

Comparative Anatomy of Respiratory System in Vertebrates

Dr Poonam kumari

Associate Professor

Dept Of Zoology

Maharaja college, Ara

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Respiration is the process of obtaining oxygen from the external environment & eliminating CO₂.

- External respiration - oxygen and carbon dioxide exchanged between the external environment & the body cells
- Internal respiration - cells use oxygen for ATP production (& produce carbon dioxide in the process)

Adaptations for external respiration:

1 - Primary organs in adult vertebrates are external & internal gills, swim bladders or lungs, skin, & the buccopharyngeal mucosa

2 - Less common respiratory devices include filamentous outgrowths of the posterior trunk & thigh (African hairy frog), lining of the cloaca, & lining of esophagus

Fishes

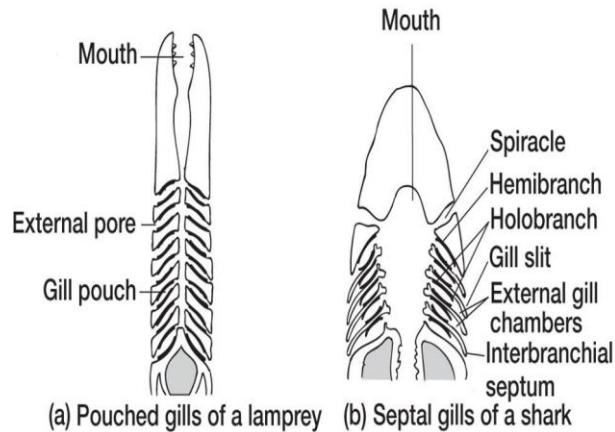
Agnathans

The pharynx is subdivided; the ventral part forming a respiratory tube that is isolated from the mouth by a valve called the velum. This is an adaptation to how the adults feed, by preventing the prey's body fluids from escaping through the gills or interfering with gas exchange, which takes place by pumping water in and out of the gill pouches instead of taking it in through the mouth.

Sharks

Sharks are fish and, like other species of fish, use gills to breathe rather than lungs. There are usually between five and seven gill arches, each bearing one gill slit. In most other fish species, these gills are covered by the operculum, which acts as a lid over the gill. However, sharks do not have this covering. There is also a modified slit, called the spiracle, which lies immediately behind the eye on the shark's head.

Sharks use these gill slits to oxygenate their blood. The spiracle assists in the process of taking water in. As the shark moves forwards, water is taken into the mouth and over the gills. This is called "ram ventilation". When at rest, the shark actively pumps water over its gills. There are gill rakers, which are perpendicular to the gill arches. The rakers support the secondary bars, which direct the water.



Bony Fishes

The operculum of osteichthyans is bony or cartilaginous. It provides a protective cover over the branchial arches and gills they support. In addition, the operculum is part of the dual pump used to ventilate the gills. In cross section, each gill is V-shaped and composed of primary lamellae (gill filaments) that are subdivided into secondary lamellae and supported on a branchial arch. Tiny adductor muscles cross between filaments to control the arrangement of adjacent gills that govern the flow of water across the secondary lamellae. As in most other fish gills, the blood in the secondary lamellae flows one direction and water flows in the opposite direction to establish a countercurrent exchange.

