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Anatomy of the Respiratory System

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The major function of the respiratory system is to deliver oxygen to and remove carbon dioxide from the blood. Air is delivered into the lungs through a series of conducting airways that connect the ambient air to the alveoli where gas exchange with blood takes place. These conducting airways include the nares, nasal cavity, pharynx, larynx, trachea, bronchi, and bronchioles. Gas exchange occurs in the alveolar ducts and alveoli, both of which are lined by an extensive pulmonary capillary network so that there is a huge vascular surface area for oxygen and carbon dioxide diffusion. Blood reaches the pulmonary capillaries from the right ventricle through the pulmonary arteries and returns to the left atrium via the pulmonary veins. In addition, the bronchial circulation, which is a branch of the systemic circulation, provides nutrients to the bronchi, large vessels, and pleura. This chapter describes the gross and microscopic structure of the respiratory system and forms a basis for future chapters. The structures are described in the sequence that they might be approached during a clinical examination.

The Nose

The external nares and false nostril

The respiratory system begins at the external nares, which provide very mobile valves that can be closed to prevent water entry during swimming or can be opened maximally during exercise to facilitate high airflow rates. The alar cartilages provide rigidity to the external wall of the nostril. Movements of the external nares are a result of the action of the muscles (levator nasolabialis, dilator naris lateralis, and transversus nasi) that attach to these cartilages. The lateralis nasi inserts into the cartilaginous extension of the ventral turbinate so that it draws the lateral wall of the nasal vestibule outwards and compresses the false nostril, thereby enlarging the nasal opening.

The junction between the skin and the nasal mucosa is visible just within the external nares. On the ventral aspect of this mucocutaneous junction is the opening of the nasolacrimal duct. This is one source of the small amount of moisture frequently seen on the horse's external nares.

If one extends an index finger into the nose and up the lateral surface of the external nares, one enters the blind,

hair-lined cavity known as the false nostril. It is approximately 10 cm in depth and its function is unknown. The sebaceous glands in the walls of the false nostril can give rise to epidermal cysts.

The nasal cavity

Extending a finger up the medial and ventral aspect of the external nares, one enters the nasal cavity through its narrowest part known as the nasal valve. On the medial side of the nasal valve is the nasal septum while on the lateral side is the alar fold, which is a mucosal extension of the ventral turbinate. The nasal septum separates the two sides of the nasal cavity. In its caudal portion it is bony but rostrally it is cartilaginous. It is covered with a highly vascular mucosa. The rostral end of the mucosa to the level of the second or third cheek tooth is covered by a non-ciliated stratified cuboidal epithelium with a low density of mucous cells. Caudally, the epithelium becomes ciliated pseudostratified columnar and mucous cell density increases progressively.

Nasal turbinates

Each side of the horse's nasal cavity has two turbinates that divide the cavity into three air passages, the ventral, middle and dorsal meatuses. The ventral meatus, which has the largest cross-sectional area, provides the direct pathway for airflow between the external nares and the nasopharynx and is the primary path for an endoscope or stomach tube. The dorsal meatus extends into the ethmoid region. The turbinates enlarge the mucosal surface of the nasal cavity, which facilitates its air-conditioning and defense functions.

It is easiest to understand the gross structure of the turbinates if one imagines them initially as a mucosa-covered bony plate extending into each nasal cavity from its lateral wall. To be accommodated within the nasal cavity, each of these structures must scroll. The ventral turbinate scrolls upwards while the dorsal turbinate scrolls downwards (Fig. 1.1). This scrolling results in the shell-like structures known as the nasal conchae. The conchae of both the dorsal and ventral turbinates form dorsal and ventral conchal sinuses. The dorsal conchal sinus is contiguous with the frontal sinus and the ventral conchal sinus with the maxillary sinus (Fig. 1.2).

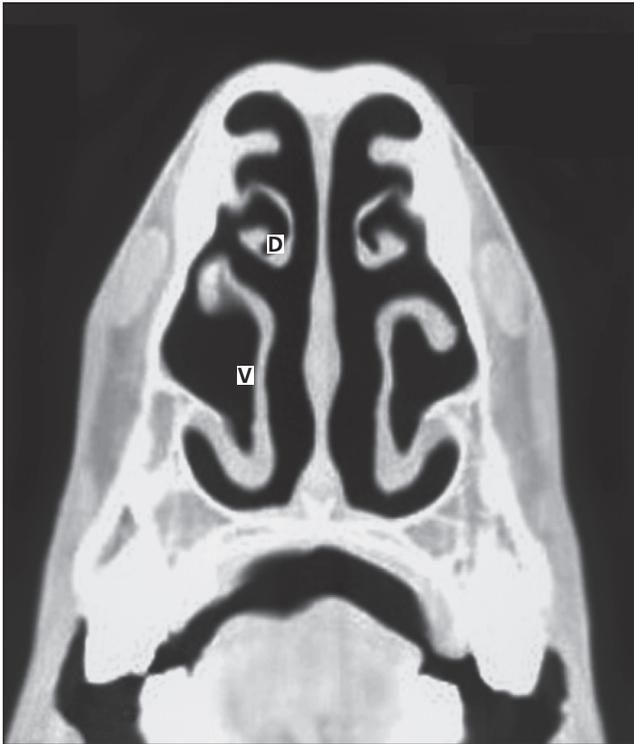


Fig. 1.1. Cross-sectional image of the nose at the level of the first cheek tooth. The scrolling of the dorsal (D) and ventral (V) turbinates is clearly visible.

The ventral turbinate is the shorter of the two turbinates extending between the first and sixth cheek teeth. Rostrally, the ventral turbinate continues to the external nares as the alar fold. The longer dorsal turbinate terminates rostrally at the first cheek tooth and caudally extends to the ethmoid region. The epithelial lining of the rostral portion of the alar fold is stratified squamous epithelium with numerous duct openings from the large number of submucosal glands. Caudally, there is a progressive transition of epithelium through stratified non-ciliated cuboidal, and ciliated pseudostratified columnar, to typical respiratory epithelium with numerous mucus cells (Kumar et al 2000) (Fig. 1.3).

The submucosa of the nasal cavity is highly vascular allowing it to warm inspired air and regulate mucus production. Postganglionic sympathetic nerves (supplied via cervical sympathetic preganglionic fibers synapsing in the superior cervical ganglion) innervate the nasal blood vessels. Upon release of norepinephrine these nerves cause vasoconstriction. Congestion of the nasal mucosa is a feature of Horner syndrome and is a consequence of loss of the sympathetic nerve supply. Parasympathetic innervation of the nose is from the facial nerve (CN VII) and has little effect on the diameter of blood vessels, suggesting that vasodilatation is a largely passive process. When activated,

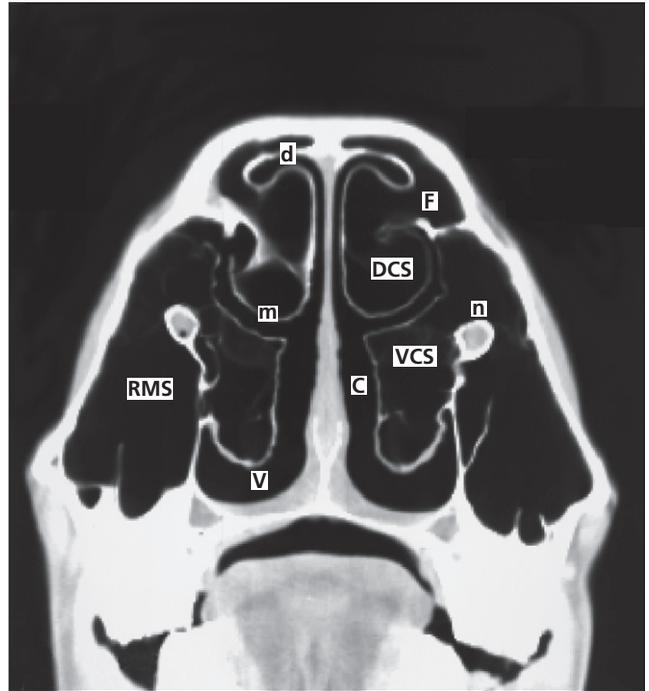


Fig. 1.2. Cross-sectional image of the nose at the level of the junction of the fourth and fifth cheek teeth. The dorsal (d), middle (m), ventral (v), and common (c) meatuses are visible. The ventral conchal sinus (VCS) communicates with the rostral maxillary sinus (RMS) over the nasolacrimal canal (n). The dorsal conchal sinus (DCS) communicates with the frontal sinus (F).

the parasympathetic nerves in the nose chiefly regulate glandular blood flow and secretion.

