Comparative Reproductive Biology

Edited by

Heide Schatten, PhD
Gheorghe M. Constantinescu, DVM, PhD, Drhc

Blackwell Publishing

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Heide Schatten, PhD, is an Associate Professor at the University of Missouri, Columbia. She is well published in the areas of cytoskeletal regulation in somatic and reproductive cells and on cytoskeletal abnormalities in cells affected by disease, cellular and molecular biology, cancer biology, reproductive biology, developmental biology, microbiology, space biology, and microscopy. A member of the American Society for Cell Biology, American Association for the Advancement of Science, Microscopy Society of America, and American Society for Gravitational and Space Biology, she has received numerous awards including grant awards from NSF, NIH, and NASA.

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Foreword

I was honored when my colleague and friend Dr. Heide Schatten asked me to write a foreword for this book. It is a great pleasure to strongly recommend Drs. Heide Schatten and Gheorghe M. Constantinescu's latest scholarly work *Comparative Reproductive Biology.* Both editors are internationally known scientists and well qualified to oversee and contribute to such a comprehensive task. Furthermore, they have recruited an exceptional group of reproductive biologists to author chapters in their areas of expertise.

When considering the physiological systems of the body, the degree of species variation within the reproductive system compared to other systems is remarkable. Furthermore, it is essential that researchers, educators, and students alike remain acutely aware of the fundamental comparative differences in the reproductive biology of domestic species (carnivores, pigs, ruminants, and horses). As a researcher, understanding the comparative differences in ovarian and uterine function among mammalian species has been essential in helping me develop new approaches to a problem. Too many of us are guilty of basing our understanding of mammalian reproduction on our species of interest. Therefore, this book will be especially helpful in educating a broad audience of readers regarding the important differences in how domestic species reproduce.

As a teacher, I consistently emphasize that "structure dictates function." Therefore, I appreciate the strong morphological approach that the editors have taken in organizing and preparing the chapters. This book does an excellent job of synthesizing the classical information on reproductive biology (anatomy, histology, endocrinology, etc.) with an extensive list of reproductive biotechnologies: transgenic animals, gender selection in mammalian semen and preimplantation embryos, artificial insemination, embryo transfer and *in vitro* fertilization, comparative cryobiology of preimplantation embryos, animal cloning, comparative placentation, and pregnancy diagnostics. Consequently, this book will serve as an excellent reference for those with an interest in the reproductive biology of domestic species.

It is with enthusiasm that I endorse Drs. Schatten and Constantinescu's most recent contribution to the field of reproductive biology.

Michael F. Smith, Ph.D.
Professor of Animal Sciences
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Preface

Rapid progress in reproductive biology and the desire of many new and established scientists to find classic as well as contemporary aspects in one comprehensive book has inspired this work. *Comparative Reproductive Biology* offers both broad and specific knowledge in areas that have advanced the field in recent years, including advances in cell and molecular biology applied to reproduction, transgenic animal production, gender selection, artificial insemination, embryo transfer, cryobiology, animal cloning, and many others. It includes topics in animal reproduction that are usually only found as part of other books in animal science such as anatomy, developmental anatomy, developmental biology, histology, cell and molecular biology, physiology, radiology, ultrasonography, and others. We have made an effort to design a book that includes most, if not all, relevant areas of animal reproduction. The book is intended for a large audience as a reference book on the subject, rather than as a handbook or course textbook. It will fill a gap in the literature and is meant to be of interest to scientists in animal science, to teachers in the professional curriculum, to veterinarians, to clinicians, to professional students, to graduate students (PhD and Masters trainees), and others interested in animal reproduction.

There is currently no comparable and competitive book on the market. Most existing books are limited to various aspects of reproductive biology, such as oestrus cycles, pregnancy and parturition, dystocia and other conditions and/or disorders associated with parturition, surgical interventions, infertility, embryo transfer, physiology (the endocrinology of reproduction included), and mating and artificial insemination in domestic animals. An abundance of research papers are published in all fields, including the large field of physiology of reproduction of domestic animals. Many are referred to in the specific chapters of this book. This comprehensive book on various aspects of reproduction is timely due to the growing interest in the field. It provides insights into fascinating new approaches that have grown steadily since the introduction of the now well accepted *in vitro* fertilization and nuclear cloning techniques with applications for human health and agricultural and biomedical research.

The chapters are written by renowned scientists in their respective fields and their presentations include the biological aspects of reproduction in domestic animals such as dogs, cats, pigs, large and small ruminants, and horses. The specific chapters start with the developmental anatomy of reproductive organs, continuing with anatomy, histology, cellular and molecular biology, comparative reproductive physiology, transgenic animals, gender selection in mammalian semen and pre-implantation embryos, artificial insemination, embryo transfer and *in vitro* fertilization, comparative cryobiology of preimplantation embryos, animal cloning, comparative placentation, pregnancy diagnostics in domestic animals, and ultrasonography in small ruminant reproduction.

We are grateful to all of the authors for contributing their unique expertise and we hope the reader will find this book of value.

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Comparative Reproductive Biology

Chapter 1

Developmental Anatomy of Reproductive Organs

Ileana A. Constantinescu

Male and Female Reproductive Systems

The male and the female reproductive systems consist of the gonads, the reproductive tracts, and the external genitalia (the mammary glands are also included in this section). Although functionally distinct, the urinary and reproductive systems are intimately associated in origin, development, and certain final relationships in the adult anatomy. Common features of the two systems include the following:

- Both systems originate in the intermediate mesoderm.
- The (excretory) ducts of both systems initially share a common cavity—the *urogenital sinus* (a subdivision of the *cloaca*).

The common origin and close spatial association of the urinary and reproductive systems render a rather complicated organization. Some of their common primordia will differentiate in accordance with the established sex of the emerging new individual. Some of the organs are formed by association of structures that arise independently at different times and places. Some structures form and degenerate without ever becoming functional, while others undergo partial degeneration and their remnants are incorporated into a new organ for a new function.

The reproductive organs of both sexes develop from common primordia that follow a similar, consistent pattern of formation well into the fetal period. This development includes transition through an "indifferent" (undifferentiated) stage during which all component structures are present and appear the same in both sexes. When the primordia of the reproductive system are established (before differentiation), all embryos are potentially bisexual. As a result, developmental errors may lead to various degrees of intermediate sex.

Development of Gonads

During their development the gonads pass through two distinct stages: the Indifferent stage and the Differential stage.

Indifferent Stage

The outline of the gonads appears (in most mammals) when the embryo possesses from 38 pairs to 40 pairs of somites (at about 24 days in dogs, 27 days in horses, and 28 days in oxen). The *gonadal primordium* is represented by genital (gonadal) ridges—paired longitudinal condensations of intermediate mesoderm (with contribution from the adjacent coelomic mesothelium) along the axis of, and medial to, the *mesonephros* (the primordium of the excretory system).

The cells of the ridges become aligned to form a number of irregularly shaped cords, the primitive sex cords, which extend into the center (medulla) of the ridge and connect to the surface epithelium. At this stage the embryos exhibit gonads, which show no evidence as to whether they will develop into testes or ovaries (hence, the "indifferent" stage in gonadal development).

Differential Stage

Although genetic sex is established at the time of fertilization, the gonads do not attain morphological sex characteristics until toward the end of the embryonic period. This differentiation is much accelerated (and slightly earlier in males) at the beginning of the fetal period.

Regardless of their future fate, the primordia of all reproductive male and female structures form in both sexes. At this stage in development, the primordia are represented by the undifferentiated gonad and two duct systems—the paired *mesonephric* and *paramesonephric ducts.* It is these primordia that, remodeled by complete or partial regression, addition to, or incorporation into present or later-to-emerge structures, will form the adult, functional reproductive male and female organs.

The mesonephric (Wolffian) duct is the salvaged remnant of the mesonephros (one of the three overlapping kidney systems). In amniotes, the mesonephros regresses by the end of the embryonic period; the exception is the mesonephric duct (and part of its tubules), which is retained and remodeled as genital ducts in the male. The paramesonephric (Müllerian) duct forms as an epithelial invagination ventrolateral to the mesonephros. Cranially, each tube opens into the abdominal cavity; caudally, each fuses with its counterpart to enter the urogenital sinus ventral to the mesonephric duct. In females, the Müllerian duct forms most of the genital duct system.

Testes

Developmental processes represent an extensive panorama of complex, interdependent, precisely sequenced and

coordinated interactions of genetic and environmental modulators that work together to create an unique organism. The sexual identity of an individual is established with the process of fertilization; the individual's sexual distinction is the result of exposure to gonadal hormones, which start to be secreted as soon as the gonads emerge from the indifferent stage. The gonadal differentiation reflects morphogenic changes that involve the sex cords and *interstitial cells* (cells between the cords). Toward the end of the third week after fertilization (a few days later in species with longer gestation), primordial germ cells (future gametes) migrate from the endoderm of the yolk sac and become embedded into the indifferent gonad.

In a genetically male embryo, the germ cells carry an XY chromosome. The Y chromosome possesses the SRY gene, which encodes the testis-determining factor (TDF) that directs testicular differentiation, thus establishing the gonadal sex. In the presence of TDF, the sex cords become organized into *s*eminiferous tubules—elongated, tortuous cords that extend into the center (medulla) of the gonad and contain differentiated germ cells, spermatogonia. Seminiferous tubules connect to the retained mesonephric tubules of the mesonephric duct via the rete testis (a network of thin tubules located in the medulla of the testis and originating from sex cords that lack germ cells). The cord cells (which form the walls of the seminiferous tubules) differentiate into Sertoli (sustentacular) cells that secrete a glycoprotein, a Müllerian-inhibiting substance (MIS), which is responsible for the regression of the paramesonephric ducts. The interstitial (Leydig) cells begin secreting testosterone that induces sexual differentiation of the duct system and of the external genitalia.

As the medulla becomes the functional part of the testis, the cortex is reduced and separated from the surrounding surface epithelium by a thick layer of connective tissue—the *tunica albuginea*. The tunica albuginea serves as a pathway for blood vessels.

Ovaries

In the genetic female embryo with an XX chromosome complex, the absence of the Y chromosome redirects differentiation of the indifferent gonad to become an ovary. The cells of cords dissociate into clusters surrounding individual or groups of germ cells, which together form primordial follicles (the proliferation of both types of cells is completed before birth). Within the follicles, germ cells differentiate into primary oocytes that remain arrested in meiosis I until ovulation. The medulla of the gonad is greatly reduced and replaced by vascular stroma. In the absence of a Y chromosome with its supportive contribution, the mesonephric ducts degenerate.

Development of Reproductive Tracts

In mammals, the gonads develop in close association with the two paired duct systems—the mesonephric and paramesonephric ducts, present in both sexes.

Development of Male Reproductive Tracts

Testosterone secretion by fetal testes triggers the morphogenic changes in the duct system and external genitalia (if exposure to testosterone is denied, the embryo, regardless of its genetic sex, will develop as a female).

The cranial portion of the mesonephric duct (and associated tubules) regresses while the reminder undergoes regional differentiation. Its tubules that become connected with the sex cords via rete testis will form the efferent ductules (those left out persist as functionless vestiges, either as the "appendix of epididymis" or as the "paradidymis"). The mesonephric duct in the area of the testis becomes extensively elongated and convoluted to form the epididymis; its caudal end extends to enter the urogenital sinus (the mesoderm of the caudal region of the duct differentiates to form the seminal vesicles).

In amniotes, as a rule, the paramesonephric ducts degenerate completely by the beginning of the fetal period. Vestigial structures are seen either as the "appendix testis"—a tiny portion of its cranial extent, or as the "uterus masculinus"—a small diverticulum wherein the fused ducts open into the urogenital sinus.

