
MAMMARY GLAND

Contents

Anatomy
Growth, Development, Involution

Anatomy

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Introduction

Dramatic development of the mammary gland during gestation and subsequent differentiation of alveolar cells to allow onset of milk synthesis and secretion in precise correspondence with parturition is indeed a biological marvel. The initial mammary secretion produced after parturition is called colostrum. Along with the mature milk subsequently produced, these secretions provide the neonate with a spectrum of nutrients and antibodies necessary for good health and early development. Nutritionally, milk of all mammals contains variable amounts of proteins, carbohydrates and fats suspended in an aqueous medium. Thus, milk provides each of the major classes of nutrients to the neonate. Although there are species differences in milk composition, having the birth of the offspring and functionality of the mammary gland coincide is clearly critical.

The mammary gland evolved in all mammalian species to nourish the newborn young. However, in dairy animals such as the cow, through genetic selection and advances in milking technology, the mammary gland or udder now yields far more milk than a calf can consume and far greater quantities than the original organ was designed to accommodate. The selection for greater milk production and the removal of the product by machine milking impose unnatural stresses on the bovine udder. Thus, a basic understanding of mammary gland anatomy,
supporting structures, milk storage, and the processes involved with milk secretion, letdown and removal from the udder should aid in the development of procedures to harvest efficiently large volumes of milk from the mammary gland. For the placental mammals, the number of mammary glands varies markedly between classes and species. However, among those studied to date, each mammary gland has a teat or nipple. It is nonetheless worth remembering that only a few of the known mammals have been studied. Because the dairy cow is the most important milk-producing animal from an economic standpoint, the following information is primarily based on the bovine mammary gland. However, some consideration is given to differences in udder development between dairy ruminants.

**Gross Anatomy**

Regardless of the specific arrangement or number of mammary glands for a given mammal, milk synthesis and secretion requires development of a functionally mature mammary gland. In reproductively competent animals, the mature mammary gland consists of a teat or nipple, associated ducts which provide for passage of milk to the outside, and alveoli composed of epithelial secretory cells and supporting tissues. The epithelial cells are arranged to form the internal lining of the spherical alveoli and the cells synthesize and secrete all milk. Secretions are stored within the internal space of the hollow alveoli and larger ducts between suckling episodes.

Given the variety of mammals and the environmental niches occupied, it is no surprise that there is much variation in number of mammary glands, location and composition of secretions. Unlike common dairy species (cows, goats or sheep) aquatic mammals especially those in cold environments, produce milk very high in lipid content with relatively less lactose. High lipid content is essential for the suckling young to rapidly produce a layer of insulating fat to protect from the cold and to provide a source of metabolically derived water. This illustrates the relevance of lactation to provide a strategy for survival of offspring and reproductive success. Table 1 illustrates some of the variety in numbers and location of mammary glands in some common species.

Although the basics of mammary development are generally similar between species, the unique anatomy of the udder deserves special attention. In the cow and other ruminants, the mammary glands are clustered together into groups of two (goats or sheep) or four (cattle) mammary glands to form the udder. This arrangement provides a practical advantage. Because the mammary glands and teats are close together, the portion of the milking machine attached to the animal (teat-cups and teat cluster) can be relatively compact. For those not familiar with milking and management of modern dairy cows, the udder of a lactating Holstein cow for example can be rather massive. It is not unusual for a single cow to yield 25 kg or more of milk at a single milking. Combined with the mass of the udder tissues, this means that the connective tissue elements of the mammary glands have to support as much as 70 kg of tissue and stored milk just before milking. Given the ventral inguinal

<table>
<thead>
<tr>
<th>Order</th>
<th>Common name</th>
<th>Position of glands</th>
<th>Total glands</th>
<th>Opening per teat</th>
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<td></td>
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<td>Thoracic</td>
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<tr>
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<td>Domestic dog</td>
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<td>Perissodactyla</td>
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<td>Primate</td>
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(See Mammals.)
orientation of the udder, this is no trivial matter. Support is provided by strong, flat suspensory ligaments, which are attached to the pelvic bone and to the strong tendons of the abdominal muscles in the pelvic area.