The ethmoids

The ethmoid region of the nasal cavity is clearly visible when an endoscope is directed dorsally from within the ventral meatus of nasal cavity (Fig. 1.4). One sees the rostral surface of the ethmoturbinates, a mass of highly vascularized, scroll-like plates of bone that ramify toward the olfactory region of the brain (Fig. 1.5). The ethmoid region receives most of its blood supply from intracranial sources (Bell et al 1995). The olfactory epithelium that lines the ethmoturbinates contains three types of cells: sensory neurons, exhibiting odor receptors that transmit electrical signals to the brain; sustentacular cells, which provide protection to the neurons and secrete mucus; and basal cells, which differentiate to replace dead sensory neurons. The axons of nerves in the olfactory epithelium converge to form the olfactory nerve (CN I) giving rise to the sense of smell. Progressive ethmoid hematoma is a slowly growing, uncommon, hemangiomas mass that originates in the ethmoidal region and can cause chronic epistaxis.

The maxillary sinus drains into the caudal part of the middle meatus of the nasal cavity via the nasomaxillary

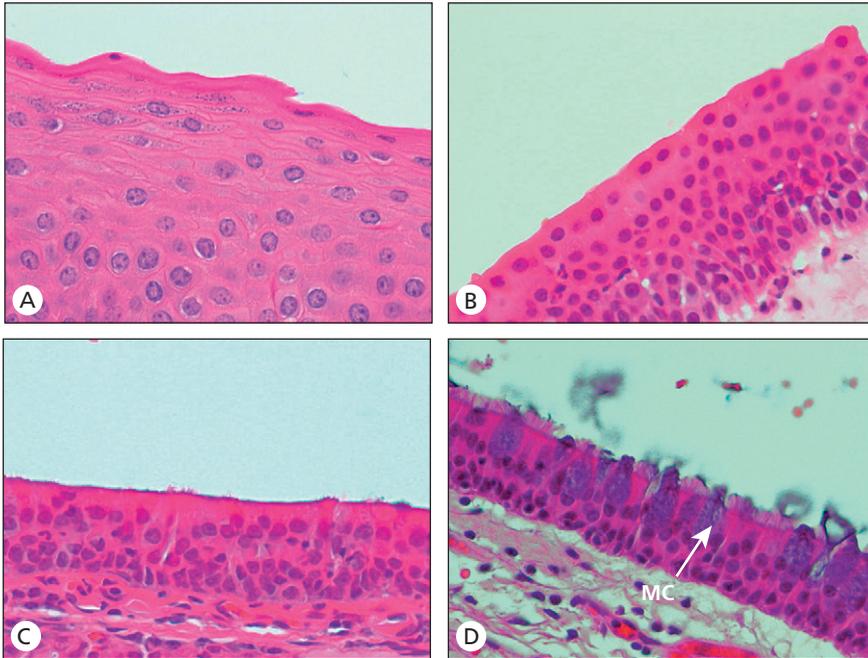


Fig. 1.3A–D. Types of epithelium found in the equine nose. (A) Stratified squamous epithelium typical of the most rostral part of the ventral turbinate. (B) Non-ciliated stratified cuboidal epithelium with low mucus cell count found on the rostral third of the nasal septum and the alar fold. (C) Transitional epithelium that occurs on the rostral third of the turbinate bones and the middle third of the nasal septum. (D) Ciliated pseudostratified respiratory epithelium with many mucus cells (MC) typical of caudal parts of the turbinates and nasal septum.

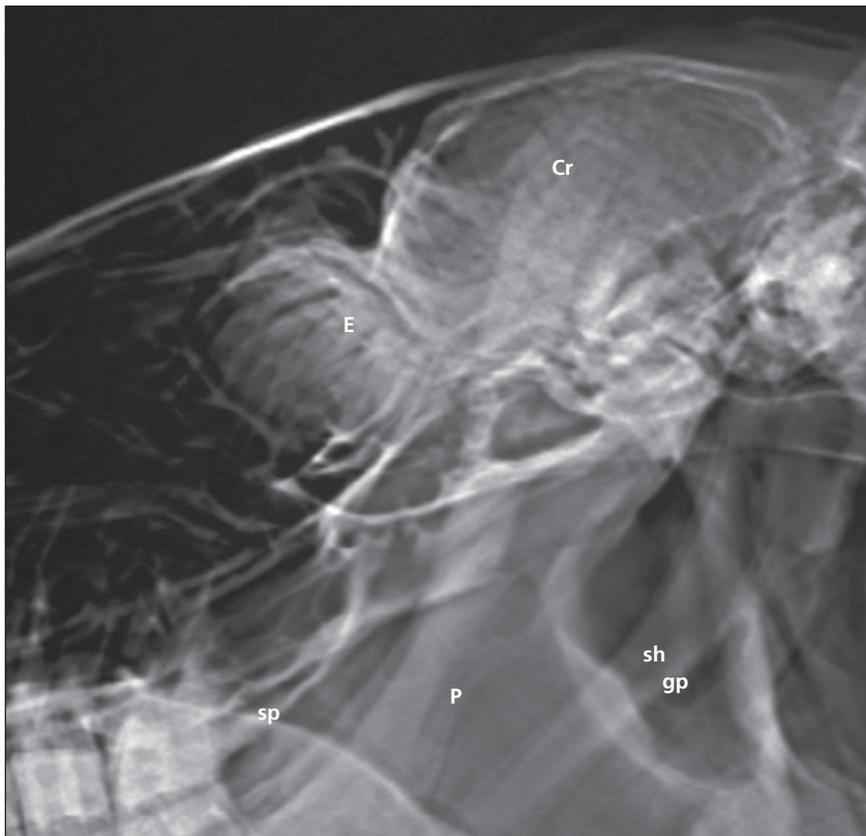


Fig. 1.4. Lateral radiograph of the caudal nasal cavity and pharynx (P) showing the cranium (Cr), ethmoturbinates (E), guttural pouch (gp), stylohyoid bone (sh) and soft palate (sp).

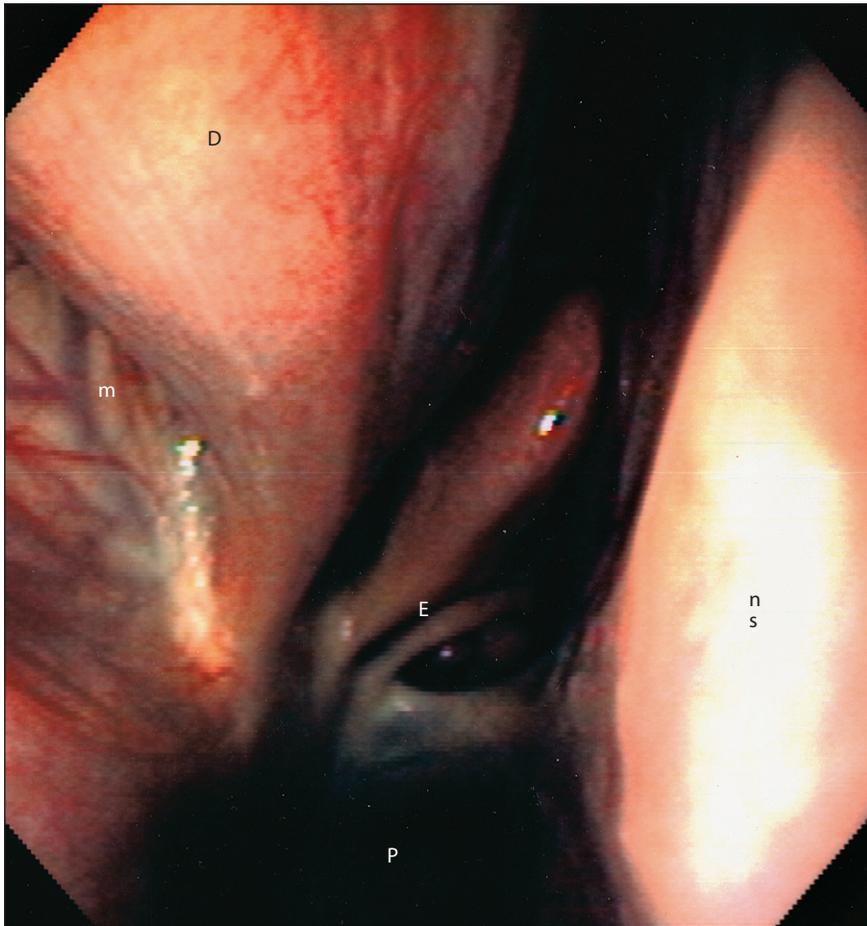


Fig. 1.5. Endoscopic view of the caudal nasal cavity showing the ethmoid turbinates (E), caudal end of the dorsal turbinate (D), nasal septum (ns), and the pathway that leads to the maxillary sinus opening (m). The nasopharynx (P) is at the bottom of the picture.

opening. Although this opening cannot be seen directly with an endoscope, purulent drainage from the sinus appears lateral to the caudal part of the dorsal turbinate where it joins the ethmoid region (Fig. 1.5).

