and camel (Moniem et al., 1980). Apart from the three major types of peritubular tissue, minor additional features of the internal cellular layer of myoid cells have been outlined by some authors. In the rabbit (Leeson and Forman, 1981), as in the rat (Clermont, 1958) and hamster (McCord, 1970), two basal laminae are present in relation to the myoid cells, one adjacent to the internal noncellular layer and one located on the external surface. In the mouse, however, a basal lamina has been reported only in relation to the external surface of the myoid cells (Ross, 1967).

Contractility of the myoid cells was first demonstrated by Roosen-Runge (1951), who utilized cinematography to record motility of the seminiferous tubules of rats and dogs. More recently, Buhrley (1975) reported that the peritubular tissue isolated from mice, hamsters, rabbits, and ground squirrels is capable of contractions. In thes species, then, it is confirmed that microscopically defined myoid cells do confer contractility to the seminiferous tubules. Although no in vitro studies of human tubules have been made, Furuyo et al. (1977) have identified two types of cytofilaments, thin filaments (50-80A) that are actin or actin-like and 100A filaments, in human peritubular cells and have suggested that the cells play a role in the movement of nonmotile spermatozoa out of the seminiferous tubules.

The development of the peritubular tissue has been followed in numerous mammals and myoid cells within the internal cellular layer generally appear to differentiate early in the postnatal period. In male lambs, such cells are present within one week after birth (Bustos-Obregon and Courot, 1974). At that time, the internal noncellular layer consists of numerous wavy lamellae external to which are elongated cells that contain concentrations of cytoplasmic filaments. More peripherally are typical, unmodified fibroblasts. By two months after birth, the contractile cells are well differentiated, displaying numerous cytoplasmic filaments, some dense attachment plaques and coated vesicles. By 80 days, testis growth increases abruptly and thereafter the structural pattern of the peritubular tissue depends more on testis size, which correlates well with live-weight, than upon the age of the animals. In the rat, at birth the seminiferous epithelium rests upon a basement membrane that separates it from a layer of low cuboidal cells (Leeson and Leeson, 1963). External to this, there is a narrow intercellular zone containing scattered fibrillar material and a region consisting of numerous processes of mesenchymal cells. By ten days postnatal, four definite layers are established due to the differentiation of the external cellular layer of flattened cells from the mesenchyme and intracytoplasmic filaments have appeared within cells of the internal cellular layer, component cells of which now are very attenuated. By 22 days postnatal, the peritubular tissue is virtually adult in appearance. These results generally have been corroborated by Kormano and Horvatta (1972), who noted that rat tubular motility is initiated by 15 days after birth, at a time when filaments make their appearance within myoid cells of the internal cellular layer. Additionally, they reported that myoid cells of 25-day-old rats had the same number of intracytoplasmic filaments as those of the adult. Similarly, Ross (1967) noted contractile filaments are present within myoid cells of the mouse peritubular tissue by 13 days after birth. By 17 days, the cytoplasmic filaments are more numerous and by 19 days the cells closely resemble the peritubular myoid cells of the adult. In the rabbit, at birth and at five days postnatal, the peritubular tissue consists of two to four layers of spindle-shaped cells oriented circumferentially around each tubule (Leeson and Forman, 1981). The cells are closely packed and there is little intervening intercellular material. In some of the cells immediately in relationship to the seminiferous epithelium, there are occasional microtubules and small bundles of filaments concentrated in the peripheral cytoplasm. At 14, 21 and 28 days postnatal, the peritubular tissue appears more condensed, component cells are more attenuated, and they form only one to two layers. By 29 days postnatal, the peritubular tissue contains two cellular layers, and cells of the internal layer possess numerous cytoplasmic filaments. The filaments within these cells are associated with localized densities by 91 days postnatal and by 112 days postnatal the peritubular tissue is indistinguishable from that of the adult. This corresponds approximately to the time when myoid cells within the testicular capsule complete their differentiation (128 days postnatal) and to the time when spermatogenesis becomes established.