In the cow and other ruminants, the udder is divided into two distinct halves, separated by the medial or median suspensory ligament, which provides most of the strength to hold the udder attached to the ventral body wall. Fibres of the lateral ligaments are continuous with the medial ligament but spread over either side of the udder so that it appears to be held in a sling of connective tissue. The medial ligament is somewhat elastic but the lateral ligaments are not. As the milk accumulates in the udder, the normally vertical orientation of the teats is lost as teats progressively protrude laterally. As animals age, excessive degradation of the fibres of the medial suspensory ligament can reduce its support capacity so that the udder becomes pendulous irrespective of time relative to milking. This can lead to difficulty with milking, i.e. problems maintaining attachment of teat cups as well as problems with teat injury and increased mastitis risk. The mammary glands of the udder are directly connected to the abdominal cavity only via passage through the inguinal canals. These are paired narrow oblique passages through the abdominal wall on either side of the midline, just above the udder. These canals allow passage of blood and lymph vessels and nerves to the udder.

Interestingly, the two halves of the udder can easily be dissected by cutting along the medial suspensory ligament, but there are no evident gross anatomical barriers between the front and rear glands (quarters) on either side of the udder. However, there are no direct connections between front and rear quarters. This is easily demonstrated following the injection of dye into the teat opening of one of the mammary glands. The dye stains only the tissue of the gland that is injected. This demonstrates that the mammary glands of the udder are independent. This is sometimes an advantage in some experimental situations since one mammary gland, or more often one udder half, can be given an experimental treatment with the opposite side serving as a control. This of course is only relevant if treatments can be shown to have only local effects.

The surface epidermis of the udder is composed of a stratified squamous epithelium and is covered with fine hair; however, the teats are hairless. Although the fore teats are usually longer than the rear teats, the capacity of the rear quarters is greater than that of the fore quarters; the ratio is approximately 60:40 (Figure 1).

The milking goat and milking sheep industry in the United States is not extensive, but in many parts of the world, these ruminants provide a much greater portion of the milk and dairy products in the local economy than dairy cows. In the case of dairy sheep, international protocols for evaluation of the udder were developed in the early 1980s. Using this standardized protocol, the udder structure and development in many dairy breeds has been systematically studied, especially related to machine milking. Production and milk composition are of course critical elements, but udder shape, teat length and size, and ease of machine milking are also important. Comparisons of external udder morphology and typology are used to standardize groups for machine milking, choice of animals to create a milking flock, or for culling of breeding animals. A number of researchers have suggested that an ideal udder of a lactating dairy sheep should have the following characteristics: (1) large volume with a globular shape and clearly defined teats, (2) soft and elastic tissues, with an evident, palpable gland cistern, (3) moderate udder height, no lower than the hock, (4) an apparent demarcation or groove between udder halves, and (5) teats of medium size (length and width), oriented in a nearly vertical position. When morphological traits are related to milk production, udder width and height are usually most consistently positively correlated with milk yield, confirming the importance of udder volume to milk yield. Interestingly, mammary cistern cavity size in some dairy sheep is nearly as large as that in cows, but of course, total gland size is much less than that in cows. This does, however, suggest that a proportionally greater amount of the milk obtained at milking from dairy ewes comes from cisternal storage rather than the alveolar storage. For example, differences in udder anatomy reflect greater daily milk yields in Lacaune (1.91 day⁻¹) sheep compared with Manchega (0.91 day⁻¹). Cisternal milk volume

![Figure 1](image-url) Cross-section diagram of the four quarters of the udder illustrating the gross anatomy.
and tissue area is more than doubled in Lacaune ewes but alveolar milk yields are essentially identical. This suggests that differences in udder anatomy are important determinants of lactation performance, and in this case, the cistern capacity is especially important. Moreover, it may be that the relative need for oxytocin release at milking might differ between dairy sheep breeds or perhaps between various dairy ruminants depending on the proportion of milk obtained from alveolar compared with cisternal storage. Patterns of milk flow during an individual milking can be characterized as occurring in one, two, or three or more peaks. However, there seems to be little if any relationship between the number of peaks and total milk yield. There are also apparent differences in patterns of oxytocin release between animals within breed as well as average differences in oxytocin release between breeds in response to machine milking. Regardless, it is difficult to define an optimal pattern of oxytocin release since some animals in both high-yielding and low-yielding breeds show minimal secretion of oxytocin but apparently normal milk yields. On the other hand, it is generally accepted that the volume of milk obtained during the primary phase of machine milking (prior to stripping) is greater in animals with more oxytocin release and if there is a bimodal release of oxytocin. These observations simply indicate that relationships among udder anatomy (alveolar vs. cisternal space), effectiveness of udder stimulation or milking to cause oxytocin release, and lactation performance are complex. Considering differences in the degree of selection for milk yield between breeds and differences between dairy ruminants (cows, goats, sheep and camels), this finding is hardly surprising.

