Bovine Reproduction
“Let our cattle bear, without mishap and without loss”
Psalms 144: 14, New American Standard Bible
To Donna
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Gregg P. Adams  DVM, MS, PhD, Diplomate ACT  
Professor  
Veterinary Biomedical Sciences  
Western College of Veterinary Medicine  
University of Saskatchewan  
Saskatoon, Saskatchewan, Canada  

James Alexander  DVM  
Alexander Veterinary Services  
Bentonia, Mississippi, USA  

Divakar J. Ambrose  MVSc, PhD, PAg, PAS  
Dairy Research Scientist, Livestock Research Branch  
ARD Professor, University of Alberta  
Edmonton, Alberta, Canada  

Marcel Amstalden  DVM, PhD  
Associate Professor  
Department of Animal Science  
Texas A&M University  
College Station, Texas, USA  

Mark L. Anderson  DVM, PhD, Diplomate ACVP  
Professor  
School of Veterinary Medicine  
University of California  
Davis, California, USA  

Frank W. Austin  DVM, PhD  
Professor  
Department of Pathobiology and Population Medicine  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA  

Jennifer P. Barfield  PhD  
Department of Biomedical Sciences  
Animal Reproduction and Biotechnology Laboratory  
Colorado State University  
Fort Collins, Colorado, USA  

Callie V. Barnwell  PhD  
Department of Animal Science  
North Carolina State University  
Raleigh, North Carolina, USA  

Albert Barth  DVM, MS, Diplomate ACT  
Large Animal Clinical Sciences  
Western College of Veterinary Medicine  
University of Saskatchewan  
Saskatoon, Saskatchewan, Canada  

Brittany Baughman  DVM, MS, Diplomate ACVP  
Mississippi Veterinary Diagnostic Laboratory  
Jackson, Mississippi, USA  

Wes Baumgartner  DVM, PhD, Diplomate ACVP  
Assistant Professor  
Department of Pathobiology and Population Medicine  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA  

Myra T. Blanchard  CLS, MS  
School of Veterinary Medicine  
University of California  
Davis, California, USA  

Patrick Blondin  PhD  
L’Alliance Boviteq Inc.  
St-Hyacinthe, Quebec, Canada  

Gabriel A. Bó  DVM, PhD  
Instituto de Reproducción Animal  
Córdoba (IRAC)  
Cno. General Paz – Paraje Pozo del Tigre- 
Estación General Paz  
CP 5145 Córdoba, Argentina  

Kenneth Bondioli  PhD  
Associate Professor  
School of Animal Sciences  
Louisiana State University  
Baton Rouge, Louisiana, USA  

Nadine Bouchard  BSc  
L’Alliance Boviteq Inc.  
St-Hyacinthe, Quebec, Canada  

Contributors
James A. Brett DVM
Associate Clinical Professor
Department of Pathobiology and Population Medicine
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA

Leonardo F.C. Brito DVM, PhD, Diplomate ACT
ABS Global Inc.
DeForest, Wisconsin, USA

Amanda J. Cain BS
Graduate student DVM/PhD
Department of Pathobiology and Population Medicine
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA

Leticia E. Camacho MS
Graduate Research Assistant
Department of Animal Sciences
North Dakota State University
Fargo, North Dakota, USA

Butch Cargile DVM, MS
Nutrition and Management Consultant
Progressive Dairy Solutions
Twin Falls, Idaho, USA

Celina Checura MV, MS, PhD
Department of Medical Sciences
School of Veterinary Medicine
University of Wisconsin-Madison
Madison, Wisconsin, USA

David Christiansen DVM
Assistant Clinical Professor
Department of Pathobiology and Population Medicine
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA

Elizabeth A. Coffman DVM, Diplomate ACT
Theriogenology Resident
Department of Veterinary Clinical Sciences
College of Veterinary Medicine
Ohio State University
Columbus, Ohio, USA

Jill Colloton DVM
Bovine Services, LLC
Edgar, Wisconsin, USA

Catherine Dolbec MSc
L’Alliance Boviteq Inc.
St-Hyacinthe, Quebec, Canada

Tyler M. Dohlman DVM
Resident, Theriogenology
Department of Veterinary Diagnostics and Production Animal Medicine
Lloyd Veterinary Medicine Center
College of Veterinary Medicine
Ames, Iowa, USA

Maarten Drost DVM, Diplomate ACT
Professor Emeritus
College of Veterinary Medicine
University of Florida
Gainesville, Florida, USA

Misty A. Edmondson DVM, MS, Diplomate ACT
Associate Professor
Department of Clinical Sciences
College of Veterinary Medicine
Auburn University
Auburn, Alabama, USA

J. Lannett Edwards PhD
Professor and Graduate Director
Department of Animal Science
University of Tennessee
Knoxville, Tennessee, USA