The paranasal sinuses

There are seven pairs of paranasal sinuses in the horse (Fig. 1.6). These are the rostral and caudal maxillary, ventral and dorsal conchal, frontal, sphenopalatine, and ethmoid sinuses. The rostral maxillary sinus (RMS) is located dorsal to the third and fourth maxillary cheek teeth. The lateral portion of the RMS communicates with the medial portion, known as the ventral conchal sinus (VCS), over the infraorbital canal. The RMS is separated from the caudal maxillary sinus (CMS) by a bony septum usually positioned between the fourth and fifth cheek teeth. The CMS is located dorsal to the fifth and sixth cheek teeth. The frontal sinus is triangular and located dorsal to the ethmoturbinates and rostral to the cranium. The frontal sinus and the dorsal conchal sinus functionally form a single compartment known as the conchofrontal sinus. Within the ethmoturbinates lie many small sinuses that

comprise the ethmoidal sinus that drains laterally into the CMS by way of the sphenopalatine sinus that lies adjacent to CN II–VI and blood vessels (Bell et al 1995, McCann et al 2004).

Drainage of the paranasal sinuses does not strictly rely on gravity alone but also on ciliary transport directed toward the middle meatus of the nasal cavity (Barakzai 2004). The RMS and VCS drain into the middle meatus via the slit-like nasomaxillary aperture (NMA), which is located at the highest point in the VCS. The remaining paranasal sinuses drain into the CMS and thence into the posterior part of the nasal cavity via the NMA of the CMS. The drainage from these two separate NMAs merges. When the drainage from the sinuses is purulent it can be observed entering the nose lateral to the caudal limit of the dorsal turbinate (Fig. 1.5). The narrow drainage pathways are easily obstructed as a result of mild inflammation.

The Pharynx

The pharynx delivers air from the posterior nasal cavity to the larynx and is also the pathway that delivers food from the oral cavity to the esophagus. In horses, the oral cavity

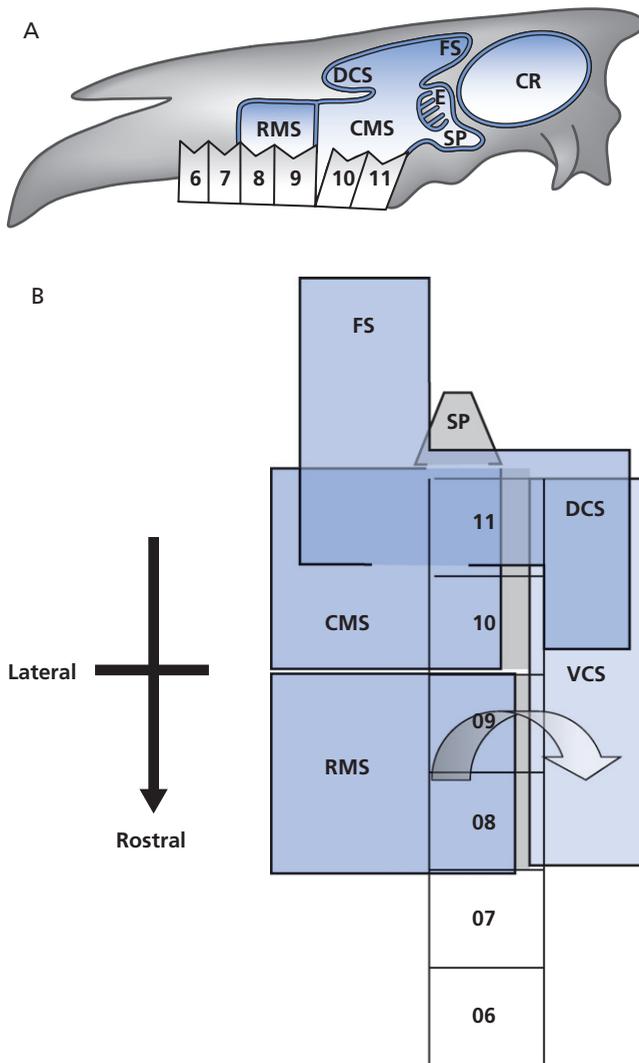


Fig. 1.6. The paranasal sinuses of the horse. (A) Lateral view. (B) Diagrammatic representation to show the relationship to the cheek teeth and the intercommunications. CMS = caudal maxillary sinus, CR = cranium, DCS = dorsal conchal sinus, E = ethmoidal sinuses, FS = frontal sinus, RMS = rostral maxillary sinus, SP = sphenopalatine sinus, VCS = ventral conchal sinus. Arrow shows communication between RMS and VCS over the infraorbital canal. Teeth are labeled in the Triadan system: 06–08 = premolars, 09–11 = molars.

and pharynx are normally separated by the soft palate except during swallowing. For this reason, horses are obligate nasal breathers.

The nasopharynx is lined with pseudostratified columnar ciliated epithelium containing goblet cells and the oropharynx is lined by stratified squamous epithelium. Lymphoid tissue that is organized into follicles is visible in rows along the dorsal wall and represents part of the equine tonsil (Kumar & Timoney 2001). In young horses, these follicles can become large and edematous. This condition, known as follicular lymphoid hyperplasia, is generally self-limiting as the horse matures. In addition, a

lingual tonsil has been described at the base of the tongue (Kumar & Timoney 2005).

Unlike the nasal cavity, larynx and trachea, the pharynx lacks rigid support from bone or cartilage. The patency of the pharynx depends on the activity of muscles associated with the hyoid bone, soft palate and tongue (Holcombe et al 1997, Holcombe et al 1998, Tessier et al 2004). These are discussed extensively in Chapter 29. Dysfunction of these muscles or their nerves has been associated with pharyngeal collapse or dorsal displacement of the soft palate, conditions that are exaggerated during exercise.

When the pharynx is viewed endoscopically from the posterior nares, the following structures are generally visible: the soft palate forms the ventral floor, the slit-like guttural pouch openings are visible on the lateral wall, and the larynx and glottis are visible ventrally (Fig. 1.7). If the soft palate is located in its normal position, the pointed epiglottis is visible. The epiglottis is held down against the soft palate by the action of the hyoepiglotticus muscle (Holcombe et al 2002). If the soft palate is displaced dorsally, the epiglottis is hidden.

When the endoscope tip is directed dorsally within the pharynx, the dorsal pharyngeal recess becomes visible. In cases of follicular lymphoid hyperplasia, the dorsal pharyngeal recess can become severely affected and edematous. In mules, a muscular sphincter surrounds the entrance into the dorsal pharyngeal recess.

The anatomy of the guttural pouches is described in Chapter 28. They are lined by ciliated epithelium with mucus-secreting cells and have a close association with the vagus (CN X), glossopharyngeal (CN IX) and hypoglossal (CN XII) nerves (Manglai et al 2000a,b). The internal carotid artery runs in the wall of the guttural pouch and it is thought that this association allows for cooling of arterial blood on its way to the brain (Baptiste et al 2000). The 5-cm long slit-like openings into the guttural pouches extend downward and backward in the lateral wall of the pharynx, beginning just caudal to the level of the posterior nares. A fold of mucus membrane that needs to be lifted to pass an endoscope into the guttural pouch covers the medial wall of the guttural pouch opening. During swallowing, the guttural pouch openings dilate widely and the mucus membrane folds almost make contact with each other in the pharyngeal midline (Fig. 1.7B).

