The Anatomy & Physiology of Sperm Production in Boars

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Introduction

The reproductive efficiency of the breeding herd depends upon the fertility of the boar. Male fertility is essential since the boar's DNA is the primary mechanism through which genetic improvements can efficiently be accomplished. In production settings, the critical event, which begins the reproductive process, is the meeting of sperm and eggs inside the female reproductive tract. To have fertile sperm in the reproductive tract of the female at the proper time depends upon several factors. These include the boar's physical willingness and ability to mate, and produce live and physically normal sperm in adequate numbers. This mating must also result in pregnancy and produce a large litter of live pigs at farrowing. In order to have a boar that can meet all of these criteria, considerable amounts of time and effort are needed to carefully evaluate and select boars for reproduction based on performance records. The overall factors that influence a male's fertility are complex. An understanding of the anatomy and physiology of sperm production in the boar can aid in selecting and managing males to ensure optimal boar fertility. This article describes the anatomy and physiology of the boar, what factors influence sperm production, and how these influence boar fertility.

Boar Anatomy & Physiology

General Boar Anatomy

The male reproductive tract is supported by the pelvis, and is housed internally in the abdomen and outside the abdominal cavity in the region of the groin (Figure 1). The testes of the boar are paired and produce sperm and hormones. Unlike most other species, the boar testes are anatomically upside down (Figure 2). This means the sperm that are produced leave the testes from the bottom, move up, and are stored near the top of the testicle. Sperm cells are produced only within the seminiferous tubules of the testes. Sperm production occurs along the entire length of these highly convoluted and densely packed tubes within the testes. All of the separate sperm producing tubes however, eventually converge into a single collection tube in the center of the testicle. The central sperm collection tube (rete testes, Figure 5) exits the boar testicle at the bottom and enters the storage and maturation tube, called the epididymis. This tube is tightly adhered to the outside of the testicle. The epididymis is highly coiled and when laid out end to end is over 189 ft in length. The testicles are contained within a pouch called the scrotum. This serves the important functions of protection and temperature regulation. Unlike some other species, the scrotum of the boar is not well defined since it is not pendulous and remains rather close to the body wall. The testes are connected to the internal components of the male reproductive system by a cord-like attachment. This connection is called the spermatic cord and passes through a small opening of the abdominal wall called the inguinal canal (Figure 2). The spermatic

cord serves as a passageway for blood vessels and nerves, which allows entry and exit for substances necessary to sustain cell life and supply hormones for reproductive regulation. The cord also contains blood, nervous and muscular systems involved with temperature regulation and movement of sperm out of the epididymis. The vas deferens leaves the testicle to become part of the spermatic cord and pass thorough the inguinal canal and enter into the abdomen. *The vas deferens is the tube that is cut and sutured in order to create a sterile, vasectomized boar (V-boars). These V-boars have been used effectively for estrous detection and are normal in every way except they do not have sperm in the ejaculate.* The two vas deferens connect with each other and merge into a single tube called the pelvic urethra at the neck of the bladder. The urethra continues forward and passes through the center of the penis where it is known as the penile urethra. The urethra is responsible for transport of both semen and urine. Urine enters the urethra by relaxation of a muscle under voluntary control. Relaxation of this muscle is prevented during erection and ejaculation by the nervous system in order to prevent urine entering into the semen. Fluids are added to sperm in the pelvic urethra during the process of ejaculation. Various accessory gland fluids are added to sperm beginning with the prostate fluids, the vesicular gland fluids and then the bulbourethral gland fluids. All of these glands add substances to the ejaculate that serve to increase volume, protect sperm cells, and provide nutrients needed for ensuring sperm fertility. The final structure for transfer of sperm into the female is the penis. The boar penis is composed of tough fibroelastic tissue supplied with blood and nerves. To deliver semen into the female when erect, the boar penis is extended through an opening called the prepuce located on the abdomen. All of the above mentioned anatomical parts are involved in production and/or transfer of fertile sperm into the female. Their unique structure and function can individually influence boar fertility and they themselves are influenced by a variety of both internal and external physiological factors that can increase or decrease boar fertility.