Development of Female Reproductive Tract

In females, the mesonephric duct degenerates, leaving the paramesonephric duct system to form the main reproductive tracts. The cranial-most portions of the paired duct remain continuous with the peritoneal cavity, narrow and convoluted to form the *oviducts* (uterine tubes). The degree of fusion of the paramesonephric ducts varies among domestic species, being most extensive in horses and least in carnivores; in rodents and rabbits there are two cervices that open into a single vagina, while in marsupials, the tubes do not fuse to any extent. Therefore, the marsupials are provided with a double vagina. Caudally, the unfused portions form the uterine horns. As the embryo assumes its rounded shape, the caudal portions of the tubes are shifted medially and fuse together to differentiate into the body of the uterus, the cervix, and the cranial one-third part of the vagina. The extent to which the urogenital sinus participates in the formation of the vagina varies with the species. This involvement is demonstrated by the positioning of the urethral and vaginal openings and the length of the vestibule.

Vestigial structures of (particularly) the caudal end of the mesonephric duct are consistently represented by Gärtner's ducts, seen in the cow as small openings into the vestibule; in the sow as tubular cords in the wall's uterine horns or vagina; and in carnivores, in the wall of the vagina.

Development of the Male and Female External Genitalia

In this subsection, the urogenital sinus, the Indifferent stage and the Differential Stage for both male and female will be discussed.

Urogenital Sinus

The urogenital sinus is a developmental structure common to the male and the female.

In early mammalian embryos, the caudal end of the primitive gut (caudal to the origin of the *allantois*—a ventral evagination of hindgut that collects and disposes of fetal urinary wastes) is represented by the wide diverticulum—the cloaca, temporarily closed by the cloacal membrane. Toward the end of the embryonic stage, with the advancement of the tail fold, a mass of mesenchyme—the urorectal septum—extends caudally from the junction with the allantois, dividing the cloaca into a dorsal part, the rectum, and a ventral part, the urogenital sinus. The external surface of the wall in between the two openings becomes the perineum.

Indifferent Stage

At this point in development, the cloacal region and its associated structures represent the indifferent condition, allowing no distinction between sexes. Under the influence of gonadal hormones, the urogenital sinus and its rudiments undergo specific, sex-appropriated changes. External genitalia are derived from a series of mesodermal proliferations (swellings) adjacent to the still-existent cloacal membrane. These proliferations are the following:

- **Cloacal folds**—the paired, elongated proliferations that flank the cloacal membrane.
- **Genital tubercle**—(the primordium of the phallus and the clitoris, respectively); a median outgrowth formed by the fusion of the cranial portions of cloacal folds (cranioventral to the opening of urogenital sinus).
- **Urethral folds**—folds formed caudal to the genital tubercle. When the urogenital septum is completed, the cloacal folds are subdivided into urethral folds and anal folds.
- **Genital (labioscrotal) swellings**—paired proliferations that border the urethral folds. By the end of the embryonic stage and several weeks into the fetal stage, the sex hormones released by the differentiating gonads induce progressive modelings of these primordia and will attain distinct and recognizable male versus female characteristics.

Differential Stage—Male

Androgens secreted by the fetal testes induce rapid elongation of the genital tubercle to form the phallus (a deficiency in or an insensitivity to androgens lead to a predominance of female characteristics under the influence of maternal and placental estrogens). Elongation of the phallus pulls the paired urethral folds forward to form the lateral walls of the urethral groove along the ventral aspect of the phallus. Midline fusion of the folds over the groove establishes the penile urethra. The rapid expansion, paralleled by the cranial shift of the genital tubercle, elongates the genital raphe—the first external indication of a developing male.

In the adult, the phallus forms the body of the penis, and the original swelling, the genital tubercle, becomes the *glans penis.* In domestic mammals (except the cat), the phallus extends cranially, deep to the skin of the ventral body wall, and its free end is encircled by a ring of ectoderm, the *prepuce.* Mesenchyme in the glans and body of the penis of the dog (and other nondomestic mammals) ossifies to form an *os penis* (there is a cartilage in the cat).

The genital swellings (scrotal swellings in male) enlarge, migrate cranially (to a greater or lesser extent depending on the species), and fuse with one another on the midline. The two swellings remain separated by the scrotal septum, and each makes up half of the scrotum. The accessory genital glands are positioned around the pelvic urethra and vary greatly among species. The *prostate g*land (present in all domestic species) and the bulbourethral gland (absent in the dog) form as endodermal evaginations of the urogenital sinus. The vesicular gland arises as a mesodermal evagination from the caudal part of the mesonephric duct.

Differential Stage—Female

In the absence of androgens, feminization of the external genitalia occurs. At first, the phallus elongates rapidly (the genital tubercle in the female is larger than in the male during early stages of development), but its growth gradually slows and it becomes internalized in the floor of the vestibule to form the *clitoris* (in the bitch and mare the clitoris is well-developed, but it is poorly so in the other species).

The urethral folds enlarge to overgrow the genital tubercle. They fuse only partially—at their dorsal and ventral ends. Their unfused portions form the *labia* of the vulva. The labioscrotal swellings (labial swellings in the female) flatten laterally and undergo complete regression in female domestic animals (in humans and rabbits they form the labia majora; the labia minora originate from urethral folds). Mucus-producing vestibular glands (homologues of the bulbourethral glands) are present in cows and cats only (and sometimes in sheep). Accessory genital glands in both sexes reach full development at sexual maturity. The ligamentous attachments of the genital ducts in both sexes originate in the urogenital fold, a remnant of the mesonephros. In the female, this fold forms the suspensory ligament of the ovary, the mesovarium, the mesosalpinx, and the cranial part of the mesometrium. (In the male, it forms the mesorchium and mesoductus deferens.) The caudal extension of the fold forms the proper ligaments of the gonads in both sexes.

Mammary Glands (*Mammae*)

Mammary glands (in both sexes) begin as paired, band-like thickenings of ectoderm—the mammary ridges, on the ventrolateral surface of the body between the bases of the limb buds. The length of the ridges varies with the species: They extend from the axilla to the inguinal region (as in

carnivores and swine), are restricted to the axilla (as in elephants) or are restricted to the inguinal region (as in ruminants and horses).

Each mammary gland begins as a mammary bud—a localized condensation of somatic mesoderm and overlying ectoderm at a specific location along the mammary ridge. In many species, more buds form than are retained in the adult; some buds degenerate while others persist and develop as supernumerary teats. The epithelium of each bud branches into the underlying somatic mesenchyme as solid cords. These cords become associated with the glandular tissue and become patent (around the time of birth) to form individual lactiferous ducts. Each duct opens individually on the surface of the teat. The number of ducts in each mammary gland varies with the species, ranging from 1 (in cows and ewes) to 14 (in bitches and sows). Soon after birth, the teat (*papilla*) of each mammary gland forms by proliferation of the mesenchyme surrounding each bud.

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Chapter 2

Anatomy of Reproductive Organs

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Part 2.1
Male Genital Organs

The male reproductive or genital organs consist in all species of the testicle, epididymis, ductus deferens, spermatic cord, accompanying tunics of spermatic cord and testicle (paired structures), accessory genital glands (paired or single structures), penis, prepuce, and the male urethra.

A general presentation of these structures precedes the species-specific details.

The Testicle

The testicle is the male essential reproductive gland that produces spermatozoa through the process of spermatogenesis, and also produces testosterone, the male hormone. The testicle has an ovoid shape, a head, a tail, a lateral surface, a medial surface, a free border, and an epididymal border where the epididymis is attached.

The testicle is covered by a white fibrous capsule called *tunica albuginea*, which sends, inside of the testicle, interlobular connective tissue walls called *septa*, or *septula* when they are very small. The albuginea consists of collagen fibers and a few elastic fibers. The branches of the testicular artery and vein travel within the albuginea. This tunic also covers the ductus epididymidis. The septa/septula consist of collagen fibers, vessels, and nerves; divide the parenchyma of the testicle in lobules; and build up a loose connective tissue structure called *mediastinum testis*, which also contains vessels and nerves. The lobules contain the *seminiferous tubules*. The peripheral segment of the seminiferous tubules is *convoluted*; the tubules end as *straight* seminiferous tubules, which interconnect with each other inside of the mediastinum testis in a network of ducts called *rete testis*. The rete testis continues as *ductuli efferentes*, which are coiled (see Figure 2.1).

The Epididymis

The *epididymis* (see Figure 2.1) is the first excretory organ of the male genital system. The epididymis is attached to the testicle and consists of the ductuli efferentes and the *ductus epididymidis*, surrounded by the testicular albuginea. The ductus epididymidis is very tortuous and extremely long in all species. On the lateral aspect of the testicle, between it and the epididymis, a large space is outlined under the name of *testicular bursa*. The epididymis has a head, a body, and a tail.

The head contains the ductuli efferentes of the testicle, and the origin of the ductus epididymidis. The body encloses the coiled ductus epididymidis. Both the ductuli efferentes and ductus epididymidis are located within the lobules of the epididymis. The ductus epididymidis continues inside of the tail of the epididymis with the ductus deferens. The tail of the epididymis is anchored to the tail of the testicle by the *proper ligament of the testicle*.

The Ductus Deferens

The *ductus deferens* is the continuation of, and extends from the ductus epididymidis to the urethra. The ductus deferens is held in place by the *mesoductus deferens* while running within the spermatic cord. It then enters the abdominal cavity and, switching the direction, passes within the pelvic cavity over the dorsal aspect of the urinary bladder. It crosses the ipsilateral ureter and opens on the roof of the pelvic urethra, lateral to the *colliculus seminalis*. (The colliculus seminalis is an elevation on the roof of the prostatic segment of the male urethra at the end of the urethral crest; for details, see veterinary anatomy books).

In some species, the last part of the ductus deferens, called the *ampulla*, is thickened due to the abundance of ampullar glands. The inconstant common excretory passage lateral to the colliculus seminalis for the ductus deferens and the vesicular gland in some species is called the *ejaculatory duct*.

The ductus deferens consists of an adventitia, a muscular tunic, and a mucous membrane.

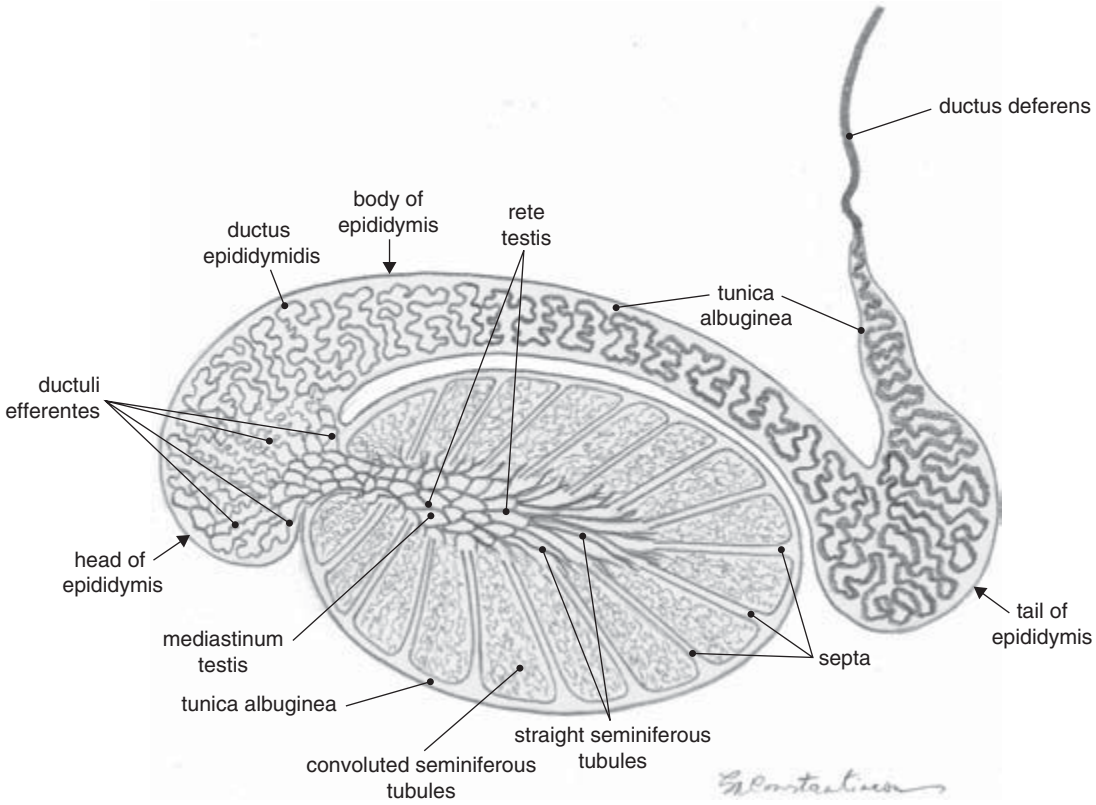

Figure 2.1. Internal organization of testicle and epididymis.