The Larynx

The main function of the larynx is to prevent inhalation of food into the lower airway during swallowing. The larynx also has evolved a second function, which is phonation. The cartilaginous support of the larynx is provided by the ring-shaped cricoid cartilage adjacent to the first tracheal ring, the large thyroid cartilage, a pair of arytenoid cartilages that support the vocal folds and the epiglottis that provides a protective flap to cover the glottis during



Fig. 1.7. (A) Endoscopic view of the pharynx showing 1, the tissue flaps that cover the openings to the Eustachian tubes and guttural pouches; 2, the dorsal pharyngeal recess; and 3, the larynx. (B) The guttural pouch openings during swallowing. Note how the tissue mucosal flaps over the openings converge in the midline of the pharynx.

deglutition (Fig. 1.8A). Corniculate and cuneiform cartilages are attached to the arytenoid and epiglottic cartilages respectively. The cricoid cartilage, which is the most caudal, has a broad dorsal surface that provides the origin of the cricoarytenoideus dorsalis muscle. It also has articular surfaces for the arytenoids and for the caudal cornu of the

thyroid cartilage. The thyroid cartilage has a narrow ventral body from which arise two plate-like laminae that form the lateral walls of the larynx and articulate with the cricoid in diarthrodial joints at their caudal cornua. The ventral borders of the laminae unite rostrally at the body of the thyroid and thereby form a ventral triangular space – the thyroid notch – that is bounded caudally by the ventral part of the cricoid cartilage. The cricothyroid membrane fills the thyroid notch, and is easily palpable. The rostral border of each thyroid lamina is attached to the hyoid bone by the thyrohyoid membrane. The paired arytenoids are mobile and under the control of the intrinsic laryngeal muscles. They lie medial to the thyroid laminae and rostral to the cricoid cartilage. At the caudal edge of the medial surface of each arytenoid is the diarthrodial cricoarytenoid articulation. On the lateral surface dorsal to the articulation is the muscular process for the insertion of the cricoarytenoideus dorsalis muscle. A notch in the arytenoid cartilage separates the caudal muscular process from the rostral corniculate cartilages that are attached to the arytenoids by cartilaginous joints. The bilateral corniculate cartilages are visible endoscopically dorsal and lateral to the glottis. In the normal horse, these abduct almost symmetrically during inhalation but, in the horse with recurrent laryngeal neuropathy, the left corniculate fails to abduct or lags considerably. The most ventral point of the arytenoid cartilage is the vocal process. This forms the attachment for the vocal ligament, a band of elastic fibers that originates on the caudal border of the thyroid body and underlies the membranous vocal fold. Movements of the arytenoids and corniculate cartilages abduct and adduct the vocal folds. The single almost triangular epiglottic cartilage is pointed rostrally and normally visible endoscopically above the soft palate. Attached to either side of its base are the bar-like cuneiform cartilages that project caudodorsally.

Three extrinsic muscles regulate the position of the larynx in relation to the head and neck. A small muscle, the hyoepiglotticus, connects the ventral surface of the epiglottis to the basihyoid bone and thereby pulls the epiglottis ventrally to enlarge the entrance to the glottis. Dysfunction of this muscle results in inspiratory epiglottic retroversion during exercise. The thyrohyoideus connects the lateral surface of the thyroid laminae to the caudal border of the stylohyoid bone. Contraction of the thyrohyoideus pulls the larynx rostrad. The sternothyrohyoideus originates at the manubrium of the sternum and inserts onto both the caudal border of the thyroid laminae and the basihyoid bone and the lingual process of the hyoid bone. Contraction pulls the larynx backward and downward.

Intrinsic muscles of the larynx (Fig. 1.8B) regulate the position of the vocal folds and the size of the glottic opening (rima glottidis). Contraction of the cricoarytenoideus dorsalis abducts the vocal folds and enlarges the rima glottidis. Paresis of this muscle results in left laryngeal

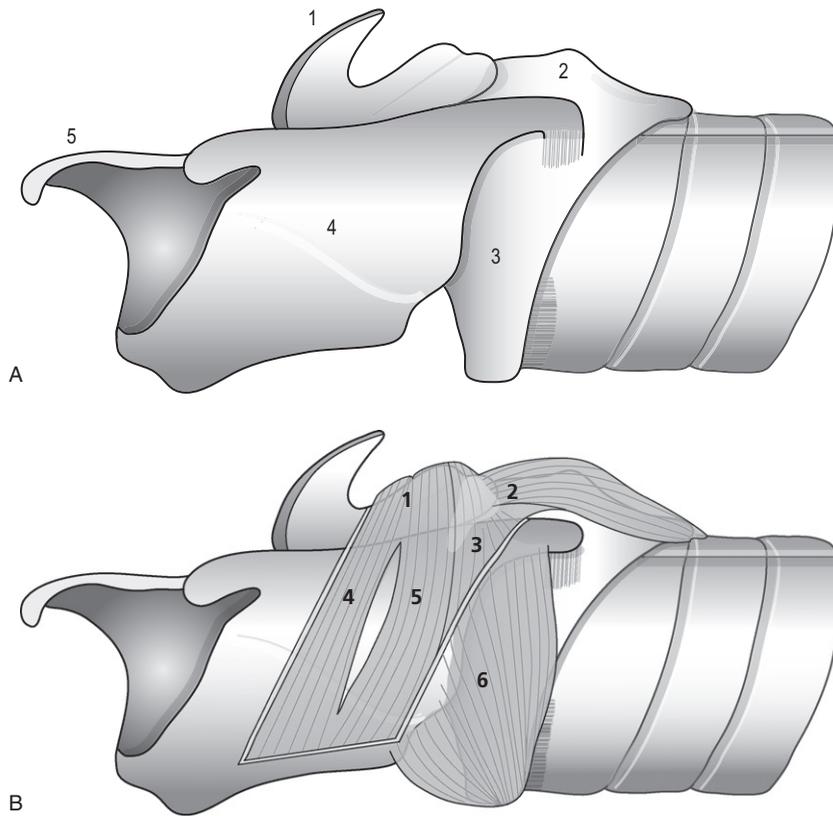


Fig. 1.8. (A) The cartilages of the larynx. 1 = cuneiform cartilage, 2 = muscular processes of the arytenoid cartilages, 3 = cricoid cartilage, 4 = lamina of thyroid cartilage, 5 = epiglottic cartilage. (B) The intrinsic muscles of the larynx. 1 = arytenoideus transversus, 2 = cricoarytenoideus dorsalis, 3 = cricoarytenoideus lateralis, 4 = ventricularis, 5 = vocalis, 6 = cricothyroideus. After Budras, Sack & Röck: *The Anatomy of the Horse* (page 44). Schlütersche GmbH & Co. KG, Hannover, Germany, 2003.

hemiplegia. Contraction of the arytenoideus transversus also abducts the vocal folds. The adductor muscles of the vocal folds are cricoarytenoideus lateralis, arytenoideus transversus, vocalis and ventralis. Contraction of the latter muscles during swallowing forms a sphincter that closes the glottis and prevents food inhalation. Innervation of the intrinsic muscles of the larynx is via the recurrent laryngeal nerves except for the cricothyroideus, which receives innervation via the cranial laryngeal nerves.

The laryngeal mucosa is contiguous with that of the pharynx and trachea. It is tightly adherent to the dorsal surface of the epiglottis, over the vocal ligaments and to the cricoid cartilage. Between the lateral border of the epiglottis and the cuneiform/arytenoid cartilages, the mucosa forms the aryepiglottic fold that can sometimes cause an inspiratory obstruction during exercise. The loose mucosal folds on the ventral side of the epiglottis can sometimes displace dorsally to entrap the epiglottis. Most of the larynx is lined by respiratory, pseudostratified, columnar, ciliated epithelium with goblet cells but the epiglottis and vocal folds are covered by a stratified squamous epithelium.

There are numerous mucus glands beneath the laryngeal mucosa, especially in the epiglottis.

The laryngeal saccules are bilaterally paired, 2.5–5.0 cm deep, mucosa-lined cavities that extend upwards and backwards on the medial surface of the thyroid cartilage. The entrance to the saccules is from the lateral ventricle of the larynx, a pocket-like depression lateral to the vocal folds. The function of the laryngeal saccules is unknown but they are thought to participate in generation of the noise characteristic of horses with recurrent laryngeal neuropathy.

The Trachea

The trachea provides a flexible connection between the larynx and bronchial bifurcation (carina). The trachea can be palpated immediately beneath the skin on the ventral midline of the neck. Its lowest point is where it enters the thoracic inlet immediately above the manubrium of the sternum and it is here that mucoid secretions tend to accumulate. The trachea then ascends and terminates at the bronchial bifurcation, which is just dorsal to the left atrium.