Phillip H. Elzer PhD
Professor and Head
Department of Veterinary Science
Louisiana State University
Baton Rouge, Louisiana, USA

Terry J. Engelken DVM, MS
Associate Professor
Department of Veterinary Diagnostics and Production Animal Medicine
Lloyd Veterinary Medicine Center
College of Veterinary Medicine
Ames, Iowa, USA

Charles T. Estill VMD, PhD, Diplomate ACT
Associate Professor
Department of Clinical Sciences
College of Veterinary Medicine
Oregon State University
Corvallis, Oregon, USA

Charlotte E. Farin PhD
Professor
Department of Animal Science
North Carolina State University
Raleigh, North Carolina, USA

William T. Farmer PhD
Department of Animal Science
North Carolina State University
Raleigh, North Carolina, USA
Julie Gard DVM, PhD, Diplomate ACT  
Associate Professor  
Department of Clinical Sciences  
College of Veterinary Medicine  
Auburn University  
Auburn, Alabama, USA

Danielle Glynn RVT  
College of Veterinary Medicine  
Purdue University  
West Lafayette, Indiana, USA

Gretchen Grissett DVM  
Clinical Resident  
Department of Clinical Sciences  
College of Veterinary Medicine  
Kansas State University  
Manhattan, Kansas, USA

Daniel L. Grooms DVM, PhD, Diplomate ACVM  
Professor  
College of Veterinary Medicine  
Department of Large Animal Clinical Sciences  
Michigan State University  
East Lansing, Michigan, USA

Sue D. Hagius BS  
Department of Veterinary Science  
Louisiana State University  
Baton Rouge, Louisiana, USA

Peter J. Hansen PhD  
Distinguished Professor and L.E. “Red” Larson Professor  
Department of Animal Sciences  
University of Florida  
Gainesville, Florida, USA

John F. Hasler PhD  
Bioniche Animal Health, Inc.  
Laporte, Colorado, USA

W. Mark Hilton DVM, Diplomate ABVP – Beef Cattle Practice  
Clinical Professor, Beef Production Medicine  
College of Veterinary Medicine  
Purdue University  
West Lafayette, Indiana, USA

Richard M. Hopper DVM, Diplomate ACT  
Professor  
Department of Pathobiology and Population Medicine  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Carla Huston DVM, PhD, Diplomate ACVPM  
Department of Pathobiology and Population Medicine  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Marianna M. Jahnke MS  
Lecturer  
Veterinary Diagnostic and Production Animal Medicine Department  
College of Veterinary Medicine  
Iowa State University  
Ames, Iowa, USA

Ram Kasimanickam BVSc, DVSc, Diplomate ACT  
Associate Professor  
Department of Veterinary Clinical Sciences  
College of Veterinary Medicine  
Washington State University  
Pullman, Washington, USA

John P. Kastelic DVM, PhD, Diplomate ACT  
Professor, Cattle Reproductive Health – Theriogenology  
Head, Department of Production Animal Health  
University of Calgary, Faculty of Veterinary Medicine  
Calgary, Alberta, Canada

E. Heath King DVM, Diplomate ACT  
Assistant Clinical Professor  
Department of Pathobiology and Population Medicine  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Tom Kroetsch MSc  
The Semex Alliance  
Guelph, Ontario, Canada

G. Cliff Lamb PhD  
Assistant Director and Professor  
North Florida Research and Education Center  
University of Florida  
Marianna, Florida, USA

Robert L. Larson DVM, PhD, Diplomate ACT, ACN, ACVPM (Epidemiology)  
Professor, Production Medicine Clinical Sciences  
College of Veterinary Medicine  
Kansas State University  
Manhattan, Kansas, USA

Jim W. Lauderdale PhD  
Lauderdale Enterprises  
Augusta, Michigan, USA

Fred Lehman DVM, MABA, Diplomate ACT, PMP  
Overland Park, Kansas, USA

Caleb O. Lemley PhD  
Assistant Professor  
Department of Animal and Dairy Sciences  
Mississippi State University  
Starkville, Mississippi, USA
Robert Linford  DVM, PhD, Diplomate ACVS  
Professor  
Department of Clinical Sciences  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Herris Maxwell  DVM, Diplomate ACT  
Clinical Professor  
Department of Clinical Sciences  
College of Veterinary Medicine  
Auburn University  
Auburn, Alabama, USA

Reuben J. Mapleton  DVM, PhD, Diplomate ACT  
Distinguished Professor  
Department of Large Animal Clinical Sciences  
Western College of Veterinary Medicine  
University of Saskatchewan  
Saskatoon, Saskatchewan, Canada

Richard W. Meiring  DVM, Diplomate ACVPM  
Clinical Professor  
Department of Pathobiology and Population Medicine  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Vitor R.G. Mercadante  DVM, MS  
Research Assistant  
North Florida Research and Education Center  
University of Florida  
Marianna, Florida, USA

