11. TESTICULAR FUNCTION

SPERMATOGENESIS

The entire process of forming sperm cells within the testis is called spermatogenesis (Fig. 11-1).

### Spermatogenesis

- **Spermatocytogenesis**
  - Cell multiplication (256-512)
- **Spermiogenesis**
  - Metamorphosis (4 phases)
- **Spermiation**
  - Release into lumen

**Figure 11-1. Stages in the process of spermatogenesis**

Prior to sexual differentiation, primordial germ cells move from the yolk sac toward the site of the undifferentiated gonads, where they proliferate forming a population of cells called gonocytes.

Gonocytes or germ cells are situated close to the basal membrane of the seminiferous tubules and in close association to the Sertoli cells. As they develop, they move within the Sertoli cells towards the center of the seminiferous tubules to which they are released (Fig. 11-2).

![Figure 11-2. Transversal cut of a seminiferous tubule showing the different stages of development from spermatogonia to spermatid](image)

### Spermatocytogenesis

Before puberty, the gonocytes become A0 spermatogonia, the source of further germ cells. These germ cells develop progressively through division into type A1, A2, A3 and A4 spermatogonia. Type A4 spermatogonia further divide to form intermediate spermatogonia which then gives rise to type B spermatogonia. Type B spermatogonia divide once or twice to produce primary spermatocytes, which in turn divide to produce secondary spermatocytes. Finally, the secondary spermatocytes undergo meiosis to form the haploid cells called spermatids. This early in development, the step involving duplication of the cells is called spermatocytogenesis or the proliferation phase. In bovines, this phase takes approximately 45 days to be completed (Fig. 11-3).

![Figure 11-3. Multiplication process during spermatocytogenesis](image)

The multiplication of spermatogonia and the further evolution of the spermatids do not result in independent cells. All cells maintain a cytoplasmic bridge, which appears to permit synchronization of the development of the spermatids, within a region of the seminiferous tubules.

### Spermiogenesis or cell differentiation

Without further division, the spermatids undergo a process of metamorphic changes leading to the formation of sperm cells in a process called spermiogenesis, which may last 10 to 11 days.

Four different phases are recognized during spermiogenesis (Fig. 11-4).
Golgi phase. This phase involves the formation of multiple proacrosomal granules within the golgi apparatus. All the granules eventually form a single acrosomal granule, which attaches to the nuclear envelope. At the opposite side of the cell, the tail starts to develop.

Cap phase. This phase involves the distribution of the acrosomal granule over about 2/3 of the spermatid nucleus, with further incipient development of the tail.

Acrosomal phase. This phase is characterized by nuclear and tail changes and the rotation of the spermatids within the sertoli cells; they rest with the tail towards the lumen of the seminiferous tubule.

The nuclear changes involve chromatin condensation and nuclear elongation with the majority of the cytoplasm moving toward the proximal area of the tail. At the same time, the mitochondria move to what is known as the middle piece of the tail.

Maturation phase. In this phase, there is further reshaping of the nucleus, most of the cytoplasm is removed and there is full development of the tail.

Spermiation

This process follows spermatogenesis and consists of the release of the metamorphosed spermatids, now called spermatozoa, into the lumen of the seminiferous tubules. After the release of the spermatozoa, the rest of the cytoplasm remains embedded in the sertoli cells as residual bodies, which are eventually catabolized. The new released spermatozoa still have a residue of cytoplasm called the cytoplasmic droplet, attached at the point of separation. This droplet prevents forward swimming by the sperm and it will be discarded during the process of maturation.

At any given time, there are about 4 to 5 cycles or waves of cells developing through the sertoli cells. The spermatogenic wave defines the developmental stage, at which each segment of the seminiferous tubules is at any given time. The developmental stage progresses as the tubule approaches the rete testis (Figs. 11-5, 11-6).
Blood-testis barrier

To protect the sperm cell, which is haploid, from immunological attack the basal membrane of the seminiferous tubules has two physical barriers that form the blood-testis barrier. First, there is a layer of contractile myoid cells sealed by light apposition; and secondly, the tight junctions between the Sertoli cells, within the seminiferous tubules, provide a more important and effective line of defense. All spermatogonia are situated below the tight junctions in the basal compartment while above the junctions, the adluminal compartment, contains the spermatocytes and spermatids.