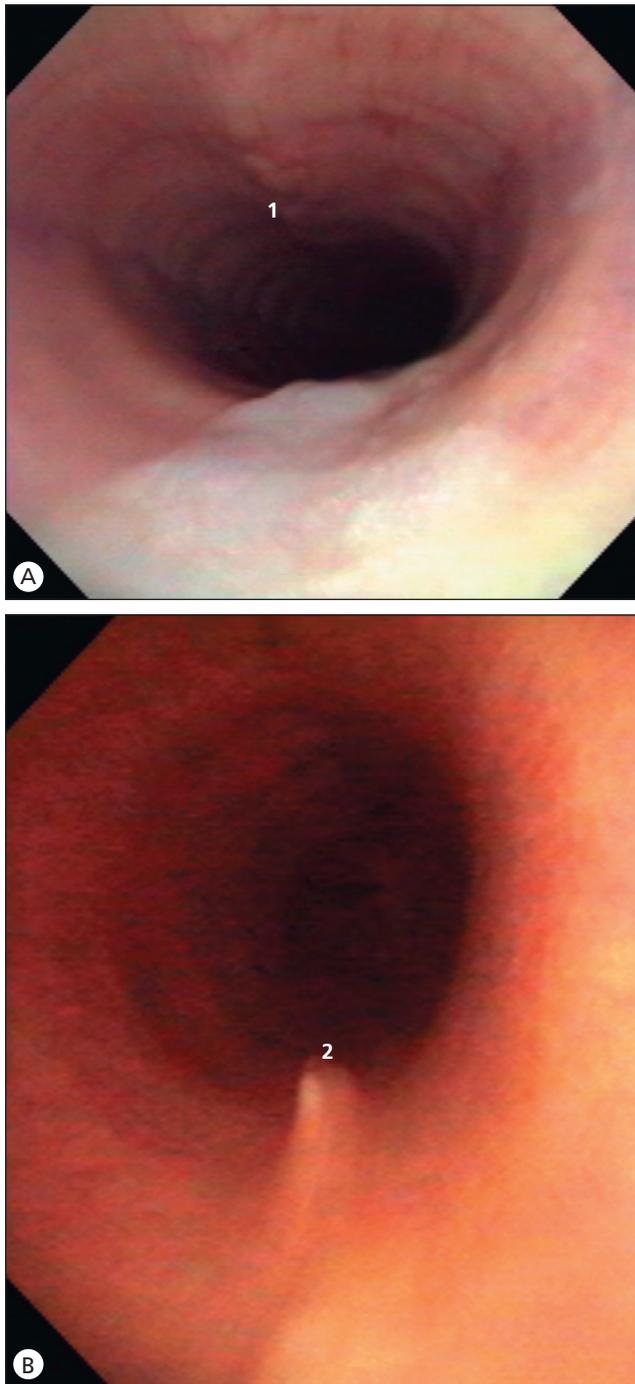


Fig. 1.9. Endoscopic views of the trachea. (A) A ventral stream of mucus in a horse with recurrent airway obstruction. The larger bronchial vessels are clearly visible as is the junction of the ends of the tracheal cartilages in the dorsal wall (1). (B) Cartilage spike on the ventral floor of the trachea (2).

The trachea is supported throughout its length by C-shaped sections of cartilage that are tightly apposed to one another so as to give rigidity to the airway (Art & Lekeux 1991a,b). A band of smooth muscle, known as the trachealis muscle, connects the free ends of the cartilages

dorsally. When this muscle relaxes, the ends of the cartilage do not meet. Contraction of the trachealis pulls the cartilage tips together so that the trachea becomes more rigid. During endoscopic examination, one can see the outline of the cartilages ventrally and laterally and often appreciate the flatter dorsal surface that overlies the trachealis muscle (Fig. 1.9). In older horses, it is not uncommon to see “spikes” of epithelium-covered cartilage protruding into the tracheal lumen on its ventral floor (Fig. 1.9B). In some horses, these can be extensive and form ridges. Their cause is unknown and they appear to be benign.

In older Shetland ponies and in Miniature Horses, the trachea often becomes flattened dorsoventrally and the region between the tips of the tracheal cartilages that includes the trachealis muscle becomes wider. In these same animals, the trachea sometimes rotates in the middle third of the neck so that the trachealis is on the right side of the neck rather than dorsal. This can cause problems if it is necessary to perform a tracheotomy. A midline incision in the neck of these animals enters the trachea near the margin of the cartilage leaving no rigid support on the right side of the tracheotomy.

The pseudostratified columnar tracheal epithelium consists primarily of mucus-producing goblet cells and ciliated cells above a layer of basal cells. The horse has few submucosal bronchial glands. The lamina propria contains many branches of the bronchial circulation that serve to warm and humidify the air and participate in the inflammatory response of the trachea. The larger of these vessels are visible endoscopically beneath the mucosa. The lamina propria is richly supplied with both sensory and autonomic nerves. Non-myelinated sensory nerves containing neuropeptides ramify into the epithelium. Parasympathetic nerves reach the cranial and caudal trachea via the cranial laryngeal nerve and vagus, respectively. Parasympathetic ganglia located along the dorsal wall of the trachea send postganglionic fibers to a submucosal and a muscular plexus. Postganglionic sympathetic fibers enter the wall of the trachea in association with the vagus nerve and terminate in the lamina propria around the bronchial blood vessels. Sympathetic nerves innervate the trachealis muscle only in its cranial third (Yu et al 1994).

The Bronchi

As an endoscope is advanced towards the carina, the openings of the main bronchi become visible. The right main-stem bronchus forms an almost straight line with the trachea, while the left bronchus deviates slightly. On each side, the first bronchus arising from the lateral wall of the main-stem bronchus is to the cranial part of the lung. There is also a large ventral branch to the region of lung

corresponding to a middle lobe. The bronchus to the accessory or intermediate lobe of the lung arises medio-ventrally from the right bronchus (Fig. 1.10). After giving off these large branches, the main bronchi then run parallel to the dorsal border of each lung toward its caudal extremity (Fig. 1.11). Branches are given off both dorsally and ventrally to various parts of the lung. The branching pattern is consistent and has been mapped and labeled (Smith et al 1994).

The bronchial branching pattern is monopodial. Each main bronchus continues almost directly toward the lung periphery and gives off a series of smaller branches (Fig. 1.11B). The exact number of branches of the horse's tracheobronchial tree has not been determined but varies with lung region. There are more branches between the carina and caudal extremity of the lung (we have counted more than 40) than between the carina and the tip of the cranial lobe. Bronchi are identified by the presence of cartilage in their walls and include all airways greater than approximately 2-mm diameter.

The trachea and bronchi are lined by a pseudostratified columnar epithelium that overlies the basement membrane and consists of ciliated and non-ciliated cells that differentiate from basal cells (Fig. 1.12). The non-ciliated cells are primarily mucus-secreting cells (also known as goblet cells). The mucus-secreting goblet cells produce the mucins, which form a large percentage of the mucoid layer that lines the airways. The horse has very few submucosal glands in its tracheobronchial tree (Widdicombe & Pecson 2002). The mucoid layer is propelled cranially by the ciliary cells (see Chapter 5). The lamina propria is immediately beneath the basement membrane and contains a rich supply of bronchial blood vessels and nerves. The former are involved in warming and humidifying the air. The nerves include non-myelinated neuropeptide-containing sensory nerves and branches of the sympathetic nervous system that supply the bronchial blood vessels (Sonea et al 1993a,b, 1994a,b, 1999). Smooth muscle encircles the bronchi and bronchioles and receives parasympathetic and inhibitory non-adrenergic non-cholinergic innervation (Broadstone et al 1991, Yu et al 1992, 1994).