Hormones & Male Reproduction

Ultimately, the process of reproduction in the boar is initiated and regulated by hormones at the level of the brain (Figure 3). The hypothalamus serves as both a neural and endocrine (hormonal) organ, and is located near the base of the brain. In response to many different stimuli, the hypothalamus releases the hormone GnRH (Gonadotropin Releasing Hormone). This hormone is important because it is responsible for inducing the release of FSH (Follicle Stimulating Hormone) and LH (Luteinizing Hormone) from the pituitary gland, which is located just below the hypothalamus.

The release of GnRH is regulated by neural and hormonal inputs. These inputs indicate physiological age, weight, nutritional level, season of the year, environmental temperature, and reproductive status of the testes. All of these factors can collectively or individually influence the release of GnRH and increase or reduce the amount of FSH and LH released into the bloodstream to alter the activity of the testicles.

FSH stimulation of the testes starts the process of sperm production (spermatogenesis) by initiating sperm cell division and development. The FSH molecule actually binds to Sertoli cells, which serve as nurse cells for the forming sperm cells (Figure 4). The Sertoli cells line the seminiferous tubules that produce sperm. Sperm cells are actually nursed inside these cells. These nurse cells also produce

proteins that function to accumulate testosterone, which happens to be produced outside of the tubules. Testosterone is needed in high levels inside the tubule to allow sperm cell production. The other gonadotropin, LH, is responsible for initiating testosterone production by the Leydig cells. These cells are located just outside of the seminiferous tubules.

The stimulation of the testes by FSH and LH regulates hormone production by the testes. These hormones act locally and also enter the blood stream where they act on other tissues and organs in order to allow normal reproductive function. The hormones produced by the testes include androgens (testosterone), estrogen, and inhibin. These hormones are important for regulating the release of GnRH, FSH and LH at the level of the brain. This feedback-regulation for hormone release between the testes and the brain, allows for positive and negative control of spermatogenesis and reproductive activity. This hormone control system is much like a thermostat that controls temperature.

Sexual Development of the Boar

Sexual development in the boar is determined by the presence of the Y chromosome and androgens. At approximately 20 to 40 days of fetal age, genes are expressed on the Y chromosome that allow germ cells (cells which will eventually produce sperm) and the cells of the male reproductive tract to begin to divide and differentiate. Within the fetus, certain cells in the fetal reproductive tract are able to bind and respond to androgen (testosterone like molecules). Although these fetal sperm cells divide, they will not be capable of producing fully fertile sperm cells until puberty. Although not clearly understood, the division of testes cells during this fetal period occurs free of both GnRH and FSH and LH control, unlike in the pubertal age boar. It is not known whether the amount of cell division occurring at this time determines sperm producing capability in mature males.

Testosterone and Steroid Production

Testosterone levels are elevated in the fetal boar between 20 to 40 days of age when germ cell division rates in the testes are high. Testosterone levels then remain low in the boar until just before puberty occurs at about 4-5 months of age. The production of testosterone depends upon conversion of cholesterol and progestogens to androgens (testosterone). Further processing of androgen by the testes, the submaxillary gland and the brain allows conversion of androgen to different forms of testosterone and even estrogen (considered the "female hormone"). Interestingly, estrogen has been found in rather high concentrations in the ejaculate. Estrogen has been shown to be important for inducing normal male pattern behaviors when converted at the level of the brain during the neonatal period. It is also thought to be important for spermatogenesis and sperm maturation. New evidence also suggests estrogen in the ejaculate may be responsible for inducing uterine contractions in the female to aid in sperm transport, and may possibly advance the time of ovulation through uterine prostaglandin release.

Androgens and forms of testosterone are responsible for male associated characteristics such as libido (mating behavior), aggressiveness, and muscling. It is also essential for the growth and development of the reproductive tissues such as the penis, testes and accessory sex glands. The production of testosterone is also essential for the process of sperm production in the testes and maturation in the epididymis.

Androgens are the substances classified as pheromones and are responsible for production of “boar odor”. In the

submaxillary gland (located below the jaw) androgen is converted to the 5-α androgen form and when aerosolized, induces the standing response in female pigs. This hormone has been synthesized and is marketed as SOA (Sex Odor Aerosol, Intervet, Millsboro, DE) for stimulating estrus in female swine when sprayed toward the snout.