The differentiation of myoid cells within the peritubular tissue in the early postnatal period raises the question as to whether or not such development may be androgen-dependent. This hypothesis has been tested by Bressler and Ross (1974), who removed testes from newborn mice and implanted them into adult hosts. Subsequent development appeared to proceed normally if the testes were placed

in normal males, but those implanted into hypophysectomized hosts retained an immature appearance, indicating that maturation of peritubular myoid cells is dependent upon normal pituitary function.

Implants into hypophysectomized hosts treated with testosterone exhibited some, but not all, of the changes observed during normal myoid cell differentiation. Leeson and Forman (1981) noted that in the rabbit the adult population of Leydig cells, which produce testosterone, becomes established at about 28 days postnatal, confirming the earlier work of Gondos et al. (1970), who found that partially differentiated Leydig cells appear between one and five weeks on. In the rabbit, structural differentiation of myoid cells in the peritubular tissue is not achieved until well after this time. In other species however, differentiation may proceed without an absolute requirement for androgens. Hypophysectomy or the administration of the anti-androgen, cyproterone acetate, to young sheep has no effect upon the architecture of the myoid cells (Bustos-Obregon and Courot, 1974) and porcine peritubular myoid cells differentiate between four and 25 days postnatal, which is prior to hypertrophy and activity of Leydig cells (Dierachs and Wrobel, 1973).

Leeson and Forman (1981) noted close-contact junctions between differentiating myoid cells of the rabbit peritubular tissue at 49 and 91 days postnatal. Similar tight junctions have been described between myoid cells of guinea pig and rat peritubular tissue (Fawcett et al., 1970). Such junctions may subserve impulse conduction between the cells. No studies of peritubular tissue to date have shown nerve fibers in relation to the myoid elements and it has been concluded that contractility of the seminiferous tubules probably is regulated by factors other than nervous stimulation (Hargrove et al., 1977).

Recently the physiology and pharmacology of the peritubular tissue have been reviewed and it appears that the contractions of the seminiferous tubules, like those of the testicular capsule, are modified by locally produced substances, the prostaglandins (Hargrove et al., 1977). Buhrley (1974), in the rat, noted that some prostaglandins stimulate the motility of the tubules at all concentrations tested, whereas one prostaglandin promoted contraction at very low concentrations but reduced contractile frequency at higher concentrations. Other studies, utilizing immunohistofluorescense techniques, have indicated that the peritubular myoid cells are hormone-sensitive but have not defined the active agent. In their review, Hargrove et al. (1977) concluded that contractile cells within the peritubular tissue, like those within the testicular capsule, have a role in emptying the seminiferous tubules of spermatozoa.

Apart from its contractile function, the peritubular tissue also may be of significance as a component of the permeability barrier surrounding seminiferous tubules. Physiological studies by Setchell (1967) and by Waites and Setchell (1969) have indicated that the barrier is capable of excluding from the lumina of the tubules many substances (including inulin, creatinine, and glutamic acid) normally present in testicular blood and lymph. The barrier has ben examined morphologically in a number of species, including rat (Dym and Fawcett, 1970), guinea pig and chinchilla (Fawcett et al., 1970), and monkey (Dym and Cavicchia, 1978). The barrier is bipartite and consists externally of the myoid elements of the peritubular tissue and internally of the seminiferous epithelium of the specialized junctions between Sertoli cells. The myoid elements possess junctional complexes that prevent passage of the electron tracer, lanthanum nitrate, into the

seminiferous epithelium (Russell, 1978). The external component of the barrier is not consistently competent, and this appears to result from the incomplete nature of the junctional complexes between myoid cells. The entire barrier, however, does prevent proteins from spermatogenic cells reaching the interstitial vasculature and inducing the formation of antibodies.