The Lungs

Apart from their first few centimeters, the bronchi are totally surrounded by the lung parenchyma (Fig. 1.11). Unlike the lungs of most other mammals, the horse lung is not divided into distinct lobes. Viewed from the costal surface, both the right and left lung have a similar shape with a ventral notch that accommodates the heart separating the smaller cranial portion from the larger caudal portion. The right lung is larger than the left in part because it includes the intermediate or accessory lobe, which fills the space caudal to the heart and cranial to the

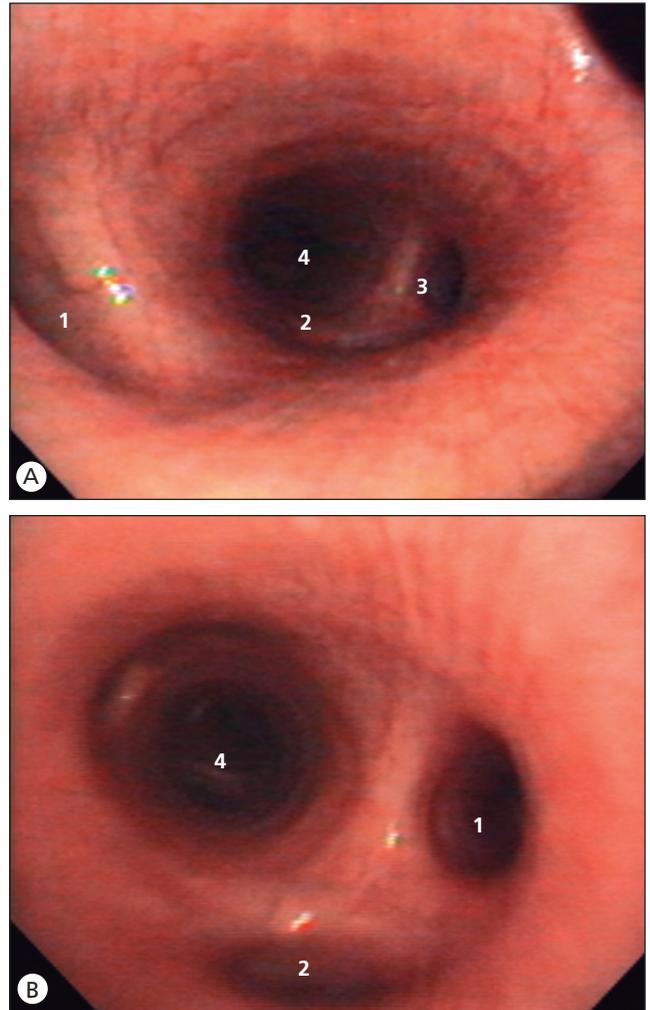


Fig. 1.10. Main branches of (A) the right and (B) the left bronchi. 1: branch to cranial region of lung; 2: branch to cardiac region of lung; 3: branch to accessory lobe; 4: branch to caudal lobe.

diaphragm. The surface of the horse lung shows the fibrous connective tissue septa that divide the lung into lobules. However, these are less distinct than in the pig or cow. The separation of the lung into lobules limits the collateral movement of air between different lung regions (Robinson & Sorenson 1978, Robinson 1982). The greatest bulk of the horse lung is in its caudodorsal region. This means that in the standing animal, much of the lung is almost dorsal to the diaphragm (Figs 1.11 and 1.13).

The bronchovascular bundle

Anyone who views a radiograph of the lung notices that the bronchi and large blood vessels run together (Fig. 1.11B). The distribution of bronchi and arteries is almost identical down to the most peripheral airways. While most veins follow the larger bronchi, some also track through the lung away from the airways and arteries.

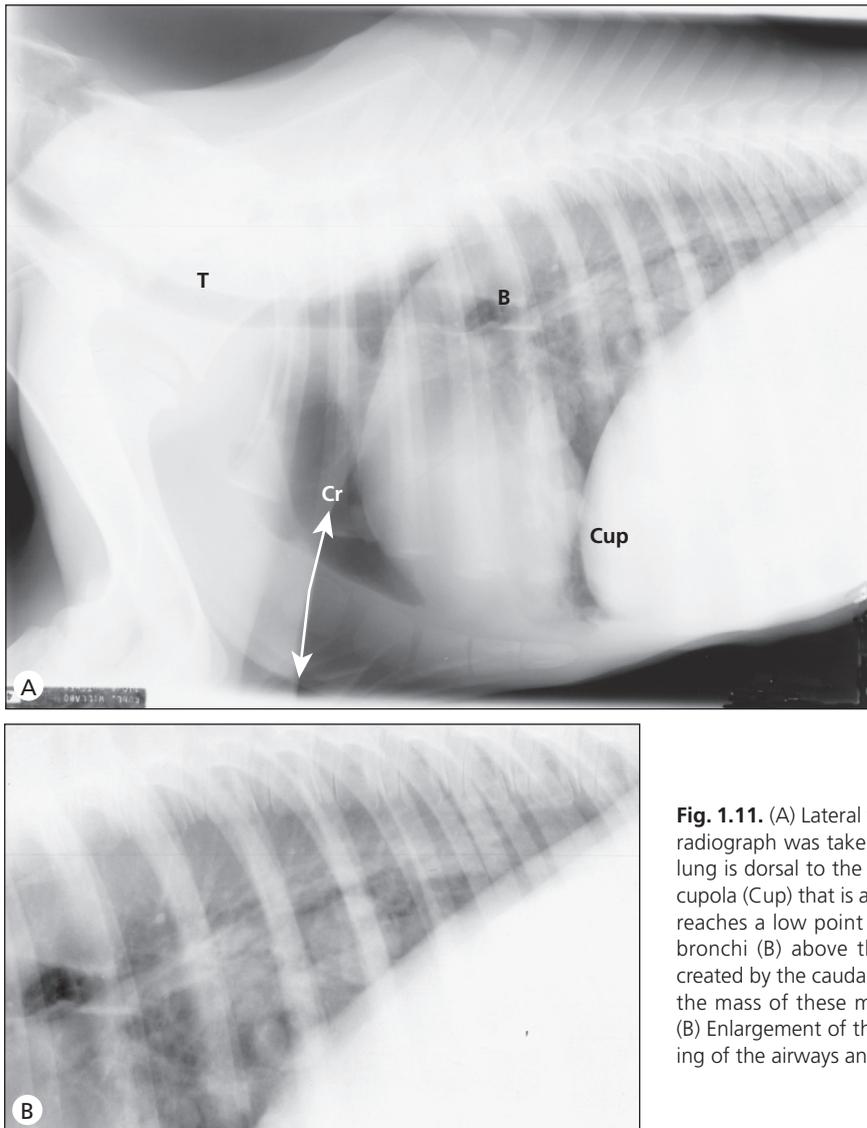


Fig. 1.11. (A) Lateral view of the thorax of a foal with pneumonia. The radiograph was taken with the foal standing. Note that much of the lung is dorsal to the diaphragm, which slopes steeply forward to the cupola (Cup) that is at the level of the sixth to seventh rib. The trachea reaches a low point at the thoracic inlet (T) and bifurcates into the bronchi (B) above the heart. The white arrow marks the shadow created by the caudal margin of the shoulder muscles. In older horses, the mass of these muscles obscures much of the cranial lung (Cr). (B) Enlargement of the caudal region of the lung to show the branching of the airways and vasculature in this abnormal lung.

The associated bronchi and blood vessels are contained in the bronchovascular bundle, which is a loose connective-tissue sheath that also contains lymphatics and nerves. The loose connective tissue is a sink in which edema accumulates whenever fluid filtration rate in the lung is increased, for example in pulmonary edema. When this occurs, the fluid increases the radiographic density in the peribronchial region.

Bronchioles

Several generations of bronchioles, which can be differentiated from bronchi by the absence of cartilage in their walls, connect the small bronchi to the alveolar ducts and alveoli. Because of their small size and the absence of cartilage, bronchioles cannot be distinguished radiographically from the surrounding alveoli. For this reason, radiographs

are not useful for the identification of bronchiolar inflammation such as occurs in inflammatory airway disease. In some mammals, there are respiratory bronchioles, the latter being identified by alveoli that open directly from the bronchiolar wall. Horses lack these respiratory bronchioles and the terminal non-respiratory bronchiole connects directly to the alveolar duct (McLaughlin et al 1961, Tyler et al 1971). In the bronchioles, the epithelium is a single layer of cuboidal cells (Fig. 1.14). The primary secretory cell is the Clara cell that has an extensive network of smooth endoplasmic reticulum (Plopper et al 1980). Ciliated epithelial cells are also present in the bronchioles but are less dense in number than in the larger airways. Mucus-secreting goblet cells do not occur in the bronchioles of young healthy horses but are found in horses that have airway inflammation (Kaup et al 1990). As in the bronchi, a layer of smooth muscle encircles the bronchioles.