Testicular Descent

During the fetal period the testes of the male begin development inside the abdomen and then at approximately 60 days of gestation, are gradually pulled out of the abdominal cavity and into the scrotum (Figure 2). They are pulled through an opening called the inguinal canal, which allows passage of the testes and formation of the spermatic cord. As the male develops, the canal becomes smaller, allowing enough room for only the spermatic cord. Failure of the testes to descend can cause sterility. Failure of one of the testicles to descend is called unilateral cryptorchidism and can lead to a male that is normal in appearance but with reduced spermatogenic capability. The reduction in spermatogenic activity occurs since sperm production by the testes must occur in the scrotum where temperatures are lower than body temperature. Testosterone levels are not affected in these males and except for reduced sperm production, all behaviors and growth are normal. In the case where both testes fail to descend into the scrotum (bilateral cryptorchidism), these males are completely sterile even though testosterone levels are normal and they appear to act like fertile males. One other abnormality associated with testicular descent is the common problem of scrotal hernia. This occurs when some of the contents of the abdominal cavity pass through the inguinal canal. This problem is thought to be genetically linked, and is often observed in castrated males. In barrows this phenomenon may be due to improper pressure applied to the supportive structures of the testes during castration.

Boar Maturity

Physiological maturation in boars after birth is an ongoing process. Between 1-2 months of age, mounting behavior is first observed in young boars. At three months of age there is a second period of germ cell division (future sperm producing cells) and a rapid increase in the testes to body weight ratio. What this indicates is that this period and the period during fetal development when germ cells also increased may be important for determining sperm production potential. It follows then, that factors that influence boar physiology at these times could influence fertility potential. At about four months of age, sperm first appear in the seminiferous tubules and erection can be accomplished in the immature boar. At 5 ½ months of age, puberty begins and sperm now appear in the ejaculate. Over the next 6-18 months, the testes increase in size and both semen concentration and ejaculate volumes continue to increase. By 18 months of age no appreciable improvements in fertility are observed and the boar is considered fully mature.

Sperm Production

Once puberty occurs, spermatogenesis is a continual process. Inside the testicle, pre-sperm cells, called spermatogonia, begin to mature near the outside wall of the seminferous tubes (Figure 6). As the cell matures, it moves closer to the center of the tube where it will be released into the sperm passageway (lumen). During maturation inside the Sertoli cell, the sperm cell changes shape from nearly a round shape to the elongated sperm head with a tail (Figure 4). Within any Sertoli cell, there are many sperm cells in different stages of development. The time period required to

change from a round cell on the outer wall of the tube to its release into the seminiferous tubule as a sperm with a tail takes approximately 34-36 days. The production of sperm cells in the testes is not synchronized within the tubules so that sperm cells can be produced for ejaculation on a daily basis. Therefore along the entire length of the seminiferous tubules there are segments that contain different stages of sperm cell development.

Sperm Maturation & Storage

Sperm leave the testicle and enter the epididymis. As sperm leave the testicle, they enter the head of the epididymis. The sperm cells are very concentrated and in this form are not motile. In this portion of the epididymis, the head of the sperm incorporates proteins into the membrane, which are thought to be essential for fertilizing the egg. As they are moved down the length of the epididymis by fluid and smooth muscle contractions, they enter into the mid-piece where they now acquire the capability for tail movement. However, although they are capable of movement, they are still too concentrated to permit motion. As the sperm are moved into the tail of the epididymis, additional proteins are added which are important for sperm fertility. Sperm are stored immotile in the tail region in concentrated form. The entire duration of the trip through the epididymis requires ~12-14 days. The sperm will acquire full motility and fertilizing capability when diluted with seminal plasma in the ejaculate. Therefore, when considering the total time needed for a sperm cell to begin development until it appears in the ejaculate, requires approximately 45 days.

Thermoregulation of the Testes

The process of spermatogenesis is highly dependent upon temperature and is especially sensitive to elevated temperatures. Therefore the role of the scrotum is to regulate testes temperature to be ~3.5° F (2° C) lower than body temperature. The scrotum has both structural features and responsive mechanisms to regulate testes temperature. The structural system includes low amounts of subcutaneous fat in order to retain less heat. One of the more intricate mechanisms for heat loss is the intertwining arrangement of the arterial and venous blood vessels that enter and leave the testes. In this arrangement, warmed arterial blood entering the testes is cooled by the returning venous blood leaving the testes. This allows the cooling of 102° F arterial blood to ~98° F before it enter the testes. In the scrotum, the response mechanisms involve heat sensors that induce body heat loss through boar panting. The scrotum also contains a surrounding muscle called the tunica dartos. In cold weather this muscle contracts and wrinkles the surface of the scrotum to minimize surface area heat loss and in warm weather relaxes and increases surface area. Another muscle called the cremaster, is found in the spermatic cord and contracts or relaxes in order to pull the testis closer to the body in cold weather or let them hang further away in hot weather.