4. CONCLUDING REMARKS

This review of contractile cells within the mammalian testis has discussed what presently is known about their location, development, and possible significance. Although there appears to be considerable support for the view that the contractile cells in both sites contribute to the movement of nonmotile spermatozoa out of the testis, other functions have been suggested for these cells. With regard to the capsule, Setchell (1978) has stated that it appears more likely that contractile cells here are involved in maintenance of the correct pressure within the testis to regulate the movement of fluid between the capillaires and the interstitium. Further, Chacon-Arellano and Woolley (1980), in their study of the horse testicular capsule, found the smooth muscle of the tunica albuginea to be continuous with the internal cremaster muscle of the spermatic cord and therefore considered that the contractile cells of the capsule may function to assist in blood or lymphatic drainage from the cord, rather than in moving spermatozoa from the testis to the epididymis. Concerning the peritubular tissue, it has been suggested that it may ensure fluid regulation between the interstitium and the lumina of the seminiferous tubules (Courot et al., 1970) as a component of the permeability barrier (Setchell, 1968; Fawcett et al., 1970). Clermont (1958) proposed that the contractile cells of the peritubular tissue might aid in the release of spermatozoa from the seminiferous epithelium as well as in transporting them to the rete testis. As Ross (1967) has pointed out, there is no evidence that spermatozoa require physical movement to effect their release from Sertoli cells of the seminiferous epithelium. In addition, Ross (1967) stated that the contractile cells of the peritubular tissue, which possess more granular endoplasmic reticulum than do smooth muscle cells elsewhere, may be concerned in the production and maintenance of the surrounding connective tissue stroma. It is apparent, however, that both the testicular capsule and the peritubular tissue, rather than being simple supportive tissues, are highly dynamic and are involved in several aspects of testicular physiology under both normal and pathological condtions.

The observation that in some species the isolated testicular capsule is capable of periodic contractions and relaxations indicates that, under normal circumstances, the capsule is in a constant state of dynamic movement, exerting pressure upon the contained mass of seminiferous tubules (Davis et al., 1970). Similarly, the contractile waves of the seminiferous tubules, as observed by Clermont (1959), Buhrley (1975), and others, no doubt affect the lumen size of the tubules and exert pressure upon their contents. Therefore, it appears very likely that contractions of the muscle cells in the testicular capsule and within the peritubular tissue serve to massage the seminiferous tubules and so to transport the spermatozoa from the tubules to the epididymis.

The possibility exists that the administration of drugs known to cause contration of the testicular capsule and of the peritubular tissue may stimulate the transport of spermatozoa out of the testis in some cases of male infertility (Davis et

al., 1970). On the other hand, a possible approach to male contraception may involve administration of drugs that cause prolonged relaxation of the testicular capsule, and possibly of the peritubular tissue as well, thereby delaying or preventing the contractile activity of these dynamic tissues.

As Leeson and Forman (1981) have pointed out, the relative contributions of contractile cells in the testicular capsule and within the peritubular tissue to the movement of spermatozoa out of the testis probably are not equal in all species. In the rat, for example, it has been demonstrated that contractile cells within the capsule are localized at the posterior pole and exhibit no regular contractility whereas the seminiferous tubules contract rhythmically. On the other hand, in the rabbit, where there are two distinct layers of contractile cells within the capsule, pronounced contractions of the capsule occur both in vivo and in vitro and contractions of the seminiferous tubules are much weaker than those found in the rat (Hargrove et al., 1977). In the emptying of spermatozoa out of the testis, the relative importance of the contractile cells, as compared with the secretion of fluid by the seminiferous epithelium or with the doubtful role of ciliary action, is difficult to quantitate. Despite this, the evidence does appear to support the hypothesis that the contractile cells within the testis facilitate transportation of spermatozoa out of the testis.

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Description of Illustrations

Plate 1

Figure 1. The outer layers of the testicular capsule from an adult rabbit. Mesothelial cells of the tunica vaginalis (arrow) are attenuated and smooth muscle cells within the outer layers of the tunica albuginea occur in two groups, the outer group sectioned transversely and the inner group obliquely. Beneath these groups are the inner layers of the tunica albuginea, consisting of dense connective tissue with elongated fibroblasts. x480.

Figure 2. The tunica vaginalis (arrow) and the outer layers of the tunica albuginea from a 49-day-old rabbit. Immediately in relation to the tunica vaginalis (above) are small bundles of smooth muscle cells, here sectioned transversely. The deeper layers of the tunica albuginea are composed of dense connective tissue containing elongated fibroblasts. x480.