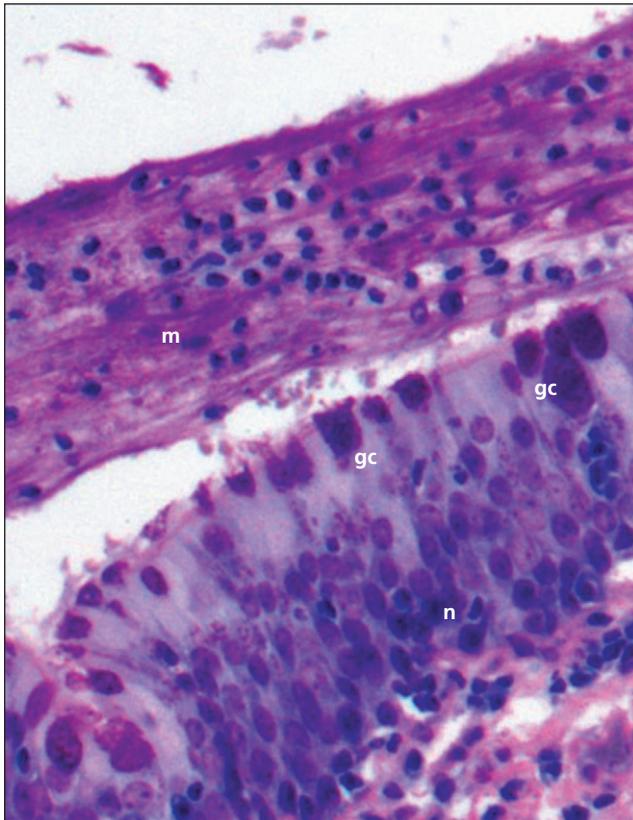


Fig. 1.12. Bronchial epithelium of a horse with recurrent airway obstruction (heaves). Note the thick layer of mucus (m) containing many neutrophils, the multiple layers of epithelial nuclei (n) in the pseudostratified columnar epithelium, and the mucus-producing goblet cells (gc) interspersed among the ciliated epithelium. (Giemsa stain.)

Alveolar ducts and alveoli

Gas exchange occurs in the alveolar ducts and alveoli. The former are extensions of the bronchioles and can form several generations, each of which has numerous alveoli in its walls. The alveolar structure of the lung results in a large surface area for gas exchange. In a 510-kg horse, the total alveolar surface area is reported to be 2,456 m² (Gehr & Erni 1980) (one-quarter of a hectare) of which about 1,500 m² is in contact with pulmonary capillaries and available for gas exchange (Gehr & Erni 1980, Stone et al 1992). Two types of epithelial cells line the alveoli. The terminally differentiated squamous type I cell covers most of the surface but the cuboidal type II cell is more numerous (Stone et al 1992). The type I cell is characterized by very thin cytoplasmic extensions that extend away from the nucleus over the alveolar surface in the same way that egg white extends away from the egg yolk in a frying pan. Its cytoplasm has few organelles other than pinocytotic vesicles and a few mitochondria. By contrast with the type I cell, the type II cell shows evidence of being metabolically very active. Its cytoplasm is rich in

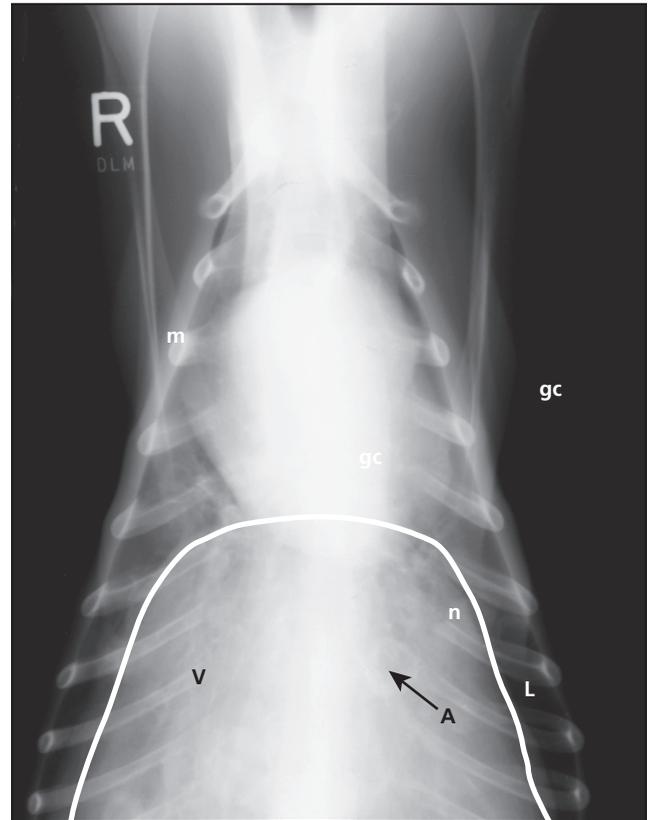


Fig. 1.13. Ventrodorsal radiograph of the lung of a foal with pneumonia. The shadow of the diaphragm is outlined. Note that the lung (L) extends far caudally and dorsally on either side of the abdomen. The bronchi and vessels (V) in the caudal part of the lung are difficult to see because the abdomen overlies that part of the lung. Without careful scrutiny, it would be easy to miss the abscess (A) because it is obscured by the abdominal contents.

endoplasmic reticulum and the Golgi apparatus is large. The characteristic feature of the type II cell is the presence of large vesicles that contain the precursors of pulmonary surfactant, the phospholipid that is essential for lung stability. Surfactant is released from the type II cells in the form of myelin coils that unfurl when they reach the alveolar surface. Type II cells also re-uptake components of surfactant to be resynthesized. In addition to production of surfactant, type II cells also reabsorb edema fluid from the alveoli, and, when the alveolar surface is injured and type I cells are lost, the type II cells differentiate into type I cells to recover the surface.

The alveolar septum

Neighboring alveoli are separated by the alveolar septum that contains the pulmonary capillaries (Fig. 1.15). The air is separated from the capillary blood by the type I epithelial cell, a basement membrane, a variable amount of interstitium and the endothelial cell. The quantitative

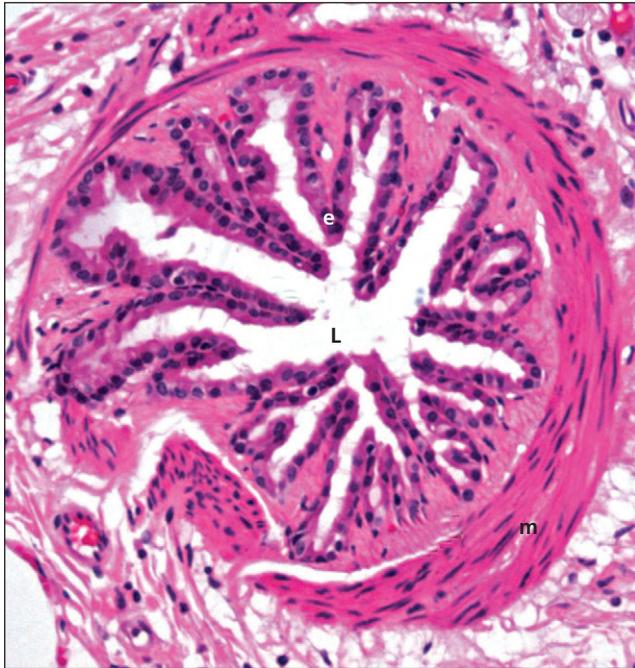


Fig. 1.14. Bronchiole from a healthy horse. The epithelial layer (e) consists of a single layer of cuboidal cells that encircles the lumen (L). The epithelium is folded because the lung was collapsed when the section was taken. In life the perimeter of the airway would form a circle. A layer of smooth muscle (m) encircles the airway. There are no mucus-producing goblet cells in this healthy bronchiole. (Hematoxylin and eosin)

characteristics of this barrier have been described in the horse and other species (Stone et al 1992). On one side of the septum, the separation of air and blood is less than $0.1 \mu\text{m}$ because there is no interstitium and few organelles in the epithelial or endothelial cells. On the opposite side, the membrane is somewhat thicker because an interstitial space separates the two cell types and they contain more organelles. It is thought that gas exchange occurs on the thin side of the septum and fluid exchange between the capillary and interstitium occurs on the thicker side

(Fig. 1.16). The capillary network in the septum is so extensive that it has been compared to a sheet of blood. Because there are no lymphatics in the alveolar septum, fluid that filters from the pulmonary capillaries must track through the interstitium to the lymphatics in the peribronchial tissue.

Lymphatic networks

The lung possesses two networks of lymphatics. One surrounds the bronchi while the other is subpleural. Both these networks connect to the hilar and mediastinal lymph nodes and drain into the thoracic duct.