The Spermatic Cord

The *spermatic cord* (see Figure 2.2) consists of the following structures:

- the ductus deferens held by the mesoductus deferens
- the blood and lymphatic vessels and nerves that supply the testicle and the epididymis, surrounded by a peritoneal fold from the *visceral lamina of the vaginal tunic* called the *mesorchium*
- smooth muscle fibers
- visceral lamina of the vaginal tunic

The spermatic cord is located within the vaginal canal and outlined by the *parietal lamina of the vaginal tunic*. The liaison between the parietal and the visceral laminae of the vaginal tunic is called the *mesofuniculus.*

The mesorchium is divided into the *proximal mesorchium*, between the vaginal canal and the epididymis, and the *distal mesorchium*, between the epididymis and the testicle. The limit between the two mesorchia is the peritoneal fold that holds the epididymis, called the *mesepididymis* (see Figure 2.3).

The Tunics of the Spermatic Cord and the Testicle

There are six tunics surrounding the testicle (see Figures 2.4 and 2.5). Three tunics come from the abdominal cavity during the descent of the testicle; the other three are outside of the abdominal cavity, as part of the body wall. Therefore, the testicular tunics may be divided into two groups of structures: intraabdominal and extraabdominal tunics.

The Intraabdominal Tunics

The *intraabdominal tunics*, those structures brought by the testicle during its descent, are the internal spermatic fascia and the visceral and parietal laminae of the vaginal tunic.

The *internal spermatic fascia* is the continuation of the transverse fascia (the endoabdominal fascia) after it passes through the deep inguinal ring. The *cremaster muscles* protected by the *cremasteric fascia* are associated to the internal spermatic fascia.

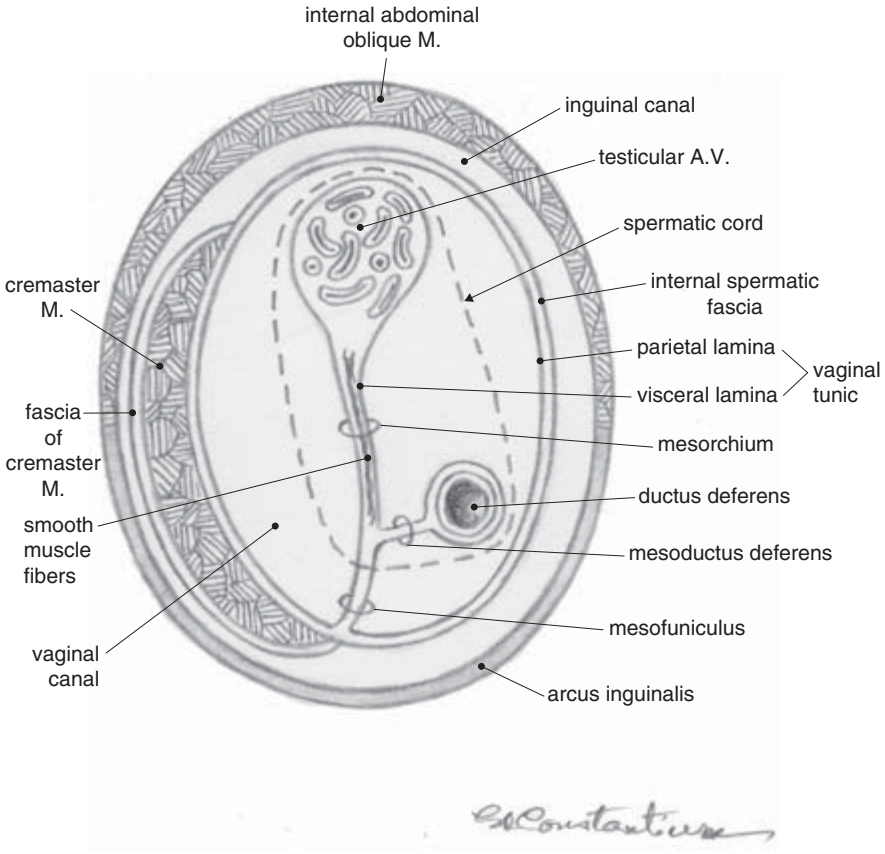

Figure 2.2. Transverse section through the spermatic cord (outlined by the broken line).

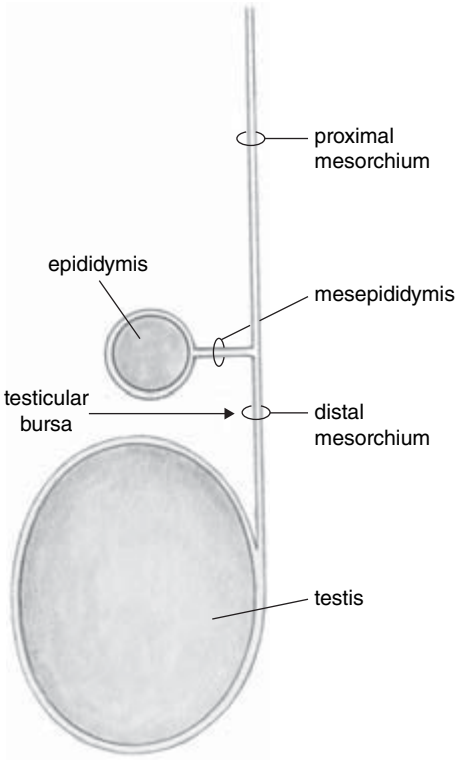

Figure 2.3. Relationship between the mesorchium and the mesepididymis.

Both the visceral and parietal laminae of the vaginal tunic are continuations of the visceral and parietal peritoneum, respectively, after they pass through the *inguinal canal* via the *deep inguinal ring*. (The inguinal canal is outlined cranially by the caudal border of the internal abdominal oblique muscle and caudally by the arcus inguinalis, and between the superficial and deep inguinal rings (for details see veterinary anatomy books). The reflection of the parietal peritoneum within the deep inguinal ring is called the *vaginal ring*. The virtual space between the two laminae around the spermatic cord is called the *vaginal canal*. The *vaginal cavity* is the space between the same two laminae around the testicle.

The Extraabdominal Tunics

The extraabdominal tunics are the external spermatic fascia and the skin. The skin consists of the tunica dartos and the scrotal skin.

The *external spermatic fascia* is the continuation of the superficial fascia that covers the external abdominal oblique muscle, associated with subcutaneous loose connective tissue. The fascia continues in the perineal region under the name of the *deep perineal fascia*.

The *tunica dartos* consists of smooth muscle fibers that surround each testicle and build up together a partition wall between the testicles called the *scrotal*

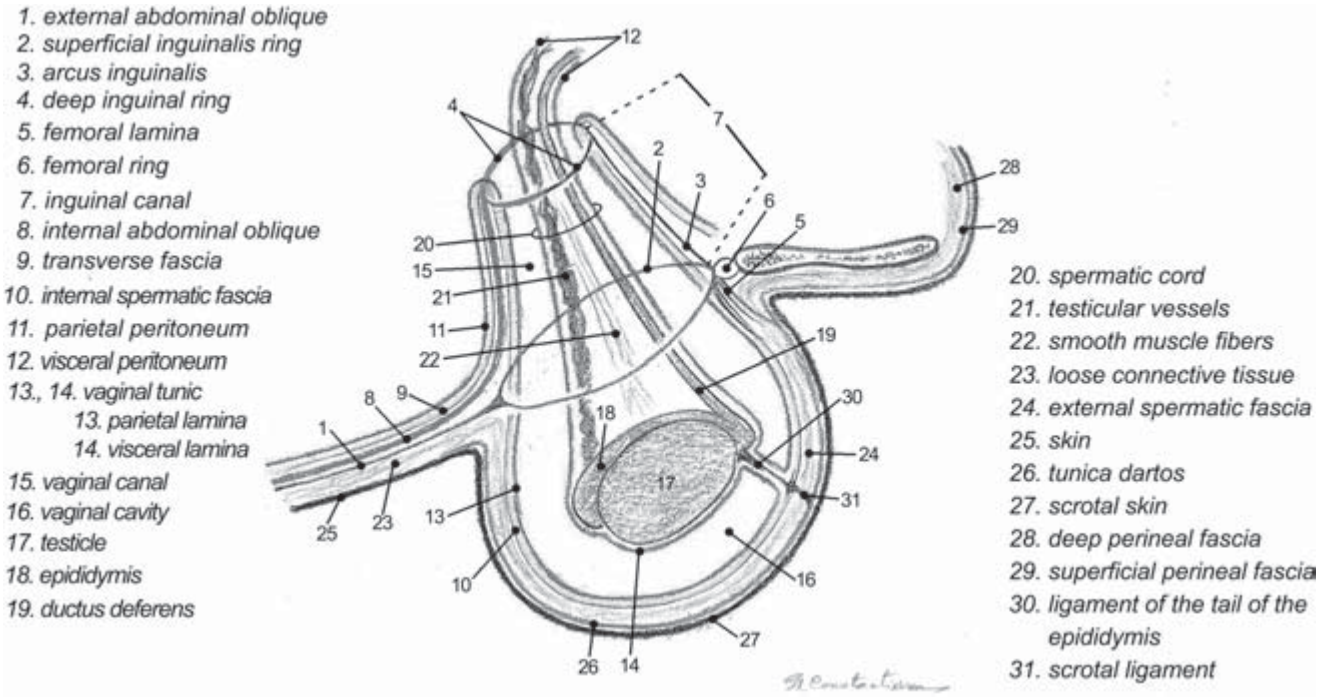

Figure 2.4. Schematic median section through the inguinal region, testicle, and testicular tunics.