Figure 3. An electron micrography of the mesothelium (M) of the tunica vaginalis and the outer layers of the tunica albuginea from an adult rabbit. Smooth muscle cells of the tunica albuginea contain packed myofilaments, some associated with dense bodies, within their cytoplasm. They are surrounded by a basal lamina (BL) and numerous collagenous fibrils, here sectioned transversely, occupy the intercellular space. x11,500.

Plate 2

Figure 4. The testicular capsule and a portion of an underlying seminiferous tubule from a 40-day-old rat. The tunica vaginalis is composed of attenuated mesothelial cells, beneath which the arrowed nucleus the tunica albuginea exhibits features of a smooth muscle cell nucleus. More deeply, the tunica albuginea has a high content of intercellular fibers. The seminiferous tubule is surrounded by the peritubular tissue which shows indistinct layering. Probably one nucleus (arrow) is that of a component cell of the internal cellular layer and the other (arrowhead) of the external cellular layer. x120.

Figure 5. An electron micrograph of a portion of a smooth muscle cell of the tunica albuginea from an adult rat. The cytoplasm contains groups of mitochondria and elements of granular endoplasmic reticulum separated by packed myofilaments, some associated with dense bodies. Micropinocytotic vesicles (arrows) occur in relation to the cell membrane. x18,000.

Figure 6. Low-power electron micrograph of the peritubular tissue from an adult rat. It consists of four layers: an internal noncellular layer, external to the basal lamina (BL of the seminiferous epithelium (right), and containing collagenous fibrils (1), the internal cellular layer, attenuated cells of which possess an electron dense cytoplasm and sparse organelles (2), a narrow external noncellular layer (3), and attenuated cells of the external cellular layer (4). x7,500.

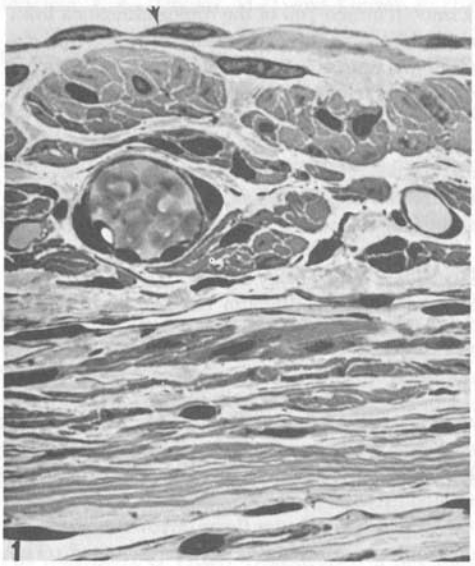
Figure 7. An electron micrograph of the peritubular tissue from a 40-day-old rat. The four layers of the peritubular tissue (1-4), external the seminiferous epithelium (E), are clearly seen. Note the tight junction (arrow) between myoid cells of the internal cellular layer. x42,000.

Plate 3

Figure 8. Seminiferous tubules from an adult rabbit. A narrow acellular zone (arrows) separates the peritubular tissue proper from the seminiferous epithelium, which exhibits active spermatogenesis. Layering of the peritubular tissue is indistinct and component cells show elongated nuclei (arrowheads) and attenuated cytoplasmic processes. x480.

Figure 9. Seminiferous tubules from a 49-day-old rabbit. The peritubular tissue (arrows) is condensed and component cells, whether contractile or fibroblastic, are attenuated. The peritubular tissue is separted from the seminiferous epithelium by a narrow, pale-staining acellular zone. x480.