Rory Meyer  DVM, Diplomate ACT  
Staff Veterinarian  
Alta Genetics  
Watertown, Wisconsin, USA

Cathleen Mochal-King  DVM, MS, Diplomate ACVS  
Assistant Clinical Professor  
Department of Clinical Sciences  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Harry Momont  DVM, PhD, Diplomate ACT  
Professor  
Department of Medical Sciences  
School of Veterinary Medicine  
University of Wisconsin-Madison  
Madison, Wisconsin, USA

Quinesha P. Morgan  PhD  
Department of Veterinary Science  
Louisiana State University  
Baton Rouge, Louisiana, USA

John L. Myers  DVM, Diplomate ACT  
Pecan Drive Veterinary Services  
Vinita, Oklahoma, USA

Ben Nabors  DVM  
Department of Clinical Sciences  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Colin Palmer  DVM, MVetSc, Diplomate ACT  
Professor, Theriogenology  
Department of Large Animal Clinical Sciences  
Western College of Veterinary Medicine  
University of Saskatchewan  
Saskatoon, Saskatchewan, Canada

Thomas Passler  DVM, PhD, Diplomate ACVIM  
Assistant Professor  
Departments of Clinical Sciences and Pathobiology  
College of Veterinary Medicine  
Auburn University  
Auburn, Alabama, USA

Augustine T. Peter  BVSc, MVSc, MSc, PhD, MBA, Diplomate ACT  
Professor  
Veterinary Clinical Sciences  
College of Veterinary Medicine  
Purdue University  
West Lafayette, Indiana, USA

Carlos A. Risco  DVM, Diplomate ACT  
Professor and Chair  
Large Animal Clinical Sciences  
College of Veterinary Medicine  
University of Florida  
Gainesville, Florida, USA

Edwin G. Robertson  DVM  
Harrogate Genetics International  
Harrogate, Tennessee, USA

Peter L. Ryan  PhD, Diplomate ACT (honorary)  
Associate Provost  
College of Veterinary Medicine  
Mississippi State University  
Starkville, Mississippi, USA

Swanand Sathe  BVSc, MVSc, MS, Diplomate ACT  
Assistant Professor, Theriogenology  
Lloyd Veterinary Medical Center  
College of Veterinary Medicine  
Iowa State University  
Ames, Iowa, USA

F. Neal Schrick  PhD  
Professor and Chair  
Department of Animal Science  
University of Tennessee  
Knoxville, Tennessee, USA
Contributors

Clare M. Scully  DVM, MA
Theriogenology Resident
Department of Clinical Sciences
College of Veterinary Medicine
Oregon State University
Corvallis, Oregon, USA

Clifford F. Shipley  DVM, Diplomate ACT
Attending Veterinarian for Agricultural Animals
Agricultural Animal Care and Use Program
College of Veterinary Medicine
University of Illinois
Urbana, Illinois, USA

Katharine M. Simpson  DVM, MS, Diplomate ACVIM
Clinical Assistant Professor
College of Veterinary Medicine
Ohio State University
Columbus, Ohio, USA

Jaswant Singh  BVSc, MVSc, PhD
Professor
Veterinary Biomedical Sciences
Western College of Veterinary Medicine
University of Saskatchewan
Saskatoon, Saskatchewan, Canada

David R. Smith  DVM, PhD, Diplomate ACVPM (Epidemiology)
Mikell and Mary Cheek Hall Davis Endowed Professor
Department of Pathobiology and Population Medicine
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA

Jack D. Smith  DVM, Diplomate ACT
Associate Professor
Department of Pathobiology and Population Medicine
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA

Ricardo Stockler  DVM, MS, Diplomate ABVP (Dairy)
Dairy Production Medicine Clinician
Veterinary Medicine Teaching and Research Center (VMTRC)
University of California Davis
Tulare, California, USA

Jeffrey L. Stott  MS, PhD
Professor
School of Veterinary Medicine
University of California
Davis, California, USA

Robert N. Streeter  DVM, MS, Diplomate ACVIM
Associate Professor
Department of Veterinary Clinical Sciences
Center for Veterinary Health Sciences
Oklahoma State University
Stillwater, Oklahoma, USA

William S. Swecker Jr DVM, PhD,
Diplomate ACVN
Professor and Associate Department Head
Large Animal Clinical Sciences
Virginia-Maryland Regional College of Veterinary Medicine
Blacksburg, Virginia, USA

Ahmed Tibary  DVM, MS, PhD,
Diplomate ACT
Professor
Department of Clinical Sciences
College of Veterinary Medicine
Washington State University
Pullman, Washington, USA

Mike Thompson  DVM, Diplomate ACT
Willow Bend Animal Clinic
Holly Springs, Mississippi, USA