In the dairy cow, each udder half is nearly independent and has its own vascular system, nerve supply and suspensory apparatus. Teats vary in shape from cylindrical to conical, and teat length is extremely variable. Both characteristics are independent of the shape or size of the udder. The teat skin is thin and devoid of sebaceous glands; however, supernumerary teats are commonly found, mainly on rear quarters. It has been estimated that 40% of cows have one or more supernumerary teats, which tend to be nonfunctional and should be removed because they can become infected with mastitis-causing bacteria.

Supporting Structures

The mammary gland is attached to the cow’s body wall under the pelvis by several strong, flat ligaments. Median and lateral suspensory ligaments provide the main support by forming a sling for the udder. The median suspensory ligaments are attached to the pelvic bone and to the tendons of the external oblique abdominal muscles in the region of the pelvis. These ligaments run parallel to each other and pass ventrally between the two udder halves, forming the intermammary groove, which separates the right and left quarters. These two layers of ligaments are joined by loose areolar connective tissue. The ligaments then separate to cover the anterior, posterior and ventral areas of the glandular tissue on each udder half but terminate at the base of the teats. The two median suspensory ligaments fuse with the two lateral suspensory ligaments at the anterior, posterior and ventral borders of each udder half (Figure 2).

The lateral ligaments of each udder half originate at the subpubic and prepubic tendons of the body wall and travel vertically, covering the outer sides of the mammary gland. Both the median and lateral suspensory ligaments have lateral branches (lamellar plates) that are inserted into the glandular tissue and become continuous with the connective tissue stroma supporting the lobules and lobes of parenchyma. The median ligaments are composed of both yellow elastic and fibrous connective tissues. Because of the elastic fibres, this ligament will stretch to absorb the shock as the cow moves about. In addition, the elasticity of these ligaments allows for the increase in udder size between milkings. As a cow matures and the udder increases in weight, the median suspensory ligaments often stretch, weaken and lose tone, allowing teats to point outward. The lateral ligaments are mainly composed of white fibrous connective tissue (collagen) and do not stretch as much; hence, they provide support in the absence of much elasticity. If both the median and lateral suspensory ligaments weaken, the udder becomes pendulous and is vulnerable to injury and mastitis.
Microscopic Anatomy

Synthetic and Secretory Tissues

Each of the four quarters functions as a separate gland within the udder and has its own milk secretory (parenchymal) tissues. The parenchyma is composed of alveoli, ducts and connective tissue; the latter supports and protects the delicate synthetic tissues. The millions of alveoli are the milk-producing units of the udder (see Mammary Gland: Growth, Development, Involution). These are microscopic globelike structures that are 50–250 μm in diameter, depending upon the volume of accumulated milk. A single layer of cuboidal to columnar epithelial cells lines the peripheral borders. Milk component precursors are absorbed from blood capillaries adjacent to the alveoli by mammary epithelial cells and converted into milk protein, lactose and milk fat. These components are released with other milk components into the lumen or interior of the alveolus for storage between milkings (Figure 3).

As milk accumulates in the alveolar luminal spaces between milkings, the pressure on the epithelial lining causes the secretory cells to become flattened. This signals the cells to stop synthesizing milk and releasing it into the lumen. In addition, capillaries surrounding the alveoli collapse because of the expanding luminal space, and the supply of milk precursors is reduced. Just prior to milking, approximately 60% of the milk synthesized by the udder is held in the alveoli and small ducts, and 40% is stored in the cisterns and large ducts. After milking, the alveolar lumina are no longer filled with milk, and secretory cells assume a columnar shape as the alveolar lining collapses; capillaries also assume their normal shape. A network of smooth muscle cells called myoepithelial cells immediately surrounds each alveolus. Myoepithelial cells also surround the small ducts, running in a lengthwise direction, and upon contraction they shorten the ducts, thereby increasing the diameter of the ductal lumina, which permits maximum milk flow.