Figure 10. An electron micrograph of the peritubular tissue from an adult rabbit. As in the rat, it consists of four layers: an acellular zone external to the basal lamina (arrow) of the seminiferous epithelium and containing unit fibrils of collagen (1), attenuated cells of the internal cellular layer, which posses an electron dense cytoplasm and numerous micropinocytotic vesicles (2), an acellular zone collagenous fibrils (3), and elongated cells of the external cellular layer which possess no myofilaments (4). x16,000.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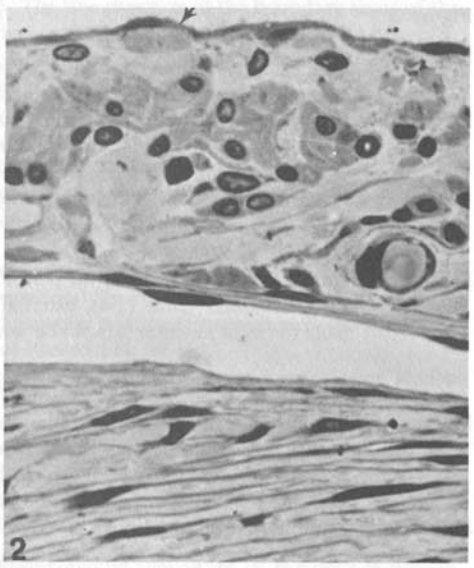
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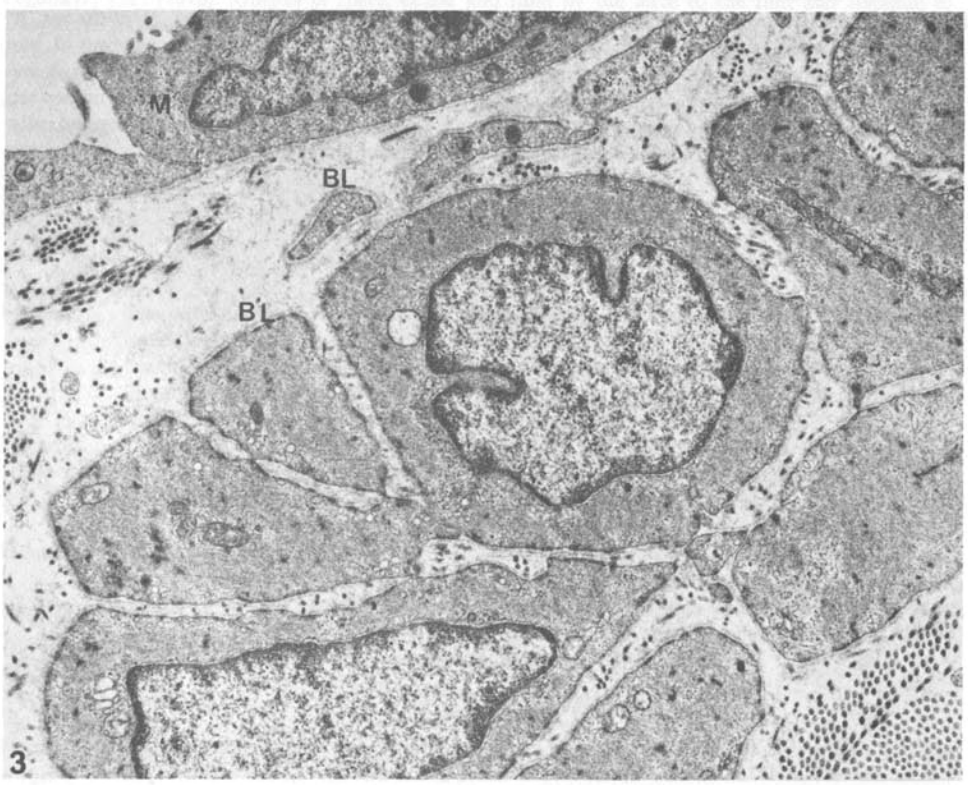
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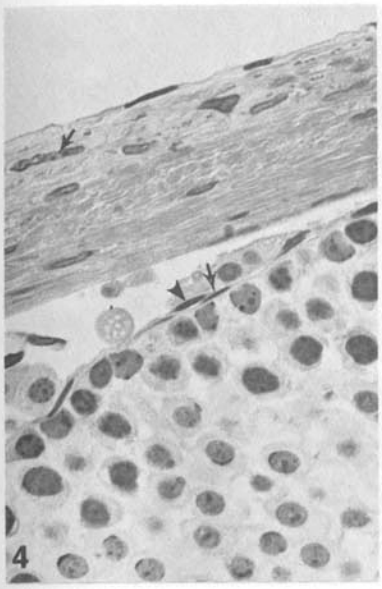
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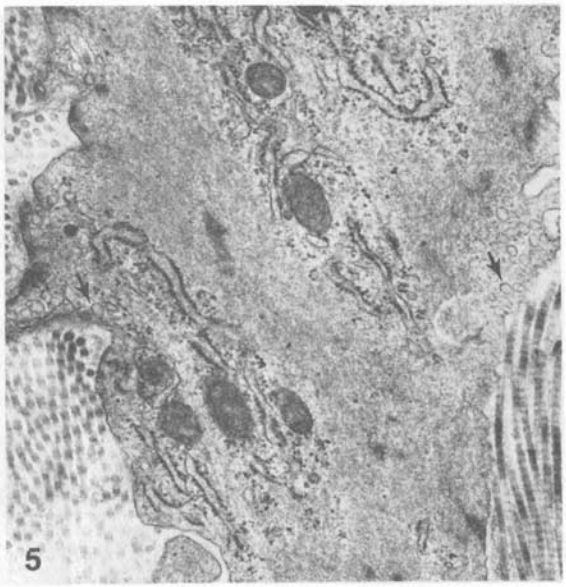
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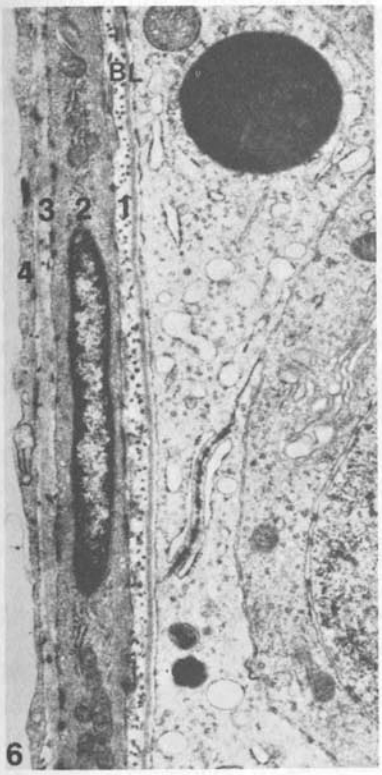