Dan Tracy  DVM, MS
Technical Services Veterinarian
Multimin USA
Auburn, Kentucky, USA

Shelley L. Underwood PhD
L’Alliance Boviteq Inc.
St-Hyacinthe, Quebec, Canada

Rhonda C. Vann PhD
Research Professor
Brown-Loan Experiment Station
Raymond, Mississippi, USA

Patrick Vincent PhD
L’Alliance Boviteq Inc.
St-Hyacinthe, Quebec, Canada

Kimberly A. Vonnahme PhD
Associate Professor
Department of Animal Sciences
North Dakota State University
Fargo, North Dakota, USA

Kevin Walters  DVM, Diplomate ACT
Assistant Clinical Professor
Department of Pathobiology and Population Medicine
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA

Gary Warner  DVM
Bovine Division
Elgin Veterinary Hospital
Elgin, Texas, USA

James K. West  DVM, MS
Armbrust Professor of Clinical Medicine
Director of Embryo Transfer Services
Iowa State University
Ames, Iowa, USA
Contributors

Brad J. White DVM, MS
Associate Professor
Department of Clinical Sciences
College of Veterinary Medicine
Kansas State University
Manhattan, Kansas, USA

Brian K. Whitlock DVM, PhD, Diplomate ACT
Associate Professor
Department of Large Animal Clinical Sciences
College of Veterinary Medicine
University of Tennessee
Knoxville, Tennessee, USA

Gary L. Williams PhD
Regents Fellow, Faculty Fellow and Professor
Animal Reproduction Laboratory
Department of Animal Science
Texas A&M University
Beeville, Texas, USA

Dwight F. Wolfe DVM, MS, Diplomate ACT
Professor
Department of Clinical Sciences
College of Veterinary Medicine
Auburn University
Auburn, Alabama, USA

Curtis R. Youngs PhD
Department of Animal Science
Iowa State University
Ames, Iowa, USA

Illustrators

Alison Anderson
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA
Chapter 76

Barbara DeGraves
Bowling Green, Kentucky, USA
Chapters 16, 17, and 18

Rachel Fishman
Class of 2017
College of Veterinary Medicine
Mississippi State University
Starkville, Mississippi, USA
Chapter 54

Mal Hoover
Medical Illustrator/Graphic Design Specialist
Kansas State University
Manhattan, Kansas, USA
Chapter 20

McRae Hopper
Starkville, Mississippi, USA
Chapters 47 and 53

Kathleen June Mullins
Germinal Dimensions
915 Allendale Ct
Blacksburg, Virginia, USA
Chapter 2

Rachel Oman DVM
Food Animal Medicine Resident
Oklahoma State University
Stillwater, Oklahoma, USA
Chapter 19

Tyla Barkley DVM
Ardmore Animal Hospital
Ardmore, Oklahoma, USA
Chapter 43
There is an old fable in which three penniless and hungry travelers come to a small town. Unsuccessful in finding work or even a handout, one concocts a novel plan. He goes to the middle of the village carrying three fist-sized rocks and announces with great aplomb that he is planning to make his famous “stone soup.” The skeptical but curious villagers gather. Well of course he needed a kettle and some water. The inquisitive villagers wondered if that was all. “Yes,” he replied, “but it is better with a little garnish to improve the flavor.” One villager thought that he could spare some carrots, another some potatoes, and a third some meat. This continued with virtually everyone in the village contributing. The result of course was a wonderful soup and everyone enjoyed a fine meal, while experiencing an object lesson in cooperation.

The story bears an ironic resemblance to the development of this text. The editor, like the plucky traveler, personally short on ability and resources but acutely aware of a need, enlisted the assistance of those who possessed both. Excellent reference texts were available on equine and small animal theriogenology, but a current bovine text was much needed. The goal was to produce a text that would service the needs of the veterinary student and bovine practitioner, as well as the graduate student and resident.

While I would readily admit that this text could be improved with respect to the choices made vis-à-vis the organization of the book or the order of some chapters, I honestly do not believe that I could have done any better than the contributors selected. The authors of this text represent a wide array of specialties and educational and experiential backgrounds. I will forever be grateful for their assistance and immensely proud of their individual contributions. I would also like to acknowledge the efforts of my graduate assistant, Amanda Cain, who in addition to contributing a chapter, prepared the glossary of terms and index. Likewise, I would like to thank everyone at Wiley for their help. Erica Judisch, the commissioning editor, was so very helpful in guiding a novice through the early phases of this book. Susan Engelken, the managing editor for this book, was incredible to work with, always patient, always competently and quickly responding to any issue or concern. Dr Joe Phillips, the copy editor Wiley enlisted, deserves the credit for identifying errors that I missed and enhancing the readability of this text.