(interdartoic) septum. From the scrotal septum the dartos extends dorsally, and surrounds and protects the penis. The dartos continues in the perineal region under the name of *superficial perineal fascia*. The *ligament of the tail of epididymis* joins the tail of the epididymis to the internal spermatic fascia (in ungulates). In Carnivores the tail of the epididymis is adherent to the internal spermatic fascia; therefore, there is no ligament of the tail of epididymis. The *scrotal ligament* joins the ligament of the tail of epididymis to the dartos in Ugulates, whereas

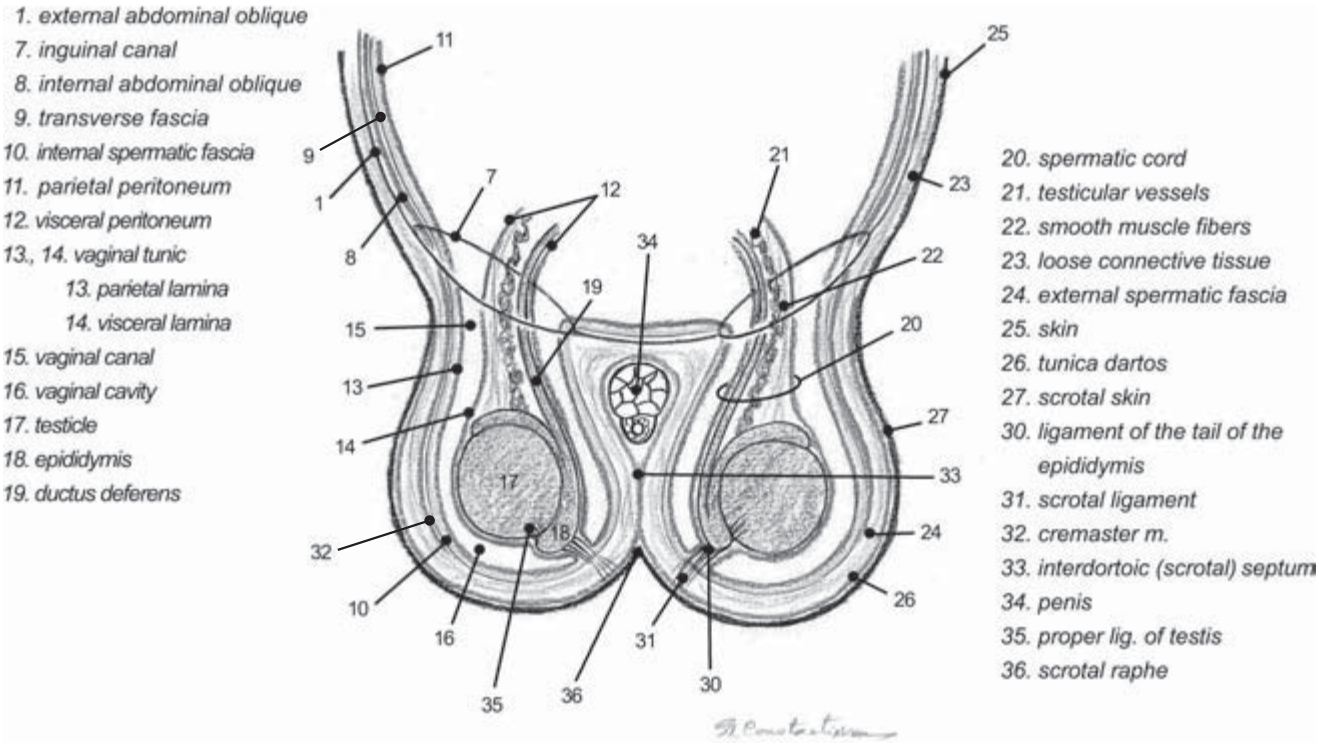

Figure 2.5. Schematic transverse section through the inguinal canals, penis, testicles, and testicular tunics.

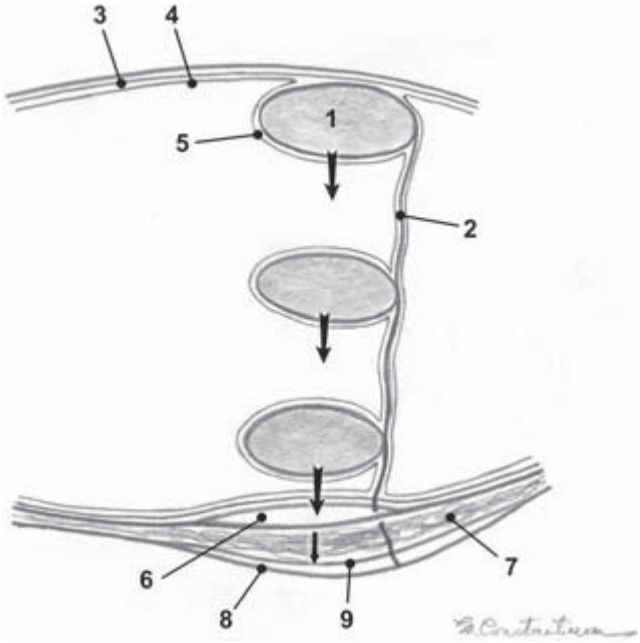

Figure 2.6. The descent of the testicle. 1. Testicle; 2. Gubernaculum testis (which will become the proper lig. of testis, the lig. of the tail of epididymis and the scrotal lig); 3. Transverse fascia (which will become the internal spermatic fascia); 4–5. Peritoneum (which will become the vaginal tunic): 4. Parietal peritoneum (parietal lamina of vaginal tunic), 5. Visceral peritoneum (visceral lamina of vaginal tunic); 6. Inguinal canal; 7. Subcutaneous connective tissue and superficial fascia (which will become the external spermatic fascia); 8–9. The skin (which will become 8. Scrotal skin and 9. Tunical dartos).

in Carnivores it joins the internal spermatic fascia to the dartos.

The *scrotal skin* that supports both testicles is separated by the *scrotal raphe* into two halves, one for each testicle.

The Descent of the Testicle

A simple and helpful description of the descent of the testicle is necessary to better understand the testicular tunics and the relationships among them (see Figure 2.6). In the early stages of the developmental life, the testicle is located on the roof of the future abdominal cavity, between the transverse fascia (on the dorsal surface of the testicle) and the visceral peritoneum (on the ventral surface of the testicle). The caudal extremity of the testicle is anchored to the skin by a mesenchymal structure, the *gubernaculum testis*, which passes through the inguinal canal on its way to the skin.

The transverse fascia is intimately lined by the parietal peritoneum, both of them passing through the inguinal canal under the name of *vaginal process.* The gubernaculum testis regresses gradually and pulls down the testicle. A short period of time before birth, which varies with the species, the testicle lands on the abdominal opening of the inguinal canal (the deep inguinal ring). At this stage of descent, the visceral peritoneum that accompanies the testicle comes in intimate contact with the parietal peritoneum. Shortly before or after birth, depending on species, the testicle passes through the inguinal canal toward the scrotum. It brings with it the visceral and parietal peritoneum and the transverse fascia, whose names will change into the visceral and parietal laminae of the vaginal tunic, and the internal spermatic fascia, respectively. These are the so-called intraabdominal testicular tunics. Outside of the body wall, the testicle finds the external spermatic fascia, the tunica dartos, and scrotal skin, all three extraabdominal testicular tunics. The remnant of the gubernaculum testis following the normal positioning of testicle is a structure divided in three parts: the proper ligament of the testicle, the ligament of the tail of the epididymis, and the scrotal ligament.

The Accessory Genital Glands

The accessory genital glands are the following: the glands of the ampullae of ductus deferentes (singular, ampulla of ductus deferens), the vesicular glands/seminal vesicles, the prostate, and the bulbourethral glands. They differ from species to species and from an intact male to a castrated male.

The *glands of the ampullae of ductus deferentes* are simple, branched tubuloalveolar glands located in the propria-submucosa of each ampulla.

The paired *vesicular glands* are compound tubular or tubuloalveolar glands, lie over the neck of the urinary bladder, and open on the sides of the colliculus seminalis.

The *seminal vesicles* are special vesicular glands found only in the horse.

The *prostate* has two parts: one compact or external part called the body, and a disseminated or internal part. The body overlaps the ampullae of the ductus deferentes and the excretory ducts of the vesicular glands, or it completely surrounds the urethra. In some species, the body is separated into a right and a left *lobe* connected by an *isthmus.* The prostate gland totally or partially surrounds the pelvic urethra, which at the area of contact with the prostate gland has a specific name, the prostatic part of the urethra. The short part of the pelvic urethra, between the neck of the urinary bladder and the prostatic part, is called the preprostatic part of the urethra. The prostate consists of individual tubuloalveolar glands. Numerous *prostate excretory ductules* open into the urethra. The disseminated part of the prostate forms a glandular layer in the wall of the pelvic urethra in some species.

The paired *bulbourethral glands* are located dorsolateral to the last portion of the pelvic urethra called the urethral isthmus. The bulbourethral gland is a compound tubular or tubuloalveolar gland.

The Penis

The *penis* is an external genital organ, the male organ of copulation. It consists of a root, a body, and a free part surrounded by the prepuce.

The *root* of the penis consists of two crura (singular, crus) and the bulbus penis. The paired *crus penis* is the proximal end of the corpus cavernosum penis. This segment

is attached to the ischiatic arch and is covered by the ischiocavernosus muscle. The *bulbus penis* is the caudal extent of the *corpus spongiosum penis.*

The *body* of the penis has a dorsal surface, with a dorsal groove only in the horse, and a ventral (urethral) surface. A urethral groove is sculpted on the ventral surface and protects the penile urethra and the corpus spongiosum penis.

The *free part* of the penis starts from the attachment of the prepuce on the penis and ends as the glans penis. The *glans penis* is the head of the penis, which contains the corpus spongiosum glandis. The glans is a cushion that overlaps the distal end of the albuginea of the corpus cavernosum penis. The dorsal process, the long part, the bulb, the crown, the septum, the neck, and the fossa of the glans penis, as well as the urethral sinus, are species specific and will be described later.

The *prepuce* is the skin that surrounds the free part of the penis like a muff. With the penis in the resting position, the prepuce is a folded skin, with external and internal laminae. The *external lamina* is a typical skin with hair and sebaceous glands, while the *internal lamina* is provided with fine hairs, sebaceous glands, and sweat glands. The internal lamina comes in intimate contact with the fully erect penis. A circular orifice called the *preputial ostium (orifice)* is outlined by the transition between the two preputial laminae. The cavity between the internal lamina and the penis in a resting position is called the *preputial cavity.* The preputial ring, fold, diverticulum, frenulum, raphe, and muscles are species specific and will be described later.

The intimate structure of the penis consists of the following: the corpus cavernosum penis with or without a septum, provided with trabeculae and cavernae, and surrounded by its own tunica albuginea; the corpus spongiosum penis with trabeculae and cavernae, and surrounded by its own tunica albuginea; the corpus spongiosum glandis; the bulbus penis; fasciae; ligaments; arteries; veins; lymph nodes; and nerves.

The paired *corpus cavernosum penis* (plural, corpora cavernosa) originate from the ischiatic arch and join with each other; in most species they are separated by the *septum penis*. The tunica albuginea sends inside the corpora cavernosa many trabeculae that separate several vascular spaces from each other. These spaces are called *cavernae*.

The *corpus spongiosum penis* is a sponge-like, erectile tissue that surrounds the urethra and is covered by its own *tunica albuginea*. *Trabeculae* and *cavernae* are also present in the corpus spongiosum penis. The *corpus spongiosum glandis* is a similar kind of structure that surrounds the glans penis.

The *bulbus penis* is the expanded caudal extent of the corpus spongiosum penis. The bulbus penis is part of the root of the penis (together with the crura of the penis). Two fasciae and two ligaments suspend the penis.

The Male Urethra

The *male urethra* is the common excretory duct for the urine and semen. The urethra consists of a pelvic part and a penile part.

The *pelvic part*, surrounded by a cavernous tissue called the spongy layer (*stratum spongiosum*) is divided into a *preprostatic* part, a *prostatic* part, a *postprostatic* part, and the *urethral isthmus.* The prostatic part is associated with the prostate gland. Inside of the prostatic part and on the roof, in a cranio-caudal order, the following structures can be identified:

- the *urethral crest*, from the *internal urethral orifice* to the colliculus seminalis, or even beyond it
- the *colliculus seminalis*, the prominence bearing on each side the ejaculatory orifice, or the separate openings of the ductus deferentes and the excretory ducts of the vesicular glands
- the *ejaculatory orifice*, the opening of the *ejaculatory duct* on the colliculus seminalis (inconstantly the ductus deferens is associated with the excretory duct of the vesicular gland in the so-called ejaculatory duct)
- the *uterus masculinus*, the rudimentary male uterus, a remnant of the paramesonephric ducts during the intrauterine life; it is also known as the utriculus prostaticus
- the *prostatic sinus*, a symmetrical recess between the urethral crest and the lateral urethral wall, where the prostatic ductules open
- the entire urethral mucosa, provided with longitudinal folds
- the muscular tunic, the smooth muscle of the pelvic urethra that surrounds the disseminated part of the prostate if present, or the spongy layer of the pelvic urethra
- the urethralis muscle, the striated muscle that surrounds the pelvic urethra.