Accessory Glands

The accessory glands are important for adding seminal plasma to the sperm cells. Recently much attention has been directed toward the importance and function of these fluids. With AI, this component is highly diluted in the semen extension process and therefore its effect has been diminished. The prostate gland is the first gland to meet the pelvic urethra. It is responsible for flushing out urine and any bacteria in the tract before entry of sperm into the urethra. The vesicular gland produces most of the volume, energy sources, buffers and ions.

The bulbourethral glands produce the gelatin plug. The gelatin plug comes out in many fractions over time during ejaculation but predominantly at the end of ejaculation. This is used to seal the large volume of ejaculate (150-500 cc) in the female uterus following natural service. The plug sets up in the cervix and may remain intact for a variable length of time. When collecting semen from the boar for AI, the first part of the ejaculate is discarded, and since the gel plug is represented in many phases, boar semen is typically filtered during the collection process.

In general, the accessory glands are responsible for providing volume to dilute and stimulate motility, provide a fluid medium for ejaculation, energy in the form of citric acid and fructose, and pH buffering. Raw semen has a pH of 7.3-7.9, is approximately 94-98% water, and contains numerous organic and inorganic molecules. Other more uncertain roles of seminal plasma may involve its ability to immunosuppress the female after breeding in order to prevent sperm from being destroyed in the female tract before fertilization.

The Boar Penis

The penis contains the penile urethra and is a common passageway for both semen and urine. The boar's penis is composed of limited erectile tissue and when sexual stimulation occurs, shows limited increase in length and width. However, the boar penis when extended is quite long. When the boar is not sexually stimulated, the muscle is contracted and forms an S-shaped bend in the penis. This S-bend keeps the long boar penis inside the boar's body and prevents extension of the penis out of the prepuce. Once the boar is excited, neural stimulation causes the retractor muscle to relax and the S-bend unfolds, and the penis extends. The boar penis exits the male's body through the preputial opening. One unique feature of the boar is the presence of a preputial pouch or diverticulum. This pouch is located just above the prepuce and accumulates urine and sloughed cells. This can become quite odorous. The pouch fluid is important because it could potentially contaminate the ejaculate. The fluid should therefore be manually massaged to empty before ejaculation.

The extension of the penis causes tension in the fibroelastic tissues of the boar penis and causes twisting of the free end of the penis to form a corkscrew shape. The corkscrew shape is perfectly formed to match the patterns of pads inside the female's cervix. Upon erection and intromission of the penis into the cervix, the locking of the penis into the cervical pads is associated with pressure. This pressure stimulus is needed to induce the ejaculation reflex in the boar.

Semen Ejaculation & Collection

Sexual stimulation (5-10 min restraint) of the boar prior to ejaculation has been shown to dramatically increase the concentration and volume of the boar ejaculate. Sexual stimulation initiates smooth muscle contractions in the tail of the epididymis and the vas deferens. The boar usually takes 7-15 minutes to ejaculate the 150-500 ml volume.

Factors Influencing Semen Quality

Breeds/Lines

Although there have been reports of breed differences in ejaculate volume, concentration, motility and even percent of live/dead cells between European breeds of swine (Duroc, Yorkshire, and Hampshire), the results appear inconclusive. Perhaps the clearest example of the effects of breed on boar fertility is illustrated when comparing Chinese Meishan boars with conventional breeds of European origin. For example, the

Meishan breed has >70% motile sperm in the tail of the epididymis at 98 days of age compared to 150 days of age for European breeds. However, despite the early puberty for the Meishan, the mature paired testes weight (269 vs. 541 g) and daily sperm production (6 vs. 12 billion) are almost half of European breeds.