Additionally, I would like to acknowledge on a personal level those who have been so important to me from the standpoint of my life and career. First of all I would thank my parents, Lewis and Barbara Hopper, who were always supportive of my goals and aspirations, and my family, wife Donna and children Tricia (her husband Caleb), McRae, and Molly, who I will always consider to be my greatest accomplishments. Also, as this goes to press I can announce a wonderful addition, a granddaughter by the name of Abigail Betty Butts.

I would also be remiss to not use this opportunity to thank some of my professors and instructors at Auburn who were so influential to me professionally and important to me personally. First on this list would be Dr Robert Hudson, but also Drs Bob Carson, Howard Jones, Donald Walker, Ram Purohit, John Winkler, and Howard Kjar. Likewise, I need to thank my colleagues at Mississippi State who have alternatively both encouraged and tolerated me through this long process.

I sincerely hope the reader finds this text useful.

Richard M. Hopper
Starkville, Mississippi
The Bull
|    | *Ben Nabors and Robert Linford* |   |
| 2. | Endocrine and Exocrine Function of the Bovine Testes | 11 |
|    | *Peter L. Ryan* |   |
| 3. | Thermoregulation of the Testes | 26 |
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|    | *Leonardo F.C. Brito* |   |
Introduction
The anatomy of the reproductive system of the bull can be grouped functionally into the components of production, transport, and transfer of spermatozoa (Figure 1.1).

Production
The testicular parenchyma contains the cellular machinery for spermatogenesis and steroid production (Figure 1.2). The parenchyma is arranged in indistinct lobules of convoluted tubules called seminiferous tubules. The seminiferous tubules contain the spermatogonia from which the mature sperm cells develop. Sertoli cells are also located within the lumen of the seminiferous tubules. The Leydig cells that are responsible for the production of the male hormone testosterone are located between the seminiferous tubules in the interstitial space.1

Testes
The testes are housed in the scrotum. The scrotum is suspended between the thighs in the inguinal region. The scrotum consists of external and internal layers. The external layer is made up of the skin, tunica dartos, superficial perineal fascia, external spermatic fascia, cremasteric fascia, internal spermatic fascia, and parietal vaginal tunic. The skin of the scrotum and tunica dartos muscle are closely adhered whereas the fascial layers are easily separated from the skin and the parietal vaginal tunic as in a closed castration technique. The coverings of the testicle itself consist of the visceral vaginal tunic and the tunica albuginea.2 The visceral vaginal tunic is the innermost layer of the vaginal tunic, an outpouching of abdominal peritoneum that passes through the inguinal canal into the scrotal sac. The potential space between the parietal and visceral vaginal tunic is the vaginal cavity (Figure 1.3). The purpose of the vaginal cavity is for temperature regulation of the testicle by raising it closer to the body through contraction of the tunica dartos and cremaster muscles. The tunica albuginea is a thick fibrous capsule that covers the testicle and maintains the testicular contents under pressure.3 Internally the tunica albuginea forms the axially positioned mediastinum testis from which connective tissue septa divide the testis into indistinct lobules. This connective tissue framework supports the vasculature, nerves, parenchyma, and tubular system of the testicle. The scrotum of the bull is pendulous due to the dorsoventral orientation of the testes contained within.1

Spermatic cord
The spermatic cord includes the ductus deferens, vasculature, lymphatic vessels, and nerves of the testicle and epididymis.4 Essentially the spermatic cord consists of all the tissue within the vaginal tunic so it extends from the vaginal ring within the abdominal cavity to the testicle.5

Transport
Spermatozoa are transported from the testicles through a tubular system consisting of the convoluted seminiferous tubules, straight seminiferous tubules, rete testis, efferent ductules, epididymis, ductus deferens, and urethra (Figure 1.4). The tubular system allows for maturation and storage of spermatozoa and provides fluid to ease movement of the spermatozoa.

Tubular transport system
The convoluted seminiferous tubules are the location of the spermatogenic process: the development of spermatogonia to primary spermatocytes, to spermatids, and finally to spermatozoa.1 This process occurs within the wall of the seminiferous tubule. Specific regions of the...
tubule are devoted to a particular stage of development, so that each stage can be identified by specific histological techniques. Upon the completion of spermiogenesis, the spermatozoa are released into the lumen of the convoluted seminiferous tubule to begin transit through the straight seminiferous tubule. The straight seminiferous tubule is simply the connection between the convoluted seminiferous tubule and the rete testis. The rete testis is a “network of irregular labyrinth spaces and interconnected tubules.” The rete testes are located within the mediastinum testis connecting the seminiferous tubules to the efferent ducts that exit the testicle at the extremitas capitata (head). The efferent tubular system continues as the epididymis on the external surface of the testis (Figure 1.5). The epididymis is divided into a head, a body located on the medial surface, and a tail located at the distal extremitas caudate.