The *urethral isthmus* is the narrow transition between the pelvic urethra and the penile urethra, around the ischiatic arch. The *penile part* of the urethra, surrounded by the corpus spongiosum penis, opens by the *external urethral orifice*.

Major Muscles, Blood Supply, Lymph Drainage, and Nerve Supply for the Male Genitalia

In addition to the cremaster muscle, the major *striated muscles* associated with the male genital organs are the following:

- urethralis
- ischiourethralis
- bulboglandularis
- superficial transverse perineal
- ischiocavernosus
- bulbospongiosus

- retractor penis (predominantly smooth)
  - anal part
  - rectal part
  - penile part
- cranial preputial (absent in the horse)
- caudal preputial (absent in the horse)

For details regarding the origin, insertion, and action of these muscles, see veterinary anatomy books, the *Nomina Anatomica Veterinaria* (*N.A.V.*), and the *Illustrated Veterinary Anatomical Nomenclature.*

The *blood supply* to the male genitalia is as follows:

- The testicle is supplied by the testicular artery and vein with species-specific differences of origin (within the mesorchium, the vein surrounds the testicular artery as a network—the pampiniform plexus, whose role is to cool down the arterial blood before it reaches the testicle). When the artery and vein reach the testicle, they perforate the albuginea, run with a species-specific design, and branch to supply the testicular tissue.
- The epididymis receives epididymal branches from the testicular artery and vein.
- The ductus deferens is supplied either by branches from the testicular artery or the prostatic artery, or by the artery of the ductus deferens from the prostatic artery (in Carnivores).
- The extraabdominal testicular tunics are supplied by the ventral scrotal artery and vein, branches of the external pudendal artery and vein.
- The pelvic urethra is supplied by the urethral artery or branch, originating from the internal pudendal artery. The urethral vein is present only in Carnivores. In the other species, the pelvic urethra is discharged by branches of the obturator and prostatic veins.
- The accessory genital glands are supplied by the prostatic artery and vein, or by branches of these vessels.
- The penis is supplied by the artery of the penis (from the internal pudendal artery), which branches into the artery of the bulbus penis (to the bulbus penis and corpus spongiosum penis), the deep artery of the penis (to the corpus cavernosum penis), and the dorsal artery of the penis. The external pudendal artery may also be involved in supplying blood to the penis. The middle artery of the penis (from the obturator artery) and the cranial artery of the penis (from the external pudendal artery), both in the horse only, contribute to the blood supply of the penis. The veins are satellite to the arteries.

  The deep artery of the penis is coiled in the resting position of the penis, especially in species with a musculomembranous type of penis. The branches of this artery have a helical arrangement and characteristic smooth muscle cells that act during the erection. In the resting position, the smooth muscle cells are organized in ridges or pads that protrude into the lumen of the vessels, causing partial obliteration. As the smooth muscle cells relax, the blood flow into the cavernae increases considerably and causes erection. The cavernae are drained by venules (Dellmann and Brown 1998).
- The prepuce is supplied by the superficial caudal epigastric artery and vein, branches of the external pudendal artery and vein.
- The penile urethra is supplied by the artery and vein of the bulbus penis.

For species-specific differences, see veterinary anatomy books, the *N.A.V.*, and the *Illustrated Veterinary Anatomical Nomenclature.*

Lymph drainage in the male genitalia occurs as follows:

- Lymph from the testicle and epididymis is drained into the lumbo-aortic and renal lymph nodes.
- Lymph from the ductus deferens (the segment included in the spermatic cord) is drained into the lumboaortic and renal lymph nodes. Lymph from the rest of the ductus deferens, the pelvic urethra, the prostate, the vesicular glands, and the bulbourethral glands drains into the medial iliac lymph nodes.
- Lymph from the scrotum is drained into the scrotal lymph nodes.
- Lymph from the penis is drained into the superficial inguinal, deep inguinal, scrotal, and/or medial iliac lymph nodes.

For species-specific differences, see veterinary anatomy books and the *Illustrated Veterinary Anatomical Nomenclature.*

The *nerve supply* for the male genital organs is as follows:

- The testicle and the epididymis are supplied by the testicular plexus, with nerve fibers from the aortic abdominal plexus, caudal mesenteric plexus, lumbar splanchnic nerves and hypogastric nerves (all sympathetic), and the pelvic nerves through the pelvic plexus (parasympathetic).
- The ductus deferens, the vesicular glands, the prostate, the bulbourethral glands, and the pelvic urethra are supplied from the pelvic plexus (sympathetic and parasympathetic fibers) by specific plexuses.
- The penis as a whole is supplied by the pudendal nerve (parasympathetic), which also supplies the scrotum by the dorsal scrotal branches and continues as the dorsal nerve of the penis, and by the nerve of the corpus cavernosum penis from the prostatic plexus (both sympathetic and parasympathetic).

For species-specific differences, see veterinary anatomy books, the *N.A.V.*, and the *Illustrated Veterinary Anatomical Nomenclature.*

Part 2.2
Female Genital Organs

The female genital organs consist of the paired ovary and uterine tube, the uterus, vagina, vestibule, vulva and clitoris, and the female urethra. The female genital organs can be systematized into the reproductive glands (the ovaries), the tubular genital organs (the uterine tubes, the uterus, vagina, vestibule, and vulva), and the clitoris. The female urethra and the vulva are considered as external female genital organs.

The Ovary

The *ovary* is the female essential reproductive gland, which produces ovules (ovocytes, oocytes), the two female hormones progesterone and estradiol, and also oxytocin, relaxin, inhibin, and activin.

Ovoidal-shaped, each ovary has a hilus, a medial surface, a lateral surface, a free border, a mesovarian border, a tubal extremity, and a uterine extremity.

The *hilus* is the area of attachment of the mesovarium and the entrance of ovarian vessels.

The *medial* and *lateral surfaces*, and the *free border* of the ovary are convex and irregular. The orientation of the surfaces is not always medial and lateral. In *the Mare only*, the free border is concave because of the depression called the *ovarian fossa*, where ovulation occurs (some veterinary clinicians prefer to call it the "ovulation fossa").

The *mesovarian border* is opposite to the free border and is the site for attachment of the mesovarium.

The *tubal extremity* is that end of the ovary facing the infundibulum of the uterine tube.

The *uterine extremity* is opposite to the previous and attached to the apex of the uterine horn by the proper ligament of the ovary.

A dense white capsule, the *tunica albuginea* covers the ovary immediately beneath a *cuboidal surface epithelium*. In all species except the horse, a peripheral parenchymatous zone called the *cortex* is located in intimate contact with the albuginea; the cortex contains follicles and corpora lutea. In the center of the ovary, a vascular zone called the *medulla* supports the blood vessels that nourish the ovary, lymphatics, nerves, and smooth muscle fibers (*in the horse the medulla is peripheral, and the cortex is central*). The loose connective tissue in both the cortex and medulla is called *stroma* (Figures 2.7 and 2.8 show the internal organization of the cow's and Mare's ovary, respectively).

Depending upon the evolution of the follicles and the sexual cycle, the following structures may be identified within the ovary:

- The *primordial ovarian follicle* is a small immature ovocyte that has not undergone recruitment and is surrounded by a single layer of flattened follicular cells; it is also called the *unilaminar ovarian follicle.*
- The *primary ovarian follicle* consists of an ovocyte surrounded by one or more layers of cuboidal or columnar follicular cells before the appearance of an antrum filled with follicular liquor; the follicle becomes surrounded by a sheath of stroma, the *follicular theca.*
- The *secondary ovarian follicle* is a growing primary ovocyte surrounded by a stratified follicular epithelium and a developing follicular theca.
- The *tertiary or vesicular ovarian follicle* (antral or graafian follicle) is a large, full-sized primary ovocyte with a central cavity called the antrum that is filled with follicular liquor, contains follicular epithelium and a very developed theca, and is surrounded by the *zona pellucida.*
- The *corpus luteum* is the yellow endocrine body formed in the site of a ruptured ovarian follicle and developed from cells of granulosa and internal theca after ovulation.
- The *corpus albicans* is the remaining structure after the degeneration of the corpus luteum. If pregnancy does not occur, the corpus luteum undergoes regression to the corpus albicans.
- The *atretic ovarian follicle* is an abnormal follicle, which began to mature but did not become a dominant follicle (a dominant ovarian follicle matures completely and forms the corpus luteum); the atretic ovarian follicle degenerates before coming to maturity.

The three ligaments of the ovary are:

- the *suspensory ligament*—joins the ovary to the diaphragm
- the *proper ligament*—joins the ovary to the apex of the uterine horn
- the *mesovarium*—the most cranial segment of the *broad ligament*. The mesovarium is in continuation with the mesometrium (which suspends the uterus) and has two segments: proximal and distal. The *proximal mesovarium* is separated from the *distal mesovarium* by the origin/attachment of the mesosalpinx. The proximal mesovarium extends from the abdominal wall (where

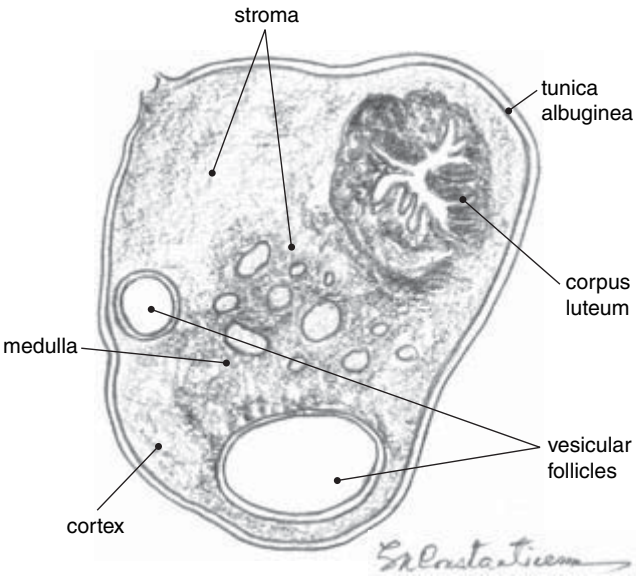

Figure 2.7. Internal organization of the cow's ovary.

the broad ligament originates) to the origin of the mesosalpinx, while the distal mesovarium is very short, from the origin of the mesosalpinx to the ovary.

Two groups of vestigial structures from the developmental life, called *epoöphoron* and *paroöphoron,* may be associated with the ovary:

- structures that originate from the epoöphoron
  - the *duct of the epoöphoron,* the vestige of the cranial part of the mesonephric duct
  - the *transverse ductules*, remnants of the mesonephric tubules, which extend from the duct of the epoöphoron to the hilus of the ovary and pass through the mesovarium and mesosalpinx
  - the *vesicular appendages*, which are pedunculated cysts near the infundibulum of the uterine tube
- the paroöphoron, a group of caudal mesonephric tubules in the mesosalpinx, near the uterine extremity of the ovary

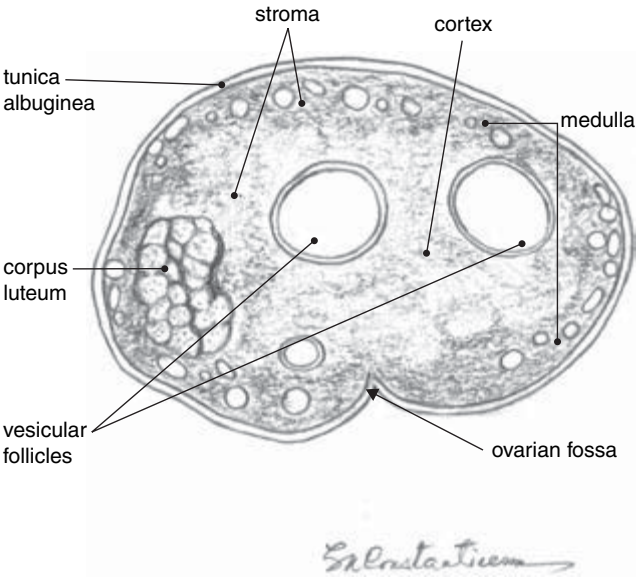

Figure 2.8. Internal organization of the mare's ovary.