Testis Size

The size of the testes is moderately heritable and has been related to early puberty in both male and female siblings and offspring. The weight of the testes at puberty, and in the adult boar, is related to sperm output and even testosterone levels. However, the relationship of testes length or width (that which could be measured in the live animal) to spermatogenic potential remains unclear. Testis size has also been reported to change due to season and is somewhat larger in cool weather and smaller in warm weather. However, testis measures in live boars of similar age and weight tend not to be closely related to fertility.

Boar Age

The boar continues to increase testes size and spermatogenic output after puberty, and it has been reported that boars less than 9 months of age have both lower ejaculate volumes and concentrations compared to boars 18 months of age or older. Therefore, in order to maximize fertility, boars less than 1 year of age should be collected no more than one time per week and boars over 1 year of age can be collected up to two times per week. There will obviously come a time in a boar's reproductive life when fertility is diminished by advanced age. This age is not well established, since there has been a high rate of boar turnover with rapid genetic improvement. The result of this is that many boars are only in stud for a period 2-4 years before culling. However, it has been observed that in older aged boars, there are higher incidences of sperm abnormalities, lower pregnancy rates and litter sizes.

Daily Sperm Production

Daily sperm production is not constant. In one study, daily sperm production over a seven-month period of time fluctuated between 12 and 14.5 billion cells produced per day.

Sperm Storage

Sperm that are stored in the tail of the epididymis are fertile for several weeks. Older or excess sperm in the tail of the epididymis are lost through minor muscle contractions, which allow sperm to be eliminated with urine. For mature boars, collection of sperm twice a day for consecutive days allows collection of 5 billion sperm per ejaculate. When boars are rested and collected only twice a week ~50 billion sperm can be collected per ejaculate. Boars that are collected once every two weeks have up to 100 billion sperm in the ejaculate. However, with long periods of sexual rest, an increase in the number of degenerating and non-fertile sperm is observed. It is reported that sperm first lose their ability to fertilize an egg, and then they lose their motility, and lastly the are observed to disintegrate.

Sperm Abnormalities

Sperm abnormalities in the ejaculate typically take 14 days to appear due to the time required for sperm that are formed at the time of the stress or injury to travel to the tail of the epididymis where they are ejaculated. After this 14-day delay, the length of time and degree to which abnormalities appear depends upon the severity and length of the stress and which stages of sperm cell development were susceptible to injury.

The presence of cytoplasmic droplets on sperm is frequently observed. The droplet

originates from separation of the sperm cell from the Sertoli cell. During the separation process, some of the cytoplasm naturally remains attached to the sperm cell. As the sperm cell is moved along the seminiferous tubule and into the epididymis, the droplet moves from the proximal position (close to the head) further down the tail (distal) and then falls off. However, in some cases of stress, the ejaculate contains higher amounts of these droplets. It appears that the stress may induce a sperm cell membrane defect or somehow alters the normal maturation function of epididymis.

Stress & Environment

Social
Libido and ejaculate volumes are lower in boars raised in physical isolation from other males or females.

Lighting
Semen quality appears not to be greatly influenced by the effects of supplemental light during short days. However, increasing or decreasing light length in the opposite season can advance the age of puberty.

Season
The wild pig is a seasonal breeder so it is not unreasonable to assume that the domestic pig still may retain some seasonal responses. Wild boars (European) typically breed from January to May, and the female wild pig is anestrus from June to December. In the domestic boar, sperm production appears to be highest between September to February compared to March through August. The differences between the wild and the domesticated boar may be a reflection of the differences in available feedstuffs, environmental housing, and management.

Temperature

Perhaps one of the best-studied stresses that affect male fertility is temperature. Low temperatures have not been found to cause great problems for boar fertility except when temperatures dip below -10° C (14° F). This occurs since boars will increase feed intake in order to keep body temperature elevated. This has the effect of allowing too much heat to be produced in the body, which has been shown to reduce fertility.
Elevated temperatures are much more of a concern. Temperatures above 85° F reduce both sperm production and motility of ejaculated sperm for up to 2 months. Temperatures above 95° F for 3 days have increased abnormalities in ejaculates beginning 2-6 weeks after the stress. The reason for the delay and length of the appearance of abnormalities depends upon the 14-day transport in the epididymis and the sperm cell stages during the 34-36 day development period. Heat stressed boars also have higher levels of basic proteins in their ejaculates and these proteins are associated with reduced sperm life of extended semen at cool storage temperatures.