The alveolar epithelial cells, limited by a cell membrane, contain the organelles necessary to convert precursors absorbed from the blood into milk constituents. The interior of the cell is composed of cytoplasm in which organelles such as the nucleus, rough endoplasmic reticulum, mitochondria and Golgi apparatus are dispersed. The portions of the cytoplasm adjacent to the basement membrane and near the nucleus are occupied by parallel cisternae of rough endoplasmic reticulum (endoplasm). The Golgi apparatus is located in the apical cytoplasm near the alveolar lumen and is composed of parallel cisternae of smooth-surfaced endoplasmic reticulum with terminal swellings that pinch off as casein-containing secretory vesicles. Milk fat droplets and secretory vesicles populate the apical cytoplasm, and microtubules are oriented perpendicular to the plasma membrane to guide the flow of secretory products toward the alveolar lumen. Mitochondria and free ribosomes are found throughout the cytoplasm (Figure 4).

Milk protein, most of which is casein, is composed of amino acids that are taken up by cells

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Figure 3 (A) Diagram of a mammary quarter illustrating the glandular tissue (alveoli are drawn out of scale), ducts, gland and teat cisterns, and teat canal. (B) Diagrammatic cross-section of an alveolus illustrating mammary epithelial cells, myoepithelial cells and capillary network.

Figure 4 Diagram of an alveolar epithelial cell typical of the lactating bovine mammary gland illustrating an extensive rough endoplasmic reticulum (R) and numerous casein-containing Golgi secretory vesicles (G) typical of the active milk-producing cell. Other structures include mitochondria (M), microtubules (Mt), nucleus (N), microvilli (Mv), and myoepithelial cells (My). The casein micelles (Cm) and lipid droplets (L) are synthesized within the cell cytoplasm and released into the alveolar lumen for storage between milkings.
from the blood. Casein is synthesized in the rough endoplasmic reticulum and transported to the Golgi apparatus, where it is concentrated and packaged in secretory vesicles for export from the cell to the alveolar lumen. Lactose is synthesized in the Golgi apparatus and is secreted from the cells in the same vesicles that transport casein. Calcium, magnesium and other ions also are secreted via secretory vesicles originating from the Golgi apparatus. Milk fat is synthesized in areas of the cytoplasm occupied by rough endoplasmic reticulum. The size of fat droplets increases from the basal to apical cytoplasm, and many small droplets probably coalesce to form larger droplets. During secretion, the droplets push through the apical cell membrane and are pinched off and released into the lumen, with each droplet limited by a unit membrane. For a more complete discussion of component synthesis and secretion as well as an electron micrograph of a lactating cell, see Milk Biosynthesis and Secretion: Secretion of Milk Constituents.

The alveoli are drained by small ducts that possess some synthetic activity. Some alveoli have a common opening into a duct, or they may open directly into other alveoli. A cluster of alveoli separated from other clusters of alveoli by fibrous connective tissue is referred to as a lobule, and the ducts draining alveoli converge into a common larger intralobular duct. A cluster of lobules forms a lobe that is drained by a common interlobular duct, and the lobes make up the glandular tissue of a quarter. Each lobe is surrounded by fibrous connective tissue to separate it from other lobes. Within each lobe, the intralobular ducts merge to form a single intralobar duct, which becomes the interlobar duct as it emerges from the lobe. This combination of alveoli and the tubular ducts supported in a connective tissue framework (stroma) classifies each quarter as a tubuloalveolar gland.

The ducts draining lobes of milk-producing tissues are composed of a double-layered epithelium and are surrounded by myoepithelial cells. These ducts converge into larger ducts that eventually drain into the collecting spaces (cisterns) near the ventral surface of the quarter. From five to 20 large ducts empty into the gland cistern of the udder. Gland cisterns are extremely variable in size and shape within an udder, and hold 100–2000 ml of milk. The shape of the gland cistern ranges from a spherical hollow cavity to one composed of folds or divisions, exhibiting a honeycomb appearance. A double-layered epithelium forms the lining of the gland cistern, and lobes of secretory tissue are found immediately adjacent to the lining.