The Pulmonary Circulation

The pulmonary circulation receives the whole output of the right ventricle and delivers it through the pulmonary capillaries and back to the left atrium. It is the branch of the circulation involved in the uptake of oxygen and removal of carbon dioxide. Its anatomy and function are described in Chapter 3.

The Bronchial Circulation

The bronchial circulation is a branch of the systemic circulation from which it receives about 2% of the cardiac output (Magno 1990). It provides the nutritional blood flow to the walls of the bronchi and large blood vessels and to the pleura. In the bronchi, the submucosal plexus of bronchial vessels is important for warming and humidifying air and in the immune response. As the intensity of exercise increases, so does the magnitude of bronchial circulatory blood flow (Manohar et al 1992). The venous drainage of the bronchial circulation is complex. Some returns to the azygos vein but some also enters the pulmonary veins thereby adding venous blood to the oxygenated blood that is leaving the capillaries. If the blood supplied by the pulmonary circulation becomes reduced in

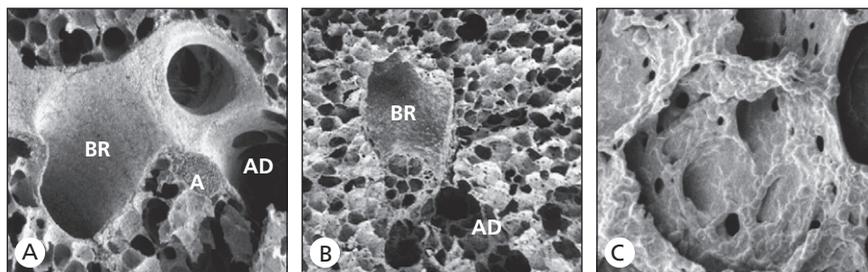


Fig. 1.15. Scanning electron micrographs of the alveoli of a horse. (A) An artery (A) adjacent to several bronchioles (BR). An alveolar duct (AD) and alveoli are also visible. (B) A bronchiole (BR) terminating in an alveolar duct (AD) and surrounded by alveoli. (C) Several alveoli that have been overdried during preparation so that the outlines of the numerous erythrocytes in the alveolar capillaries are visible. Reproduced with the permission of W.S. Tyler, University of California, Davis, CA.

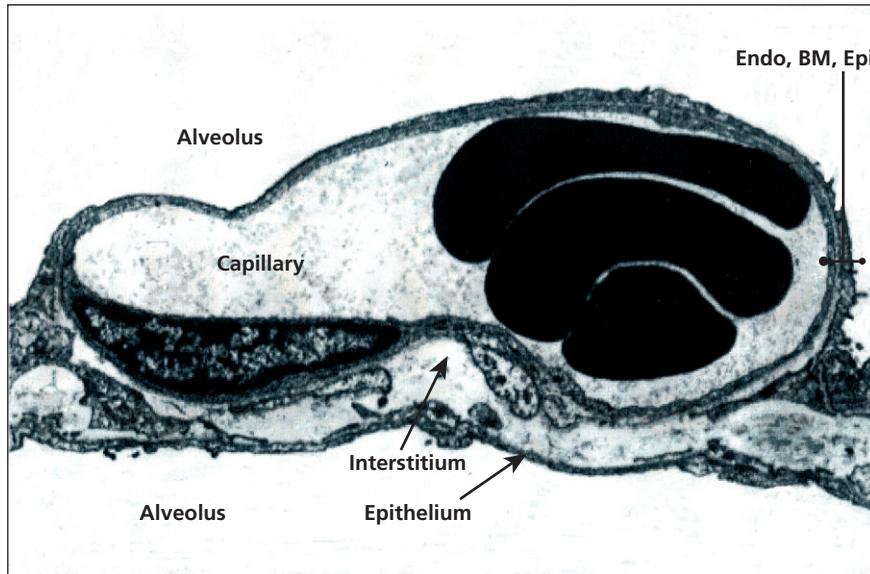


Fig. 1.16. Transmission electron micrograph of a pulmonary capillary in the alveolar septum. The septum separates two alveoli. On the lower side of this capillary, the endothelium and epithelium are separated by a thick layer of interstitium that allows movement of interstitial fluid within the alveolar septum. On the upper side, the endothelium (Endo) and epithelium (Epi) are separated only by a thin common basement membrane (BM). This thin side, which is less than $1\ \mu\text{m}$ in thickness, is probably where most gas exchange occurs.

a region of lung, the connections between the pulmonary and bronchial circulations allow blood to enter that region from the bronchial circulation thereby tending to reduce the chance of ischemia.

The bronchial circulation is involved in inflammation, healing and remodeling of the lung. In horses with lesions of exercise-induced pulmonary hemorrhage, the bronchial circulation proliferates in the walls of the inflamed airways (O'Callaghan et al 1987). In humans, this neovascularization can be a cause of hemoptysis.

The Thorax

The horse's thorax has 18 ribs that form a fairly rigid protection for the intrathoracic organs. Each rib articulates dorsally with the vertebral column and is extended ventrally by a costal cartilage. The costochondral junctions can be palpated beneath the skin in a line that follows roughly a line drawn between the tuber sacrale and the elbow. The first eight ribs articulate directly with the sternum. The costal cartilages of ribs 9 to 17 are attached to each other by elastic tissue to form the costal arch. The last rib is a floating rib. The thorax is long and laterally compressed at its anterior end. Because of the downward curvature of the vertebra in the anterior thorax, the thoracic inlet is only 18–20 cm high and it is about 10 cm wide. The proximal forelimb covers the cranial part of the thoracic wall to the level of the fifth or sixth rib (Fig 1.11), while the thinner serratus ventralis thoracis muscle covers much of the first eight or nine ribs. The thoracic wall con-

sists of the skin, subcutaneous tissues, intercostal muscles, ribs, parietal pleura, sternum and thoracic vertebrae.

The diaphragm is attached to the thoracic wall along the eighth to tenth costal cartilages, then to the costochondral junctions of ribs 10 to 13 and then to the ribs at increasing distances from their costochondral junctions until it reaches the last intercostal space. In the median plane, each hemidiaphragm extends cranially to the level of the fifth or sixth rib, which approximates to the level of the olecranon in the standing horse. Because the cupola of the diaphragm extends so far cranially and its attachments are to each rib, much of the thoracic cavity is lateral to or above the abdomen (Figs 1.11 and 1.13). For this reason, borborygmi originating in the intestines are frequently heard during auscultation of the lung. The diaphragm consists of a tendinous center through which passes the vena cava. The striated muscle is arranged around the diaphragm's periphery. It consists of the pars costalis, which originates from the ribs and inserts into the central tendinous portion, and the left and right crura, which are connected to the vertebrae by tendons and insert in the tendinous center of the diaphragm. The left crus is pierced by the aorta, esophagus and vagus nerve. The phrenic nerve innervates the muscles of the diaphragm.

The pleurae

The pleurae cover all of the surfaces of the thoracic cavity without interruption. The visceral pleura covers the lungs and joins the mediastinal pleura at the hilar region. The

parietal pleura is described as costal, diaphragmatic and mediastinal where it covers the ribs, diaphragm and mediastinal structures, respectively. In some horses the two pleural sacs communicate via small fenestrations where the two thin layers of mediastinal pleura are apposed in the caudal mediastinum. The pleural and peritoneal cavities communicate via diaphragmatic pores and lymphatics. The parietal pleura has numerous stomata connected to subpleural lymphatics that serve to remove excessive pleural fluid, protein, and cells. The pleural cavity is a potential space that normally contains only a small volume of clear to slightly turbid yellowish, non-clotting pleural fluid. The chest wall and parietal pleura, but not the visceral pleura, are well endowed with sensory nerve fibers from the intercostal nerves, and consequently pleural inflammation can cause overt pleurodynia (thoracic pain). The parietal pleura receives its blood supply from the intercostal vessels, with the principal vessels running immediately caudal to each rib. Blood supply to the visceral pleura is from the pulmonary and bronchial vasculature with capillary loops occupying the deep aspect of the pleura.

The pleurae comprise a single layer of mesothelial cells and underlying connective tissue. Mesothelial cells not only act as an envelope lining the pleural cavities but also have an active role in trans-serosal transport of fluid and electrolytes, aided by apical microvilli that increase their surface area for absorption. Mesothelial cells also synthesize components of the underlying connective tissue, cytokines, growth peptides and chemotaxins. Inflammatory stimuli activate mesothelial cells leading to increased production of biologically active compounds, fibrinolysis and possibly phagocytic function.

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