The Uterine Tube

The *uterine tube* is a duct that extends from the apex of the uterine horn toward the ovary on the lateral side of the broad ligament. The uterine tube is flexuous to allow distension during pregnancy, and it has an uneven size. The uterine tube, also called the *salpinx or fallopian tube*, consists of a folded mucosa, a smooth muscular coat that is thicker toward the uterus, and a serous layer lined by loose connective tissue. The serous layer is that part of the mesosalpinx that surrounds the tube.

The following structures are parts of the uterine tube: the ovarian end provided with the abdominal opening, the infundibulum, fimbriae of the infundibulum, ovarian fimbria, ampulla, isthmus, and the uterine part provided with the uterine ostium.

- The *abdominal opening/ostium of the uterine tube* is the far most and very narrow opening of the salpinx.
- The ovarian end of the uterine tube is also called the *infundibulum of the uterine tube*. It is funnel-shaped and mobile with regard to the ovary. When the ovulation occurs, the infundibulum embraces the ovary for receiving the ovocyte. The contact between the infundibulum and the ovary is enhanced by the fimbriae.
- The *fimbriae of the infundibulum*, fringe-like processes, are scattered around the border of the opening of the infundibulum and do not allow the ovocytes to drop into the peritoneal cavity. The *ovarian fimbria* is that fringe attached directly to the ovary.
- The *ampulla of the uterine tube* is the relatively wide part of the salpinx, between the abdominal ostium and the isthmus.
- The *isthmus* is the narrow part of the salpinx, in some species without a visible delimitation between it and the ampulla. Also the lumen of the isthmus is not always different from that of the ampulla.
- The *uterine part* is the shortest segment of the uterine tube. The uterine part passes through the wall of the apex of the uterine horn and in some species even ends on a papilla, whereas in other species the salpinx gradually continues with the uterine horn. The *uterine orifice/ostium of the uterine tube* opens at the end of the uterine part of the salpinx.
- The salpinx is held in position by a segment of the broad ligament called the *mesosalpinx*. This is a serous fold that originates from the lateral aspect of the mesovarium. The latter is therefore divided into the proximal and the distal mesovarium. The mesosalpinx surrounds the ovary in a species-specific manner. Between the ovary,

the distal mesovarium, and the mesosalpinx, a cavity called the *ovarian bursa* is outlined. The opening of this bursa is medially oriented.

The Uterus

The *uterus* is the organ of gestation. It has three distinct segments: the horns, body, and cervix. In most animals the uterus has two horns, a body and a cervix, and it is called the *uterus bicornis*. In the Rabbit, for example, the horns, body, and cervix are paired; this type of uterus is called *uterus duplex*. In primates, including humans, and in other species the uterus has only one compartment and the cervix, which is characteristic for the *uterus simplex*.

The uterine horns of the uterus bicornis have mesometrial and free borders, and corresponding cavities. The uterine body has right and left borders, dorsal and ventral surfaces, and a cavity. The uterine velum and fundus are species-specific structures. The endometrium, with species-specific features, the myometrium, and the perimetrium are layers of the constitution of the entire uterus. The cervix has a prevaginal part and a vaginal part, and is centered by a cervical canal. The latter communicates with the uterus cranially, and with the vagina caudally.

The *uterine horns*, right and left, are very different from species to species in terms of the shape, location, and size. The uterine horns are the most cranially extended components of the uterus, and they continue caudally with the body of the uterus. Each uterine horn has two openings/communications: at the apex (tip), it communicates with the uterine tube; the uterine orifice of the uterine tube makes the transition to the salpinx. Caudally the uterine horn opens into the body of the uterus in species-specific different manners. Each uterine horn has a *mesometrial border* where the mesometrium is attached, and a *free border* on the opposite side.

The *body of uterus* is a unique compartment located caudal to the uterine horns, between them and the cervix. The body has *a right and a left border* that continues onto the cervix, sites where the paired mesometrium is attached. The *dorsal* and the *ventral surfaces* complete the external features of the body of the uterus. The *cavity of the uterus* has a different size and shape according to species.

The *cervix*, with very thick muscular walls and rich in elastic fibers, is the neck of the uterus. The *prevaginal part of the cervix* is located cranial to the vagina, while the *vaginal part of the cervix* protrudes into the vagina. The cranial extent of the vagina surrounds the vaginal part of the cervix like a niche; this "niche" is called the fornix. The *cervical canal* is much narrower than the uterine cavity. This canal communicates with the body of the uterus by the *internal orifice of the uterus*, and with the vagina by the *external orifice of the uterus*. *Longitudinal folds* and other species-specific features are characteristic for the cervical mucosa.

The entire uterus has a mucosa called the *endometrium*, a muscular tunic called the *myometrium*, and a serous tunic—the visceral peritoneum—called the *perimetrium*. The mucous membrane of the uterine horns and body in ruminants is provided with specific structures called *caruncles*.

The myometrium consists of a three-layer smooth muscle: circular and oblique inner layers, and a longitudinal outer layer. Under the serous layer a *subserous layer* separates the perimetrium from the myometrium. The *broad ligament* suspends the ovary (mesovarium) and the horns and body of the uterus (*mesometrium*).

Originating from the floor of the pelvic cavity and continuing between the peritoneal laminae of the mesometrium, the connective tissue, smooth muscle, vessels, and nerves are collectively called the *parametrium*. The *round ligament of the uterus* originates from the tip of the uterine horn; this ligament differs widely in size, length, and position from species to species. The round ligament of the uterus extends up to, and even passes through the deep inguinal ring and the inguinal canal, accompanied by the peritoneum and transverse fascia as the *vaginal process*.

The Vagina

The *vagina* is a unique canal located between the cervix and the external urethral orifice, or the hymen. The fornix, ventral and dorsal walls, hymen, vaginal opening into the vestibule, and, in some species, the remnant of the caudal part of the mesonephric duct are the structures of the vagina.

- The *fornix* is the most cranial extent of the vagina, looking like a blind pouch that surrounds the vaginal part of the cervix. In some species the fornix is discontinuous due to the presence of dorsal and/or ventral frenula (singular, frenulum) of the cervix.
- The *ventral* and *dorsal walls* are held in place by the pelvic diaphragm. The pelvic diaphragm consists of the levator ani and coccygeus muscles, and the internal and external fasciae of the pelvic diaphragm in the retroperitoneal space.
- The *hymen*, poorly developed in domestic animals, is a transverse fold of the vaginal mucosa on the floor of the vagina just cranial to the external urethral orifice.
- The *vaginal ostium or orifice* is the communication between the vagina and the vestibule.

The mucous membrane has a distinct appearance in bovine species. The muscular tunic is represented by smooth muscles. Only the cranial end of the vagina is covered by the peritoneum. As in the uterus, a subserous loose connective tissue is present under the serous layer.

The Vestibule

The *vestibule* is the transition between the vagina and the vulva, very long in domestic animals in comparison to

humans, but with the exception of the cat, shorter than the vagina. The bulbus vestibuli, and the major and minor vestibular glands are the structures of the vestibule, with species-specific differences.

- The *bulbus vestibuli* is a symmetrical cavernous tissue in the lateral walls of the vestibule.
- The *major vestibular glands*, present in several species, are symmetrical glands that lie on the floor of the vestibule; their ducts open on the lateral walls of the vestibule.
- The *minor vestibular glands* are scattered on the lateral walls and the floor of the vestibule.

The Vulva and the Clitoris

The vulva and the clitoris are considered the external female genitalia. The *vulva* is provided with labia, commissures, and the pudendal fissure.

There are two pairs of *labia: major* and *minor*, that are not distinguishable in domestic animals, with some exceptions. The major labia are lateral to the minor labia.

The *dorsal* and the *ventral commissures of the labia* outline the *pudendal fissure*, the external urogenital fissure.

The *clitoris* is the rudimentary homologue of the penis; the clitoris is located on the floor of the vestibule. The only difference between the male and the female consists in the lack of urethra within the clitoris (there is a penile urethra in the male). The clitoris consists of two crura and the body with the corpus cavernosum, the glans with the corpus spongiosum, and the fascia of the clitoris. There are significant species differences of the clitoris.

- The *right* and *left crura* originate from the ischiatic arch and join into the body of the clitoris.
- The *body of the clitoris* is the result of fusion of the crura.
  - The *corpus cavernosum of the clitoris* is the erectile tissue of the crura and body. There is a partial *septum* of the corpus cavernosum.
  - The *glans* provided with a corpus spongiosum is the free end of the clitoris, protected in the *fossa of the clitoris*, which is similar to the preputial cavity of the male. The fossa of the clitoris is almost obliterated by adhesion of the prepuce to the glans in the cat, sow, and ruminants. The *prepuce of the clitoris* is formed by the ventral commissure of the labia and by a transverse fold of the vestibular mucosa to which the *frenulum* is attached. The frenulum is present only in the dog and the mare.
  - The *fascia of the clitoris* surrounds and protects the organ. It is well developed in the mare.

The Female Urethra

The *female urethra* corresponds to the male preprostatic urethra. The female urethra extends from the *internal urethral ostium* to the *external urethral ostium*.

The urethra consists of a mucosa, a muscular tunic, and the adventitia; it is surrounded by a cavernous tissue called the *corpus spongiosum*. A *urethral crest* similar to that of the male urethra is found starting from the internal urethral ostium and extending up to the middle of the urethra. *Urethral glands* and *lacunae (evaginations)*, *paraurethral glands*, and *ducts* differ from species to species and are associated with the female urethra.

Major Muscles, Blood Supply, Lymph Drainage, and Nerve Supply for the Female Genitalia

The major *striated muscles* associated with the female genital organs are the following:

- urethralis (in the female species the urethralis originates from the vagina and forms a sling ventral to the urethra)
- ischiourethralis
- bulboglandularis (associated with the major vestibular glands)
- ischiocavernosus (rudimentary in the female species)
- bulbospongiosus (because of the elongated vestibule, the bulbospongiosus is divided into:
  - constrictor vestibuli
  - constrictor vulvae
- retractor clitoridis (predominantly smooth)
  - anal part
  - rectal part
  - clitoridean part

For species-specific differences, see veterinary anatomy books and the *Illustrated Veterinary Anatomical Nomenclature*.

The *blood supply* to the female genitalia is as follows:

- The ovary is supplied by the ovarian artery and the ovarian vein with species-specific differences of origin. The ovarian artery also supplies the distal part of the salpinx by the branch of the uterine tube, and the apex of the uterine horn by the uterine branch.
- The whole uterus—with the exception of the apex of the uterine horn—is supplied by the uterine artery, which is a branch of the vaginal artery in carnivores, of the umbilical artery in the pig and ruminants, and of the external iliac artery in the horse. In the horse only, the uterine horns and part of the uterine body are supplied by the uterine artery from the external iliac artery; the rest of the body and the cervix are supplied by the uterine branch of the vaginal artery. In the pig, ruminants, and horse, the cervix is supplied by the uterine branch from the vaginal artery. The uterine vein is a branch of the vaginal vein in carnivores. In the other species, the vaginal vein is joined by the uterine branch. In the pig, the uterine vein is a branch of the ovarian

vein, in the ruminants is a slender and inconstant branch of the internal iliac vein, and in the horse is a branch of the internal iliac vein.
- The vagina is supplied by the vaginal artery and vein.
- The vestibule is supplied by the middle rectal artery, the artery of the bulbus vestibuli and the urethral artery, and also by the corresponding veins.
- The vulva is supplied by dorsal and ventral labial branches of the internal pudendal and external pudendal arteries, respectively.
- The clitoris is supplied by the artery of the clitoris.