Teat

The gland cistern empties ventrally into the teat cistern, and, at their union, there may be a slight constriction known as the annular fold. The teat cistern is also lined by a double-layered epithelium; however, the superficial (luminal) epithelial cells are more columnar than cuboidal, and the basal cells are smaller and cuboidal. This cistern holds 10–50 ml of milk, and the surface structure varies greatly. It may be smooth or it may exhibit longitudinal and horizontal folds, giving a pocketed appearance. Lobules of secretory tissue are sometimes present adjacent to the teat cistern lining, which drain directly into the teat cistern (Figure 5).

The teat cistern terminates distally at the teat canal, the opening through which milk is removed. The teat canal terminates distally at the teat meatus or orifice. Just above the union of the teat cistern and teat duct, the six to 10 longitudinal folds of the cistern lining converge to form Fürstenberg’s rosette. The tissue folds appear to provide no mechanical function in preventing milk leakage as previously theorized. The increased epithelial surface area and connective tissue stroma provided by the folds, however, appear to recruit protective leucocyte populations, especially lymphocytes and plasma cells, which may function in the local defence against mastitis-causing organisms.

Teat Canal

The teat canal is 5–13 mm in length and averages about 8.5 mm. The diameter ranges from 0.4 mm at the distal end to 0.77 mm at the proximal end and averages 0.46 mm at its mid-portion. With advanced lactation age, the teat canal lengths and increases

![Figure 5](image_url) Diagrams of longitudinal sections of the teat highlighting (A) the teat canal keratin and (B) sphincter muscle.
in diameter. At the union of the teat cistern and teat canal at Fürstenberg’s rosette, the double-layered epithelium abruptly changes ventrally to a stratified squamous epithelium, which is continuous with that of the outer teat skin. Continued desquamation of the cells surrounding the teat canal lumen results in the formation of keratin, which occludes the canal lumen between milkings, serving as a barrier to bacteria penetration. If keratin is lost or removed, the effective barrier is compromised, and the teat canal may be unable to resist bacterial invasion (see Mammary Resistance Mechanisms: Anatomical). If the milk flow-induced shear stress is excessive because of prolonged milking time, excessive vacuum or improper pulsation, some of the keratin may be lost.

The teat canal is surrounded by bundles of smooth muscle fibres. Fibres are arranged longitudinally immediately adjacent to the epithelial lining and in a circular fashion around the canal deeper in the connective tissue. The circular smooth muscles in their contracted state function to maintain tight closure of the canal between milkings to prevent leakage and to keep keratin occluding the canal lumen compressed as an aid in preventing bacteria from progressing upward into the teat cistern. Teats with weak, relaxed or incompetent circular smooth muscle bundles (sphincters) are termed ‘patent’ or ‘leaky’. Cows having such teats milk out in 2–3 min, but the incidence of mastitis is higher in quarters with patent (sphincters) are termed `patent' or `leaky'. Cows

Cows having teats with tight sphincters are called ‘hard milkers’ because milk is expressed as a fine spray and milk flow is very slow.

Vascular System

Arterial Supply

The vascular system reaches the udder via the right and left inguinal canals in the abdominal wall. Arterial blood from the heart is supplied initially through the posterior dorsal aorta, which becomes the abdominal posterior dorsal aorta after entering the abdominal cavity. This vessel runs parallel to the vertebral column until it reaches the sixth lumbar vertebrae, then it diverges into the right and left iliac arteries, which in turn diverge into the internal and external iliacs. The external pudic or mammary artery arises from the external iliac and passes through the inguinal canal to the dorsal surface of the udder. Upon emerging from the inguinal canal, the mammary artery and the associated mammary vein follow a tortuous route forming an S-shaped curve. This allows for the lengthening of the blood vessels as the median suspensory ligaments stretch to accommodate the full and distended udder.

The mammary arteries enter the right and left halves of the udder just anterior to the rear teats and divide into the anterior and posterior mammary arteries, branching into arterioles that supply the fore and rear quarters, respectively. The subcutaneous abdominal artery usually arises from the mammary artery before it divides into the anterior and posterior branches. This artery supplies blood to the anterior dorsal portion of each side of the udder. The anterior and posterior mammary arteries spread vertically through the parenchyma of the fore and rear quarters of each side, respectively, and divide, ultimately terminating in capillaries that form a network surrounding the alveoli (Figure 6).