Figure 1. Boar Reproductive Tract. (From Scientific Farm Animal Production, Taylor & Field)

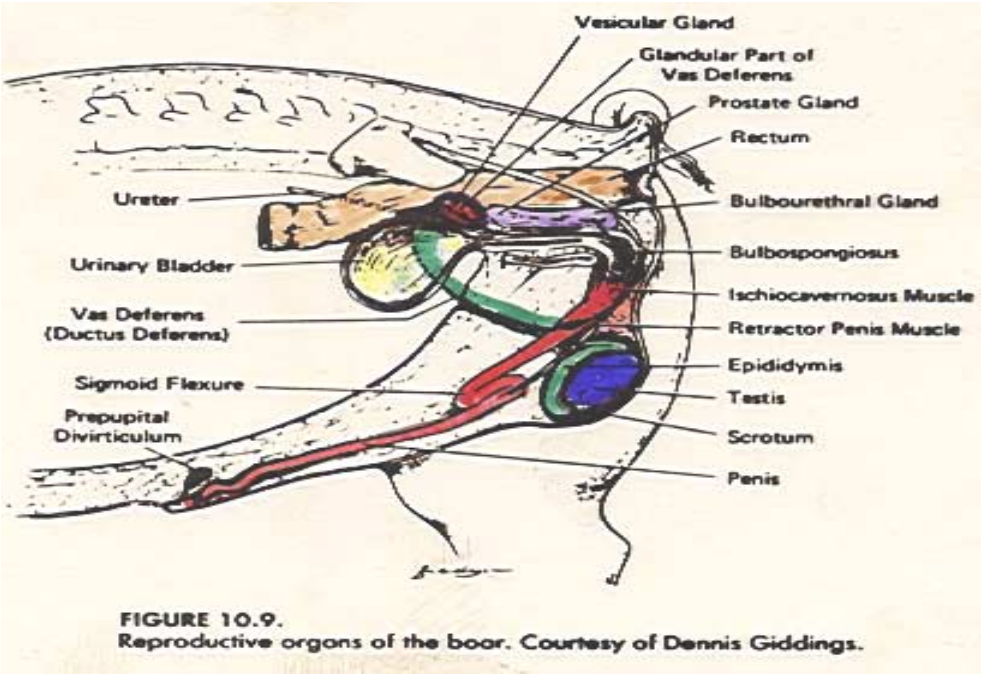

Figure 2. Boar Reproductive Tract (from Anatomy and Physiology of Farm Animals, Frandson).

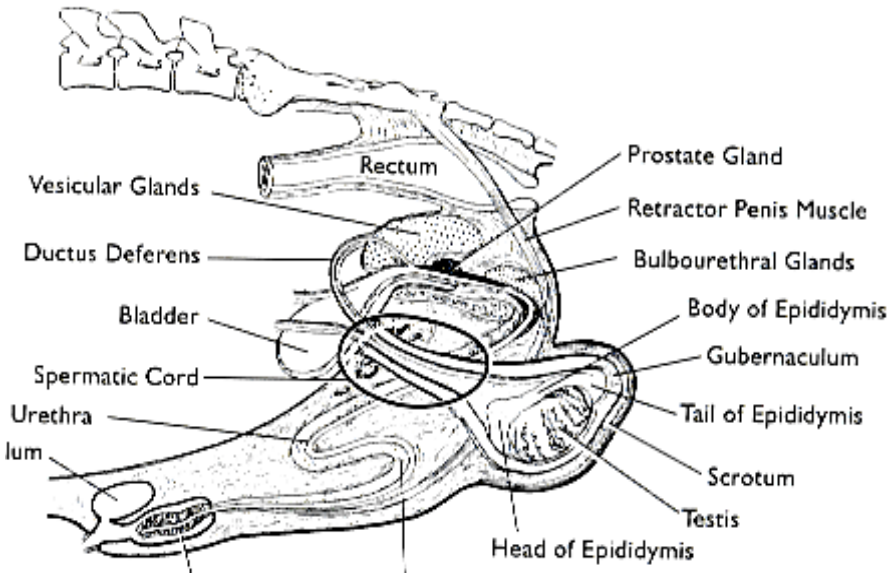

Figure 3.