For species-specific differences, see veterinary anatomy books, the *N.A.V.,* and the *Illustrated Veterinary Anatomical Nomenclature.*

L*ymph drainage* in the female genitalia occurs as follows:

- The lymph from the ovary and uterine tube drains into the lumbo-aortic lymph nodes.
- The lymph from the uterus drains in the lumbo-aortic lymph nodes (for the horns), and in the medial sacral lymph nodes (for the body and the cervix).
- The lymph from the vagina drains into the internal iliac, ano-rectal, and sacral lymph nodes.
- The lymph from the vestibule, vulva, and clitoris drains into the ano-rectal lymph nodes.

The *nerve supply* is provided by the following nerves and plexuses:

- The ovary and the uterine tube are supplied by the ovarian plexus, which originates from the cranial mesenteric plexus (both sympathetic and parasympathetic) and the last lumbar sympathetic ganglia.
- The uterus is supplied by the cranial mesenteric plexus via the ovarian plexus and by the uterovaginal plexus (from the pelvic plexus, both sympathetic and parasympathetic).
- The vagina and the vestibule are supplied by the vaginal nerves from the uterovaginal plexus (from the pelvic plexus, both sympathetic and parasympathetic).
- The vulva is supplied by the labial nerves, branches of the superficial perineal nerve (of the pudendal), and by branches of the pelvic plexus, both sympathetic and parasympathetic.
- The clitoris is supplied by the dorsal nerve of the clitoris, the branch of the pudendal nerve, and by branches of the pelvic plexus, both sympathetic and parasympathetic.

The Mammary Gland (*Mamma*)

This is intended to be a unique subsection on the topic for all species. The *mammary gland*, a modified cutaneous (sweat) gland, is by definition one mammary complex that consists of one body and one papilla (see Figure 2.9). In the ruminants and equine species, the mammary glands are collectively called *udder.* The papilla is also called *nipple* in carnivores and sows, or *teat* in ruminants and equine species. In all species, the papilla are paired, but their number differs from species to species. The numbers typically are 10 in dogs, 8 in cats, 14 in pigs, 4 in cows, and 2 in small ruminants and horses. There are normal and abnormal variations in number.

The mammary glands are attached to, and suspended from the ventral body wall. According to the position of the glands, there are species-specific thoracic (in humans, monkeys, and elephants), thoracoabdominal (in cats), thoracoinguinal (in dogs and pigs), or inguinal mammary glands (in all ruminants and horses).

The body, which is conical shaped, consists of skin, glandular tissue, and connective tissue. Adjacent mammae are superficially separated by longitudinal or transversal intermammary grooves in ruminants and equine species.

A single gland consists of glandular tissue and a duct system. The glandular tissue is separated in lobes by connective tissue. Each lobe is divided in lobules, which are clusters of up to 200 alveoli that secrete into a central ductule (the lactiferous alveolar ductule). The lobules are separated from each other by a thin layer

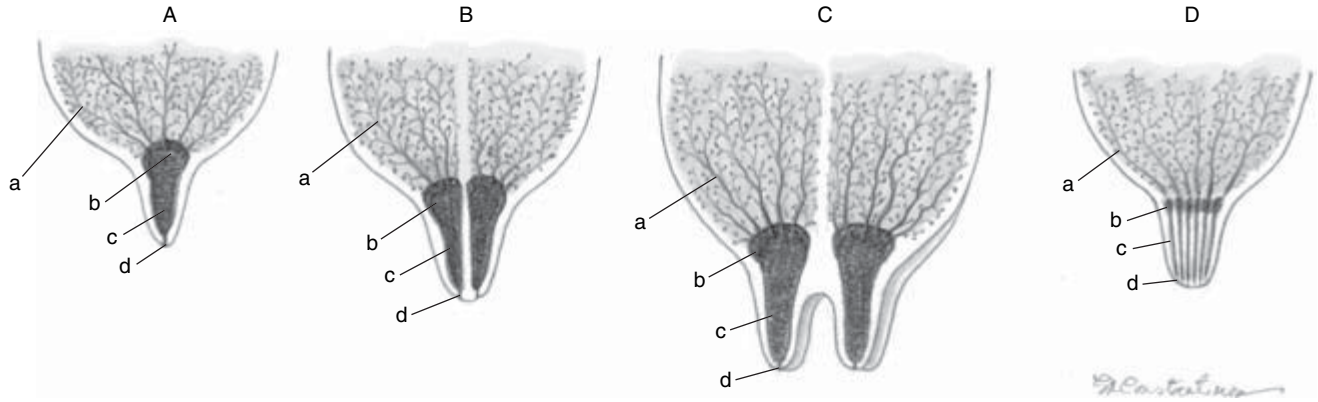

Figure 2.9. The duct system and lactiferous cistern in mammary glands (schematic): **A.** small ruminants; **B.** mare and sow; **C.** cow; **D.** carnivores; **a.** lactiferous ducts; **b.** gland cistern (**b** and **c** form the lactiferous sinus s. cistern); **c.** papillary cistern; **d.** papillary ducts.

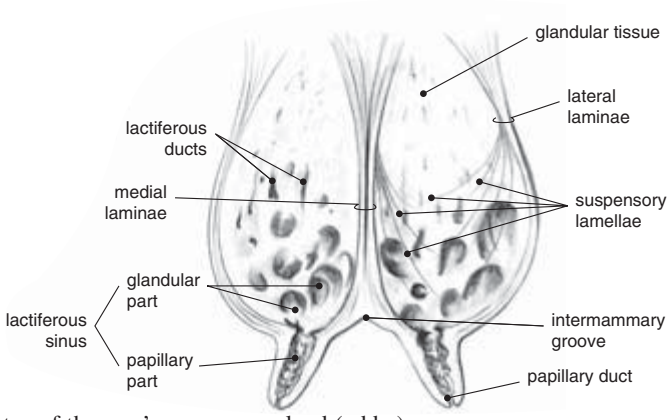

Figure 2.10. Suspensory apparatus of the cow's mammary gland (udder).

of connective tissue. The lactiferous alveolar ductules continue with intralobular and interlobular ductules. All the above-mentioned structures are located within a lobe. At the end of each lobe, the duct system is represented by a lactiferous duct. The lactiferous ducts are the first visible structures of the duct system, and all of them convey the milk to the lactiferous sinus; the ducts become larger and larger as they approach the lactiferous sinus (see Figure 2.10).

The lactiferous sinus or cistern is the dilated part of the duct system and consists of a glandular part (gland cistern) and a papillary part (papillary or teat cistern). The glandular part is located in the ventral end of the mammary gland, whereas the papillary part is located within the papilla. At the base of papilla in the cow the mucosa makes several folds resembling a flower, known as the "rosette of Fürstenberg," with clinical importance. The papillary duct is the narrow passage of the papillary part of the lactiferous sinus at the very end of the papilla and is provided with a sphincter. This duct is also called teat or streak canal in ruminants. Its opening is called the papillary orifice or ostium. In some species, a papilla is perforated by two or more papillary ducts, each of which opens by its own ostium. There are differences among species in terms of the number of glandular complexes that open through one teat. So there are from 5 to 7 glandular complexes per teat in the cat, from 8 to 14 in the dog, from 2 to 3 in the pig, 2 in the horse, and 1 in all ruminants.

The entire mammary gland is covered and protected by a capsule, which is continuous with the interlobar connective tissue. In the large animals, especially in the cow, the udder is suspended by the so-called *mammary suspensory apparatus*. This apparatus consists of lateral laminae and medial laminae, both provided with suspensory lamellae that anchor the laminae into the glandular tissue. The lateral laminae originate from the femoral laminae of the external abdominal oblique muscles. The internal laminae originate from the symphyseal tendon and the abdominal tunic, the latter being the elastic component of the mammary suspensory apparatus. (The symphiseal tendon is the common origin of the symmetrical gracilis and adductor muscles.)

Rudimentary developed and nonfunctional mammary glands also exist in male species. These glands are located in the same place(s) as in the female species and are represented by small teats.

Blood Supply, Lymphatic System, and Nerve Supply for the Mammary Gland

The mammary gland blood supply varies from species to species, and especially during the lactating period. The *arteries* are provided by the cranial epigastric artery through the cranial superficial epigastric artery; by the external pudendal artery through the caudal superficial epigastric artery and the ventral labial branch; and by the internal pudendal artery through the ventral labial and mammary branch. In the Mare and in the cow the caudal superficial epigastric artery is called the *cranial mammary artery*, and in the same species the ventral labial branch is called the *caudal mammary artery.* In the cow the cranial mammary artery (the caudal superficial epigastric artery) anastomoses with the cranial superficial epigastric artery, whereas the caudal mammary artery (the ventral labial branch of the external pudendal artery) anastomoses with the ventral labial and mammary branch of the internal pudendal artery. (Figure 2.11 shows the blood supply to the cow's udder.)

The *veins* in general follow the arteries. In cows with voluminous and very productive udder, the cranial mammary vein (the *milk vein*) is very large and can be seen under the skin. This vein is flexuous and runs in a cranial direction, penetrating a ring in the ventral abdominal wall where the vein joins the cranial epigastric vein. The ring, which is large enough to introduce a finger within, is called the *milk well.* In accordance with the position of the cow lying down and compressing the udder and the vascular supply, the blood returns to the systemic circulation through one of the cranial mammary, caudal mammary, or external pudendal veins.

The *lymphatic system* is mainly represented by the mammary lymph nodes (superficial inguinal lymph nodes). The subiliac, ischial, or deep inguinal (iliacofemoral) lymph nodes may also drain the udder. The afferent lymphatic vessels start from widely spread papillary plexuses.

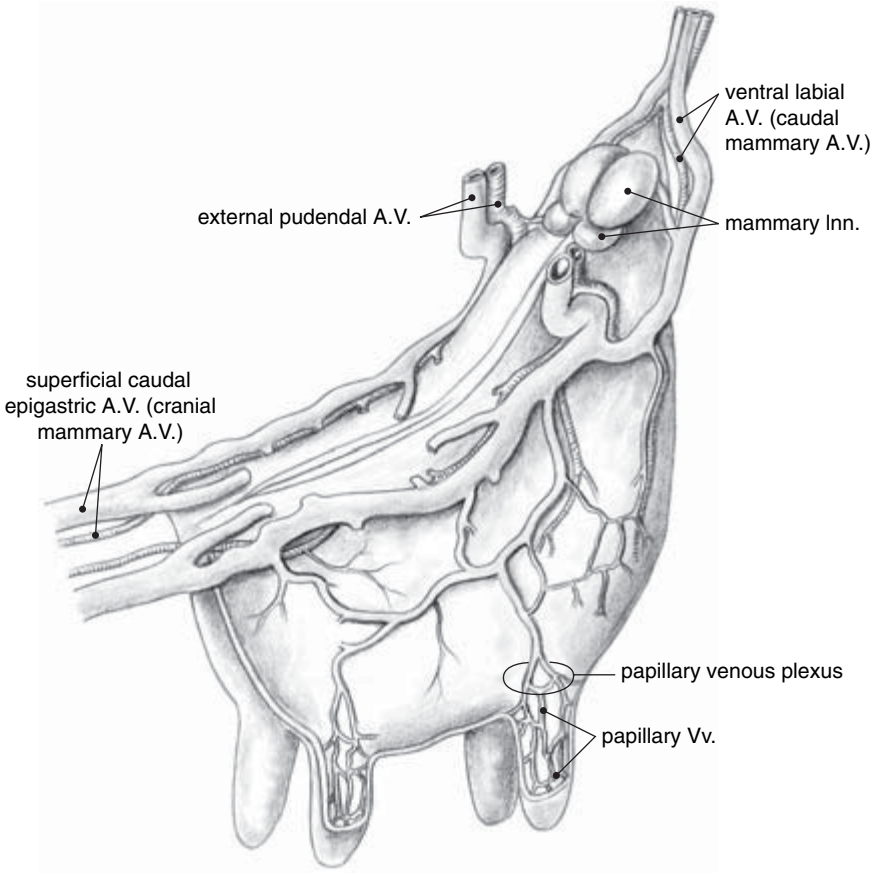

Figure 2.11. Blood supply to the cow's udder (modified and redrawn in pencil from R. Barone, Laboratoire d'Anatomie École Nationale Vétérinaire, Lyon, 1978).