Ductus deferens

The ductus deferens is attached to the medial side of the testicle by the mesoductus. The ductus deferens is the continuation of the tail of the epididymis (Figure 1.6). The ductus deferens enters the abdominal cavity through the inguinal canal, crosses the lateral ligament of the bladder, and before it ends at the colliculus seminalis in the urethra it widens into the ampulla.
Transfer

The transfer of spermatozoa from the bull to the cow is achieved by the process of intromission, which requires erection of the penis and ejaculation of sperm. The pertinent anatomy for these processes to occur includes the penis, the musculature of the penis, the vasculature, and the innervations.

Penis

The penis of the bull can be divided into a root, body, and glans penis (Figure 1.7). The root of the penis can be defined as the origin of the erectile tissue that comprises the penis as well as the origin of the muscles of the penis. The erectile tissue that makes up the bulk of the penis is the corpus cavernosum. The paired corpora cavernosa originate separately on each side of the ischiatic arch medial to the ischiatic tuberosity. These individual limbs are termed the crura of the penis. The crura pass ventromedially until they join to form the body of the penis. The corpus spongiosum is the erectile tissue that surrounds the urethra. The origin of the corpus spongiosum, called the bulb of the penis, originates between the crura along the midline of the ischiatic arch. Therefore the root of the penis is composed of the crura (corpus cavernosum) and the bulb (corpus spongiosum).

The erectile tissue is enclosed in the dense outer covering of the tunica albuginea. The tunica albuginea is a dense covering that consists of an inner circular layer and outer longitudinal layer of fibers. The inner circular layer sends trabecular scaffolds throughout the corpus cavernosum for the attachment of the cavernous endothelium.

Located caudal to the root of the penis are the muscles of the penis: the ischiocavernosus, bulbospongiosus, and retractor penis muscles (Figure 1.8). The paired ischiocavernosus muscles originate on the medial surfaces of the ischiatic tuberosities overlying the crura; the muscle fibers pass ventromedially in a “V” fashion until ending a short distance on the body of the penis. During erection the ischiocavernosus muscle contracts pushing blood from the cavernous spaces of the crura into the body of the penis. The bulbospongiosus muscle lies caudal to the bulb of the penis, originating along the ischiatic arch and continuing until the junction of the crura. The bulbospongiosus muscle fibers run transversely across the bulb of the penis and contraction of this muscle results in propulsion of the ejaculate through the urethra. The retractor penis muscle extends from the caudal vertebrae and internal anal sphincter to insert distally to the sigmoid flexure. These paired muscles relax during erection allowing the penis to extend from the prepuce and contract during quiescence, retracting the penis into the sheath.

The body of the penis begins where the two crura meet distally to the ischiatic arch; it extends cranially, along the ventral body wall to become at the mid-ventral abdomen the free part of the penis (Figure 1.9). The body of the penis is bent in an “S” shape called the sigmoid flexure. The proximal bend of the sigmoid flexure opens caudally and is located near the scrotum. The distal bend is opened cranially and the short suspensory ligaments of the penis attach the penis to the ventral surface of the ischiatic arch. The glans penis is a small restricted region at the tip of the free part of the penis (Figure 1.10). The free part of the penis is the distal extent from the attachment of the internal lamina of the prepuce to the glans penis. The free end of the penis is twisted in a counterclockwise direction as viewed from the right side, illustrated by the
oblique direction of the raphe of prepuce continued as the raphe of the penis to the urethral process (Figure 1.11). The twist of the free end of the penis is due to the attachment of the apical ligament. The apical ligament of the penis is formed by the longitudinal fibers of the tunica albuginea leaving the body of the penis just distal to the sigmoid flexure and reattaching near the apex of the penis.8

The prepuce of the penis is composed of an external and internal fold or lamina8 (Figure 1.12). The external lamina is the haired outer fold of skin attached to the ventral abdomen.

The haired skin terminates at the preputial orifice where the external fold turns inward to line the preputial cavity as the internal lamina. The internal lamina serves to attach the external lamina to the penile epithelium.

Blood supply

Before ejaculation can occur the testis must produce spermatozoa. This requires an adequate blood supply for the metabolic demands of cellular division for spermatogenesis and steroidogenesis. The arterial blood supply to each testis is provided by a testicular artery, a direct branch of the abdominal aorta arising caudal to the renal arteries. The testicular artery crosses the lateral abdominal wall and then passes ventrally through the inguinal canal.10

As the testicular artery approaches the testis it begins to spiral with the nearby tortuous pampiniform plexus of the testicular vein forming a vascular cone. This arterial/venous arrangement is an effective thermoregulatory apparatus.11