The mammary arteries also gives rise to the papillary arteries of the teats. The vascular tissues of the teat composed of the papillary arteries and venous plexus are collectively termed the corpus cavernosum. Right and left udder halves generally have their own arterial supply; however, some small arterial connections pass from one half to the other. Blood also reaches the udder, to a lesser degree, via the cranial epiigastric and perineal arteries that supply, in part, the anterior and posterior portions of the udder, respectively. The arterial blood flow pathway leads from the heart to the udder.

The primary purpose of the arterial system is to provide a continuous supply of nutrients to the milk-synthesizing cells with which to produce milk. These vessels have heavy muscular walls that aid in driving blood away from the heart to peripheral tissues. In a 500-kg cow, about 71 000 l of blood flows through the udder each day. Approximately 400 volumes of blood pass through the mammary gland to produce 1 volume of milk.

Venous Drainage

After passing through the capillaries surrounding the alveoli, and the interchange between blood and tissue fluids takes place, blood reaches the small
veins. These venules run in a dorsal direction and unite to form the larger mammary veins at the base of the udder, forming the venous circle. Veins have thin connective tissue walls and exhibit little change in diameter because venous pressure does not vary greatly. Papillary veins of the teat also course upward to meet the mammary veins and converge upon the venous circle at the base of the udder. The external pudendal vein follows the course of the external pudendal artery, passes through the inguinal canal, and becomes the external iliac vein, which then drains into the posterior vena cava (Figure 7).

Anterior extensions of the mammary veins on both sides of the udder are the very prominent and turgid subcutaneous abdominal veins, also known as milk veins in the mature lactating cow. These travel along the ventral surface in a rather tortuous route under the skin but exterior to the abdominal wall. The two veins from each side form an anastomosis in front of the udder and enter through the rectus abdominis muscle near the breast bone to become the internal abdominal veins. They penetrate the diaphragm to become the internal thoracics, which drain into the anterior vena cava. The two main routes by which blood exits the mammary gland are the external pudic and the subcutaneous abdominal veins. Approximately two-thirds of the blood exits the udder via the external pudic veins and one-third exits via the subcutaneous abdominal veins. Some blood may leave the rear quarters via the perineal veins, the pathway of venous flow from the udder to the heart.

**Lymphatic System**

Interstitial fluids originating from capillaries that nourish mammary parenchymal cells recirculate via the lymphatic system, which carries waste products away from the udder. Lymph vessels begin as small capillaries dispersed among the connective tissues of the teat and milk secretory parenchyma. These small vessels converge upon larger lymphatics toward the dorsal portions of the udder, terminating at the supramammary lymph nodes on the right and left halves of the mammary gland. These nodes are located dorsal to the rear quarters, and each side of the udder may have from one to three nodes. The nodes serve as filters that remove or destroy foreign substances and also provide a source of lymphocytes to fight infection. Lymph is filtered through the nodes by entering at the peripheral border, passing through a network of sinuses and exiting at the hilus via large vessels that pass through the inguinal canal. Vessels may then branch, and the fluid is passed through the inguinal, iliac and prefemoral lymph nodes before joining the lumbar lymph trunk. The fluid continues to the thoracic duct and empties into the anterior vena cava (Figure 8).

Movement of lymph in vessels of the udder is always in a dorsal direction, toward the supramammary lymph nodes. Lymphatic vessels are equipped with one-way valves to maintain direction of flow; however, movement is slow because there is no pump to circulate the fluid. The forces behind lymph flow include muscle movement, breathing and swaying of the udder as the cow moves about.

**Nervous System**

The major nerves of the udder are the sensory nerves that carry impulses from the four quarters to the brain. Other nerves are sympathetic and are composed of motor fibres to the smooth muscles of arterial walls and those of the teat sphincter. These fibres control the rates of blood flow through the udder by regulating the diameter of arteries and are involved in inhibiting the milk ejection reflex.