The *nerves* that supply the mammary glands originate from the thoracic, lumbar, and sacral spinal nerves. In the cow, the udder is supplied by the genitofemoral nerve (from the lumbar spinal nerves) and by the mammary branches of the pudendal nerve (from the sacral spinal nerves). The genitofemoral nerve carries efferent and afferent sympathetic fibers. There is no proof of a parasympathetic nerve supply to the mammary gland.

This is, again, a general and acceptable description for all species.

Part 2.3
The Genital Apparatus in the Carnivore

Male Genitalia

The male genitalia in carnivores are presented in four subsections, following the same pattern as was chosen for the general description. Therefore, the first subsection covers the testicle, epididymis, ductus deferens, spermatic cord, and the tunics. The second subsection covers the accessory genital glands, the third subsection the penis, and the last subsection the male urethra.

The Testicle, Epidydimis, Ductus Deferens, Spermatic Cord, and the Tunics

The descent of the testicles occurs very late during the development. The testicles take their normal place within the scrotum between the second and the third week *after* birth.

Globular in shape, the two testicles of carnivores weigh from 1/750 to 1/1850 of the body weight. The long axis of each testicle is obliquely oriented, cranioventrally. The albuginea is thick, and the *mediastinum testis* is located in the middle of the testicle. The *testicular artery*, which runs deep to the albuginea, shows a characteristic design on the surface of the testicle. Small *arterio-venous anastomoses* between the testicular artery and vein were described in the dog.

The *epidydimis* is attached to the dorsolateral border of the testicle. The head of the epidydimis starts from the medial surface of the testicle, but it reaches the dorsolateral position to continue with the body and the tail. In the dog, both the head and the tail of the epididymis exceed the head and the tail of the testicle, whereas in the cat only the head of the epididymis slightly exceeds the head of the testicle. The albuginea of the epidydimis is thinner than that of the testicle. The ductus epididymidis in the dog is between 5 mm and 8 mm long, whereas in the cat it is from 1.5 mm to 3 mm long; it is tortuous in both species. The tail of the epidydimis is attached to the tail of the testicle by a short proper ligament of the testicle, and to the internal spermatic fascia directly (there is no ligament of the tail of the epidydimis in carnivores because the internal spermatic fascia is adherent to the tail of the epididymis). The scrotal ligament joins the internal spermatic fascia to the dartos (see the general description). Figures 2.12 and 2.13 show the testicle of the dog; Figures 2.14 and 2.15 show the testicle of the cat.

The *ductus deferens* begins as a flexuous duct along the epidydimal border of the testicle and medial to the epidydimis in a caudocranial direction because of the position of the testicle. After the ductus deferens passes over the head of the epidydimis, it enters into the spermatic cord and continues up to the vaginal ring. Within the abdominal cavity, the ductus deferens makes a curve in a dorsocaudal direction to enter the pelvic cavity and reach the urethra. In its route from start to finish, the mesoductus deferens, also part of the spermatic cord, is attached to the ductus deferens. Before it reaches the urethra, the ductus deferens crosses the ureter ventrally, then dorsally over the lateral ligament of the urinary bladder. To reach the urethra, the ductus deferentes penetrate the prostate gland and open on the lateral sides of the colliculus seminalis. Before they

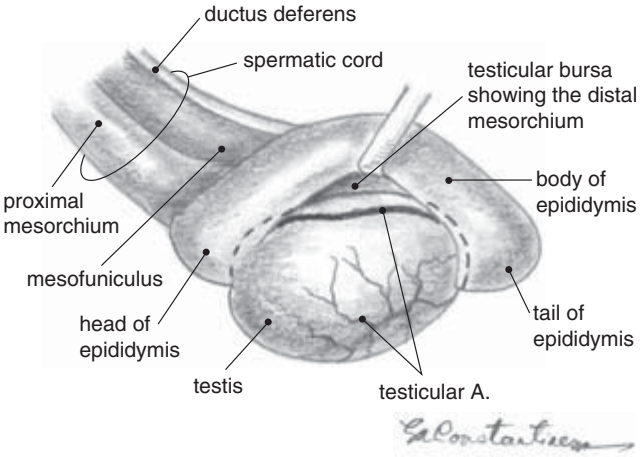

Figure 2.12. Testicle of the dog—lateral aspect.

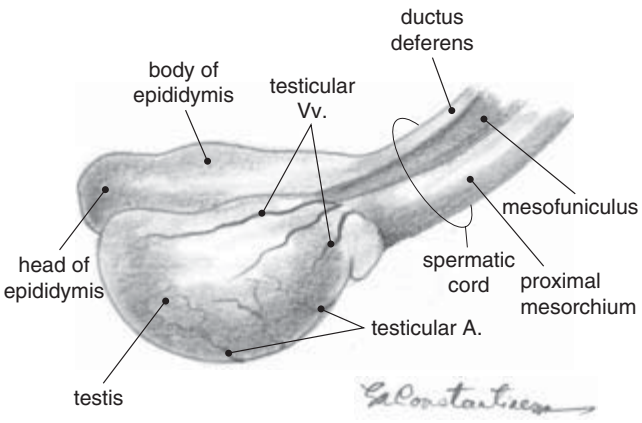

Figure 2.13. Testicle of the dog—medial aspect.

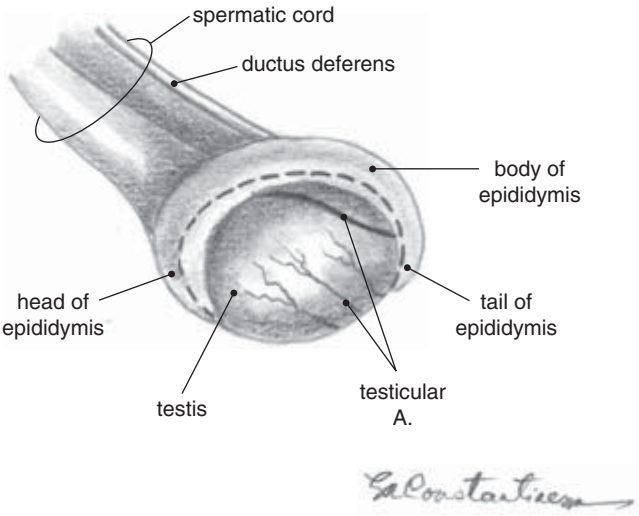

Figure 2.14. Testicle of the cat—lateral aspect.

touch the prostate gland, the ductus deferentes and the ureters are held by the genital fold, a visceral peritoneal fold. The uterus masculinus usually can be seen between the two layers of the genital fold. The ampulla of the ductus deferens with the glands is present only in the dog, but it is not too obvious.

The *spermatic cord* and the *tunics of the spermatic cord and testicle* don't differ from the general description, but they differ slightly from the dog to the cat. In the dog, the spermatic cord is from 8 cm to 10 cm long in a middle-sized individual, and it is ventrocaudally obliquely oriented. The scrotum and the testicles are situated distally in the perineal region. In the cat, the spermatic cord is horizontal and proportionally longer in comparison to that of the dog. The scrotum and the testicles are located proximally in the perineal region, in a subanal position.

The Accessory Genital Glands

In the dog, only the *prostate gland* is present, whereas in the cat, the *prostate and the bulbourethral glands* are present. No vesicular glands are present in any of these species (see Figures 2.16 and 2.17).

The *prostate gland* has two parts: the body and the disseminated part. In both species, the body has two lobes, right and left, with an uneven surface. In the dog, the body is spherical and completely surrounds the urethra, whereas in the cat, the prostate is attached only to the roof and the lateral walls of the urethra. The prostate opens on the roof of the prostatic part of the urethra. The disseminated part of the prostate is present as small lobules in both species.

The *bulbourethral glands* (present only in the cat) are very small (up to 5 mm in diameter) and lie in intimate contact with the dorsolateral wall of the urethra, at the level of the ischial arch.

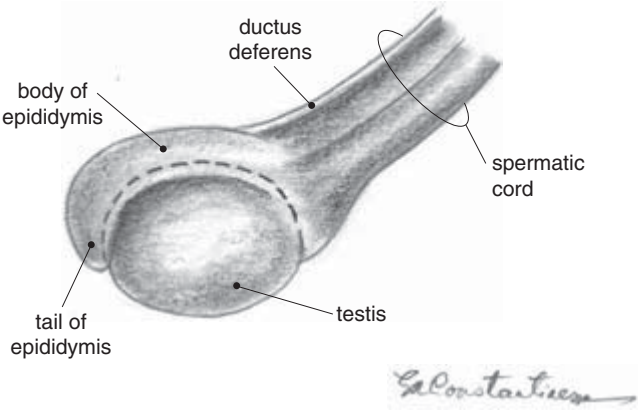

Figure 2.15. Testicle of the cat—medial aspect.

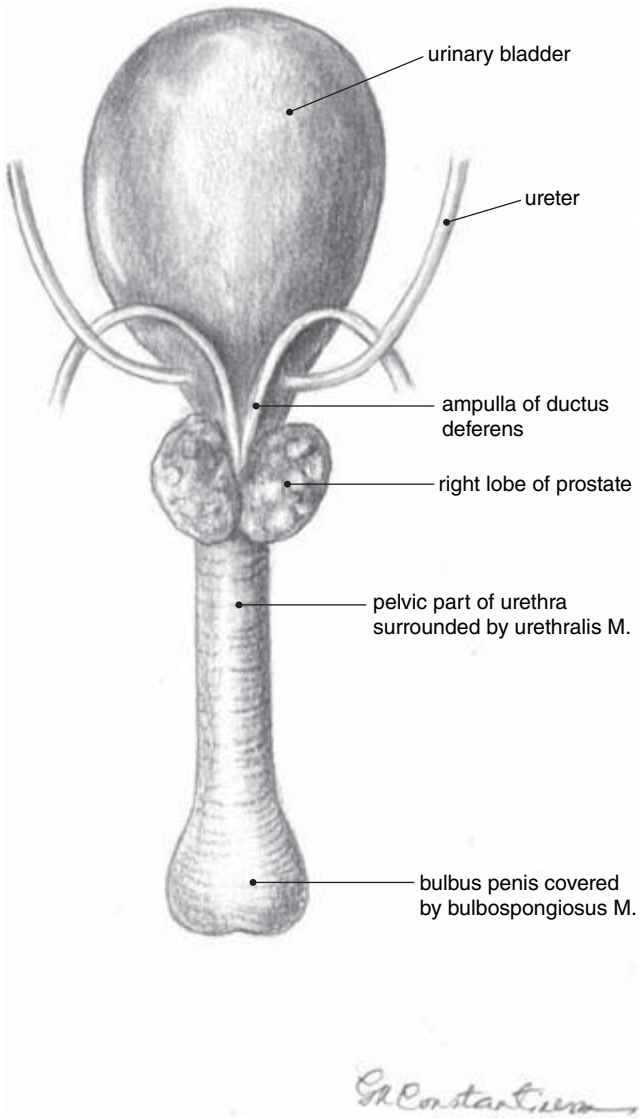

Figure 2.16. Accessory genital glands in the male dog—dorsal view.