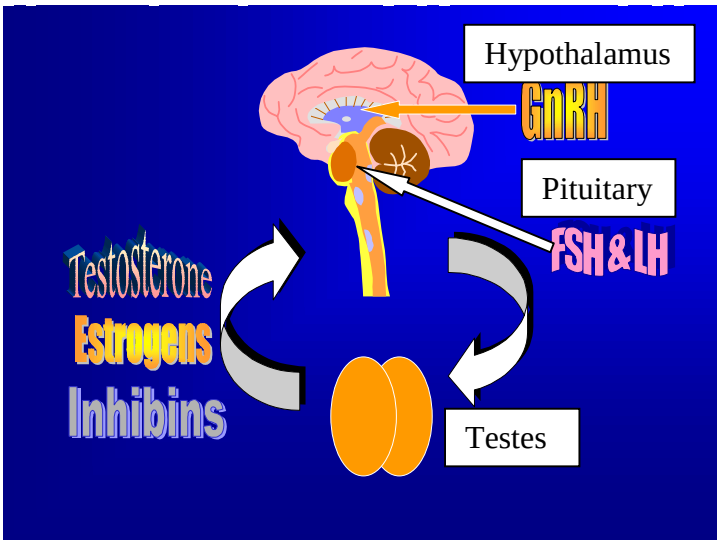

Figure 4.

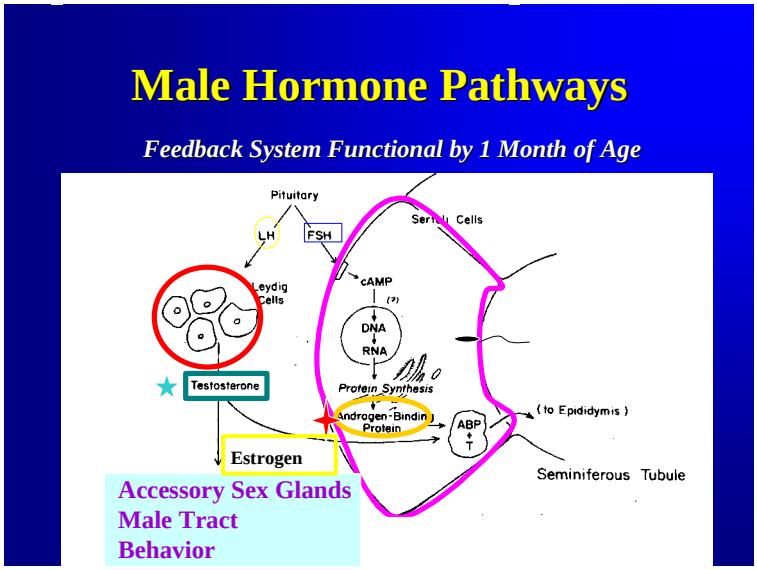

Figure 5. Cross-section of Testicle (from Reproduction in Farm Animals, Hafez)

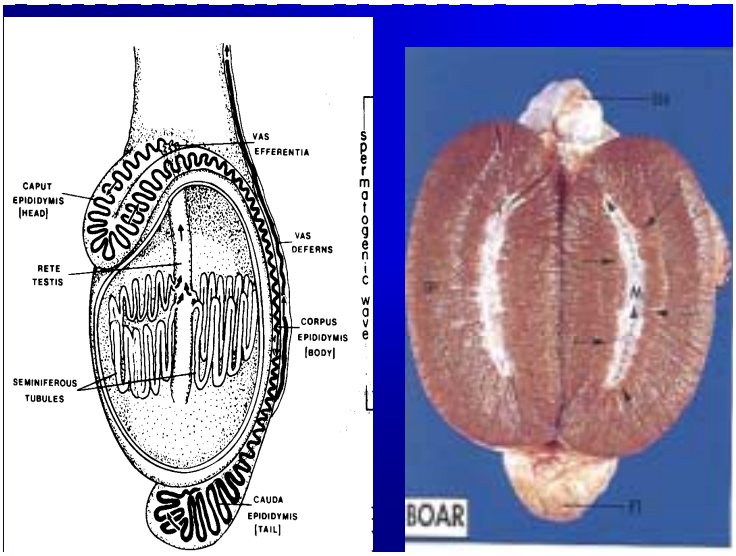

Figure 6. Seminiferous Tubule (from Anatomy and Physiology of Farm Animals, Frandson, and Applied Animal Reproduction, Beardon and Fuquay)