The main spinal nerves are the first, second, third and fourth lumbar nerves and the external spermatic nerves, which become inguinal nerves as they pass through the inguinal canal; these nerves are distributed to the glands and skin via anterior and posterior fibres. The first lumbar nerve supplies the
anterior portion of the udder but does not innervate the parenchyma. The second lumbar nerve joins the third lumbar nerve, which fuses with the second and fourth lumbar nerves, composing the inguinal nerve. The perineal nerve, derived from the second, third and fourth sacral nerves, feeds the caudal portion of the udder. Afferent fibres of the inguinal nerve send signals from the udder to the spinal cord and brain, while the efferent fibres send signals from the brain and spinal cord to the udder via ventral root ganglia.

Each quarter is supplied with nerves terminating in the dermis of the udder skin and teats, which lead to the spinal column and brain. Innervation of the udder is greatest in the dermis of the teats where pressure-sensitive receptors have been identified. These terminal endings are sensitive to physical stimuli such as pressure, touch and stretching, and they tend to be more numerous at the proximal end of the teat and close to the surface. The precise nature of the nerve endings has not been established, but the highly specialized sensory nerve endings in teats of some species have not been documented in the cow. Impulses travel via afferent fibres through the mammary nerves to the inguinal nerve. This courses through the inguinal canal to the second, third and fourth lumbar nerves, and the dorsal roots of these nerves carry the afferent signal along the spinal cord to the brain (Figure 9).

Nerves also arise from the spinal column and terminate in the muscles of the teat and arteries. The circular smooth muscle bundles surrounding the teat canal undergo continuous rhythmic contractions between milkings via impulses from the sympathetic nervous system. When these nerves are severed or blocked, the cow tends to leak milk. During milking, impulses from the brain and spinal cord cause the muscle bundles to relax, allowing the teat canal to dilate for the flow of milk.

The nervous system has no direct involvement in the synthesis and secretion of milk or in milk removal (ejection) from the udder. These processes are controlled directly by hormones circulating in blood. However, the nervous system is essential to the milking process itself because it triggers the mechanisms of hormone release from the brain to the mammary tissue.


Further Reading

Swett WW (1942) Arrangement of the tissues by which the cow’s udder is suspended. Journal of Agricultural Research 65: 19–22.
Introduction

Mammary glands are accessory reproductive organs that develop to nourish the young. Mammary gland development and lactation may occur multiple times in a mammal’s life. In fact, the mammary gland is one of a few body organs that undergoes repeated cycles of structural development, functional differentiation and regression. Careful management of this cycle is the basis for successful lactation in dairy animals. Growth and development of the mammary gland (mammogenesis) occurs through a series of phases, which are intimately associated with the specific physiology of the animal’s growth and reproductive functions. Each mammary growth phase is regulated by hormones and locally produced growth factors. The specific hormones responsible for mammary growth vary with the developmental phase. To understand mammary gland growth and its regulation first requires an understanding of the tissue components giving rise to the growing gland.

Mammary Tissue Components

Mammary parenchyma is composed of the epithelial structures, such as alveoli and ducts, and the associated stromal connective tissue (see Mammary Gland: Anatomy). Stroma of a lactating gland primarily is composed of cellular and noncellular components of the connective tissue surrounding the epithelial structures. Cellular components of the stroma include fibroblasts, endothelial cells associated with blood vessels and leucocytes localized in the tissue, while noncellular components include collagen and other connective tissue proteins. In contrast to a lactating gland, considerable white adipose tissue exists in a gland from the early phases of foetal development and extending through much of pregnancy. This fat pad often is included as part of the stroma of the developing gland, but is considered as extraparenchymal tissue.

Alveoli are the basic structures that produce milk during lactation (Figure 1). The extensive system of mammary ducts provides a pathway for removal of milk from alveoli. Ducts and alveoli are the defining structures of the mammary gland. Understanding their development has been a primary historical focus of research. Groups of alveoli are organized into clusters, with each cluster constituting a lobule (Figure 2). Each alveolus in a lobule drains into an intralobular duct, groups of which in turn are connected by interlobular ducts. Development of this lobular structure is a fundamental process of mammary growth. Prior to puberty, ductules arising from rudimentary epithelial structures near the base of the teat will elongate by growing into the fat pad. After puberty, these ductules continue to elongate in the cycling heifer, but also begin branching to form structures called terminal ductule lobular units (TDLU). These structures are characteristic of the lactating mammary gland.