The blood-testis barrier serves to prevent the entrance of some blood substances into the environment where the developing spermatocytes and spermatids are located. At the same time, the barrier retains other substances such as androgen binding protein (ABP) inside the seminiferous tubules, facilitating its action.

Hormonal control of testicular function

Initiation of spermatogenesis is LH and FSH dependent. LH, acting synergistically with prolactin, stimulates and regulates the production of testosterone by Leydig cells. In turn, some testosterone reaches circulation, and then the rest of the organism where it stimulates, among other things, the phenotypic manifestation of secondary sex characteristics. The rest of the testosterone diffuses into the inside of the seminiferous tubules, where it stimulates multiplication of germinal cells.

FSH, on the other hand, directly stimulates the Sertoli cells to support germ cell development. This is further mediated by the production of ABP, which captures and retains testosterone, helping in this manner to ensure its presence in order to exert the stimulatory effect in the germ cells (Fig. 11-7).

Some of the testosterone in the testis is converted to either DHT or estradiol. Dihydrotestosterone, testosterone and estradiol control, through negative feedback, the production of GnRH in the hypothalamus. GnRH in turn regulates LH and FSH release by the gonadotropes of the pars distalis. It appears as if Sertoli cells have more feedback control over FSH, through the production of inhibin and activin, while LH is more controlled by the ratio of testosterone:estradiol. This ratio is determined by the clearance rate of testosterone and its conversion to estradiol in target tissues.

Formation of semen

As the spermatozoa travel from the testis into the epididymis they lose the cytoplasmatic droplet and acquire motility and the capacity to fertilize. Once they reach the tail of the epididymis they are considered mature spermatozoa and they are ready for ejaculation (Fig. 11-8).

Sperm maturation (Development of swimming ability)

- Takes place in the epididymis
- Takes about two weeks

The ejaculate contains spermatozoa mixed with a variety of fluids, secreted by accessory glands to the reproductive tract. The main accessory glands are the ampullae, seminal vesicle, prostate, and bulbo-urethral gland or Cowper's gland (Fig. 11-9). The collection of fluids added to the sperm cells to make the semen is called the seminal plasma.

The ampullae are located at the urethral end of the ductus deferens. These glands are well developed in stallions, but absent in boars.
Seminal vesicles are located parallel to the bladder. They are large in bulls and boars, but are not present in dogs. They produce the large majority of the fluids of the ejaculate.

The prostate is located caudal to the seminal vesicles close to the bladder-urethral junction and is very underdeveloped in rams and bulls, but it is the principal accessory gland in dogs and primates.

The bulbo-urethral glands are absent in the dog but are very developed in the pig. They produce a very viscous gel, characteristic of the end of the boar’s ejaculate.

There are significant differences in the characteristics of the ejaculate of different domestic animals. The main variations are in volume and the total number of sperm cells ejaculated. The ranges of motility and acceptable malformations are less variable (Fig. 11-10).

The chemical composition of the ejaculate of different animals is also variable. There are some compounds whose role is not yet fully understood, that are not present in all ejaculates (Fig. 11-11).

### Contributions to semen formation

- **Testes**
  - Sertoli cells
  - Leydig cells
  - Rete testis
- **Epididymis**
  - Cauda
  - Ampulla
- **Vesicular gland**
- **Bulbo-urethral gland**

### Semen characteristics

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<th>CHARACTERISTIC</th>
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<tr>
<td>VOLUME (mL)</td>
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<td>0.8-1.2</td>
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<td>CONCENTRATION (million/mL)</td>
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<td>SPERM / EJACULATE (billion)</td>
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<td>1.6-3.6</td>
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<td>MOTILITY (%)</td>
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<td>NORMAL (%)</td>
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<td>70-80</td>
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*Garnier and Hafez (1993)*

### OTHER COMPONENTS OF SEMEN

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<td>PROTEIN (g/100mL)</td>
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<td>FRUCTOSE (mg/100 mL)</td>
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<td>CITRIC ACID (mg/100 mL)</td>
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<td>SORBITOL (mg/100 mL)</td>
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<td>0</td>
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*Garnier and Hafez (1993)*

### Figure 11-9. Components of the ejaculate, contributed by different accessory glands

### Figure 11-10. Characteristic of the ejaculate of several domestic animals

### Figure 11-11. Most common compounds found in semen of domestic animals