An adequate blood supply to the penis and associated muscles is required for the processes of erection, ejaculation, and tissue maintenance. This comes by way of the internal iliac artery. The internal iliac artery is a direct continuation of the abdominal aorta at the entrance to the pelvic cavity. The umbilical artery, a branch of the internal iliac, supplies the ductus deferens and the bladder.4 The prostatic artery leaves the internal iliac and supplies the prostate, vesicular glands, ductus deferens, ureter, and urethra.4 As the internal iliac continues through the pelvic cavity it divides into the caudal gluteal and internal pudendal.10 The internal pudendal gives off the ventral perineal artery, urethralis artery, and continues as the artery of the penis.10 The artery of the penis gives off the artery of the bulb of the penis, which supplies the bulbospongiosus muscle and the cavernous spaces of the corpus spongiosum12 (Figure 1.13). The deep artery of the penis is another branch of the artery of the penis that enters the crus of the penis and supplies the erectile tissue, the corpus cavernosum.12 After the deep artery branches off, the artery of the penis continues as the dorsal artery of the penis which passes along the dorsal aspect of the penis toward the glans penis and prepuce. It is responsible for maintenance of penile tissue during quiescence.13
Nervous supply

The innervation of the external genitalia of the bull consists of the pudendal nerve and its branches. The pudendal nerve carries motor, sensory, and parasympathetic nerve fibers. The pudendal nerve passes through the pelvic cavity medial to the sacrosciatic ligament and divides as it approaches the lesser ischiatic notch of the pelvis into proximal and distal cutaneous branches supplying the skin of the caudal hip and thigh. The pudendal nerve continues through the ischiorectal fossa, terminating in a preputial branch, a scrotal branch, and finally the dorsal nerve of the penis. The pelvic nerve provides parasympathetic innervations from the sacral plexus. The hypogastric nerve contributes sympathetic fibers from the caudal mesenteric plexus to the genital system (Figure 1.14).

Accessory glands

The accessory genital glands of the bull include the vesicular gland, ampulla of the ductus deferens, and the prostate and bulbourethral glands (Figure 1.15). The bilateral vesicular gland is the largest accessory gland in the bull and contributes the greatest volume to the ejaculate. It is a lobated gland of firm consistency. It lies dorsal to the bladder and lateral to the ureter and ampulla of the ductus deferens. The body of the prostate lies dorsal to the urethra between and caudal to the vesicular glands. The disseminate part of the prostate is concealed in the wall of the urethra and covered by the urethral muscle. The ampulla, vesicular glands, and prostate all empty their contents into the urethra through the colliculus seminalis. The bilateral bulbourethral gland lies on each side of the median plane dorsal to the urethra; it is mostly covered by the bulbospongiosus muscle. Its duct opens into the urethral recess. The presence of this structure makes it difficult to pass a catheter retrograde into the bladder.

References


Introduction

The normal bovine male reproductive system consists of paired testes retained within a sac or purse-like structure known as the scrotum, which is formed from the outpouching of skin from the abdomen and consists of complex layers of tissue. The testes are accompanied by a number of supporting structures including spermatic cords, accessory sex glands (prostate, bulbourethral, paired vesicular glands), penis, prepuce, and the male ductal system. The testicular duct system is extensive and comprises the vas efferentia found within the testes, the epididymis, vas deferens, and the urethra, all of which are located external to the testes. The reader is referred to the excellent chapter on the anatomy of the reproductive system of the bull in this book (Chapter 1). The primary functions of the testes are to produce male gametes (spermatozoa) and the endocrine factors, such as steroid (testosterone) and protein hormones (inhibin, insulin-like peptide 3), that help regulate reproductive function of the bull in concert with hormonal secretions from the hypothalamus (gonadotropin-releasing hormone) and pituitary glands (luteinizing hormone, follicle-stimulating hormone). The testes consist of parenchymal tissue that supports the interstitial tissue and includes the steroid-producing Leydig cells, vascular and lymphatic system, and the seminiferous tubules within which the germinal tissue develops with the support of the nurse cells more commonly known as Sertoli cells. Chapter 4 discusses in detail the endocrine factors responsible for testicular development and initiation of spermatogenesis in the bull, and thus this chapter focuses more on the regulation and function of the adult testes. This chapter will not undertake a treatise of those conditions that disrupt testicular function but rather will focus, as practically as is possible, on what is known of the endocrine and exocrine function of the bovine testes. Much of the endocrine and exocrine function of the testes is similar across mammalian species, and where specific information is absent for the bovine, examples will be given from other domestic species when possible. It has not been possible to cite the many significant contributions to the field of endocrine and exocrine function of the testes. Thus, where and when possible, the reader is referred to selected citations for additional reading.