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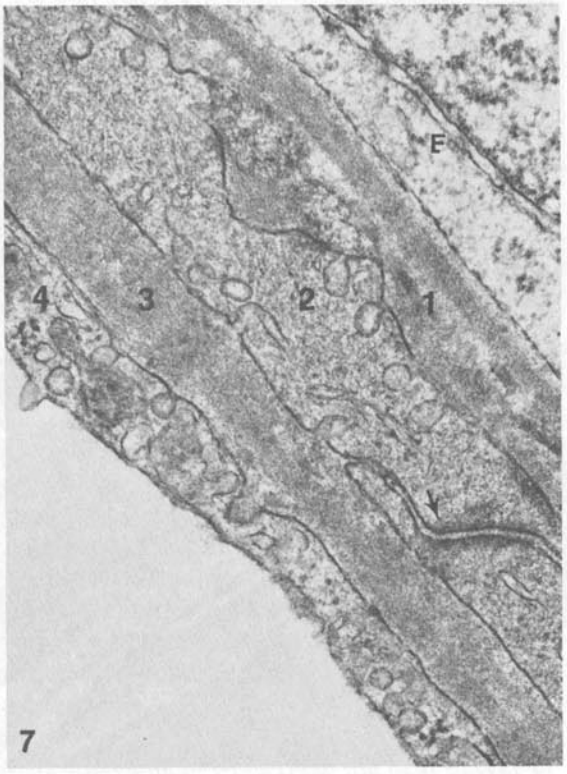
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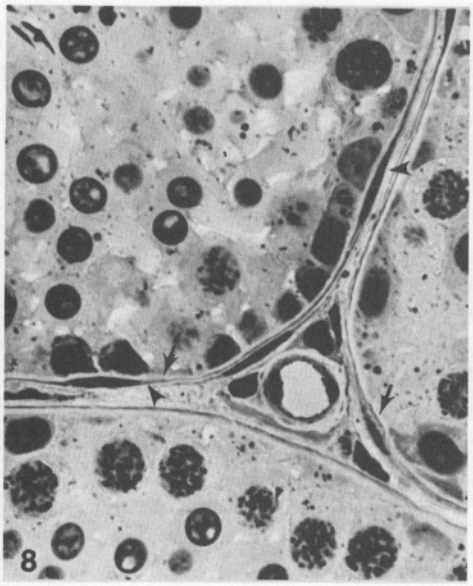
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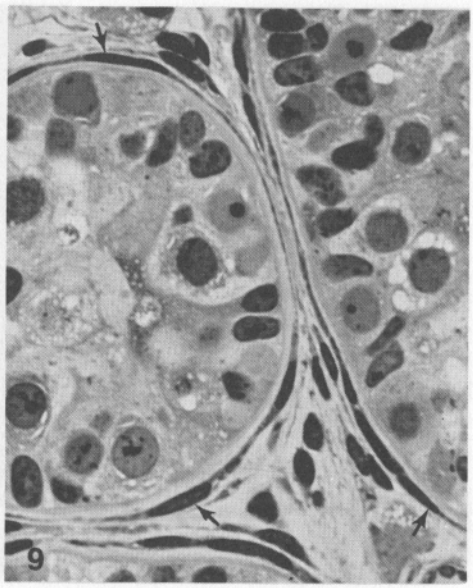
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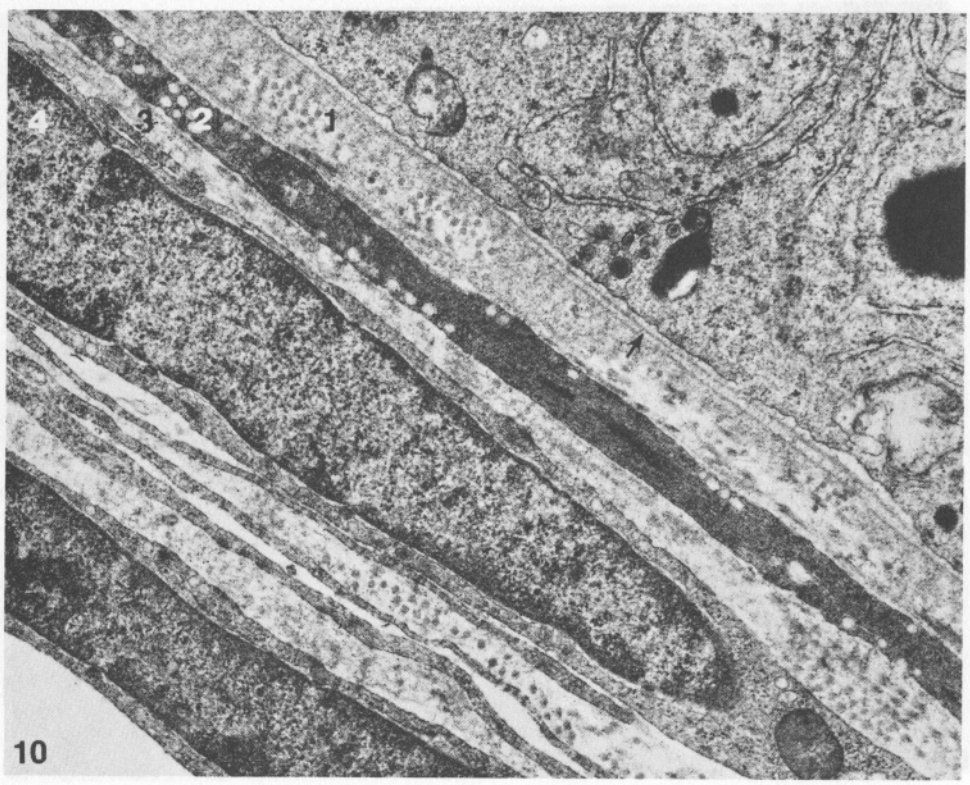
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