Historical perspective

It has been evident for many centuries that the testes exercise control over the characteristics of the male body. The results of castration in domestic animals and human males made this very clear, but provided no clues as to the mechanism of control. Pritchard noted from Assyrian records dating some 15 centuries BC that the castration of men was used as punishment for sexual offenders, which suggests that the effect of castration on fertility and behavior was recognized at that time. Knowledge of the effects of castration of livestock dates back to the Neolithic Age (c. 7000 BC) when animals were first thought to have been domesticated. The effects of castration were understood by Aristotle (300 BC) who provided very detailed and clear descriptions of testicular anatomy and function. It was not until the seventeenth century that a detailed account of testicular and penile anatomy was presented by Regnier de Graaf in a treatise on the male reproductive organs. De Graaf indicated the existence of the seminiferous tubules and suggested that the production of the fertile portion of the semen occurred in the testes. The first microscopic examination of the testes was undertaken by Antonie van Leeuwenhoek in 1667 where he demonstrated and reported the presence of germ cells in the seminal fluid.

Detailed study of the testis began in the mid-nineteenth century. In 1840, Albert von Kölliker discovered that spermatozoa develop from cells residing in the testicular (seminiferous) tubules. This major discovery was followed by Franz Leydig’s description of the microscopic characteristics of the interstitial cells. Later, Enrico Sertoli, an Italian scientist, correctly described the columnar cells running from the basement membrane to the lumen of the testis.
The testis

The bovine testes are paired, capsulated, ovoid-like structures located in the inguinal region and suspended in a pendulous scrotum away from the abdominal wall. The proximal relationship of the testes to the abdominal wall varies and may depend on season and ambient temperatures. The cremaster muscle plays an important role in thermal regulation of the testes. The size of the testis varies with breed, but typically the adult testis weighs 300–400 g and is about 10–13 cm long and 5–6.5 cm wide. The tough fibrous capsule covering each testis consists of three tissue layers: the outer layer, the tunica vaginalis; the tunica albuginea, which consists of connective tissue composed of fibroblasts and collagen bundles; and the inner layer, the tunica vaginalis, which supports the vascular and lymphatic systems. The capsule is the main structure that supports the testicular parenchyma, the functional layer of the testes, which consists of the interstitial tissue and seminiferous tubules. The interstitial tissue is found in the spaces between the seminiferous tubules and consists of clusters of Leydig cells, which are primarily responsible for steroid hormone biosynthesis and secretion, along with vascular and lymph vessels that supply the testicular parenchyma. The seminiferous tubules originate from the primary sex cords and contain the germinal tissue (spermatogonia, the male germ cell) and a population of specialized cells, the Sertoli cells, which not only support the production of spermatozoa but also form tight junctions with each other, creating one of the most important components of the blood–testis barrier. This structure prevents the entry of most large molecules and foreign material into the seminiferous tubules that may disrupt normal spermatogenesis. The most important substances synthesized by the testes and released into the vascular system are peptide and steroid hormones. However, fluids from the seminiferous tubules may pass into the interstitial tissue via the basal lamina, where they may enter the testicular lymphatic and vascular systems, or into the tubule lumen via the apical surface of the Sertoli cells.

The scrotum and spermatic cords

The scrotum is composed of an outer layer of thick skin and three underlying layers, the tunica dartos, the scrotal fascia, and the parietal vaginal tunica. The scrotal skin is extensively populated with numerous large adrenergic sweat and sebaceous glands that are highly endowed with thermal receptors and nerve fibers. Neural stimulation from the thermal receptors enables the tunica dartos, which consists of smooth muscle fibers and lies just beneath the scrotal skin, to contract and relax in response to changes in temperature gradients and facilitates the cooling of the scrotal surface via scrotal glandular sweating. Thus the scrotum plays an important role not only in housing and protecting the testes but also has a role in thermoregulation of the testes. The spermatic cord connects the testes to the body and provides access to and from the body cavity for vascular, neural, and lymphatic systems that support the testes. In addition, the spermatic cord accommodates the cremaster muscle, the primary muscle supporting the testes, and the pampiniform plexus, a complex and specialized venous network that wraps around the convoluted testicular artery. This vascular arrangement is very important in temperature regulation of the testicular environment. The plexus consists of a coil of testicular veins that provide a counter-current temperature exchange system: this is an effective mechanism whereby warm arterial blood entering the testes from the abdomen is cooled by the venous blood leaving the testes. Testicular arteries originate from the abdominal aorta and elongate as the testis migrates into the scrotum. In cattle and other large domestic ruminants these arteries are highly coiled, reducing several meters of vessel into as little as 10 cm of spermatic cord. The arterial coils and venous plexus are complex structures that form during fetal life in cattle. Because of the pendulous nature of the bovine scrotum, testicular cooling is facilitated by the contraction and relaxation of the cremaster muscle, which draws the testes closer to the abdominal wall during cooler ambient temperatures and vice versa during warmer temperatures. Figure 2.1 shows bright-field and thermal images of the bovine testes that demonstrate the change in temperature from the neck to the tip of the scrotum as the testes thermoregulate during elevated environmental temperatures. Scrotal and testicular thermoregulation is a complex process.