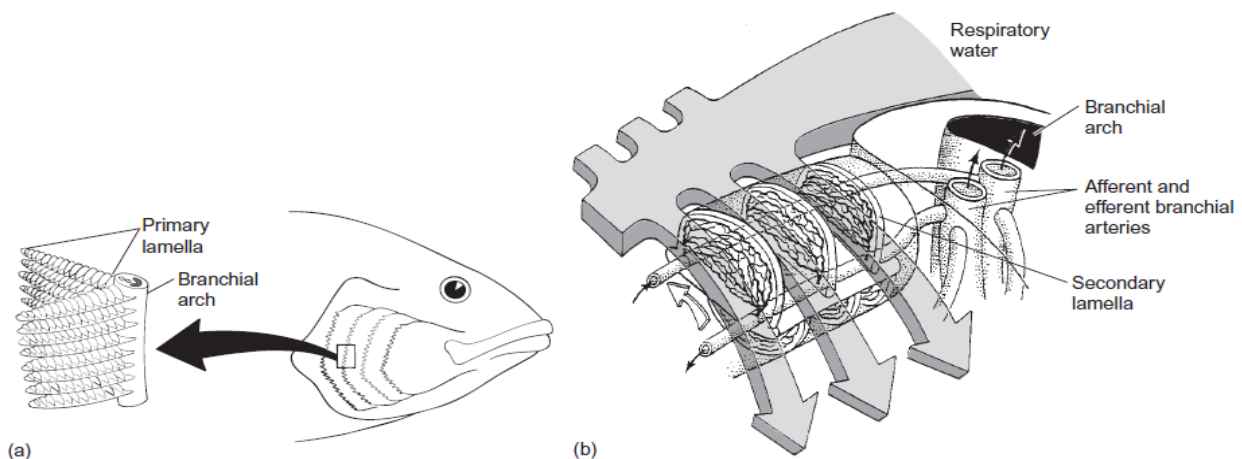
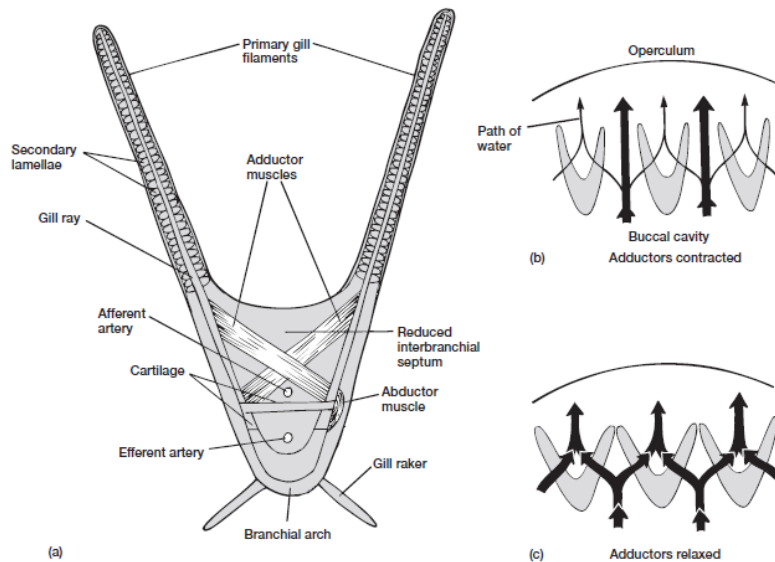


FIGURE 11.19 Gill ventilation in teleost.

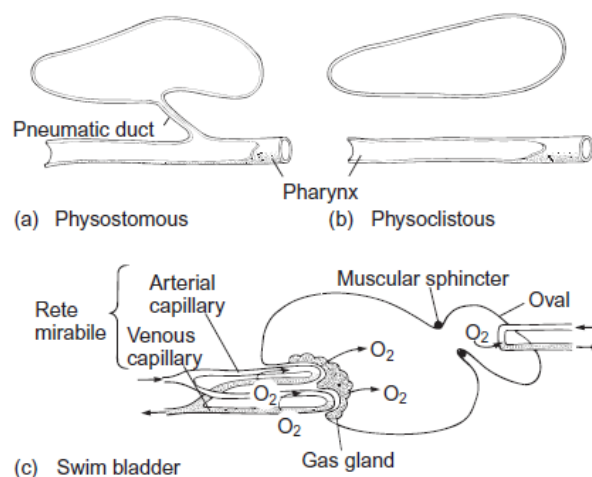
(a) One gill bar is removed, showing the stack of gill lamellae. (b) Water flow is directed across the secondary lamellae opposite to that of blood flowing within each secondary lamella, establishing a countercurrent exchange between them.



Lungs

Air-filled sacs arise early in bony-fish evolution and serve respiratory and hydrostatic functions. In lung fishes and tetra pods, the respiratory function predominates. In the Australian lungfish, the esophagus arises from the floor of the esophagus, but bends around the right side of the esophagus to join a single lung in a dorsal position within the body cavity, a location that is also favorable to buoyancy control. The lungs are subdivided into faveoli. Air forced into these lungs exchanges with capillary blood circulating in the walls of the faveoli. It is not surprising that almost all osteichthyans possess some form of gas bladder (or lung). Air-filled gas bladders give buoyancy to the fish body and help resist its tendency to sink.

Fishes that ventilate a gas bladder do so by gulping and forcing fresh air through the pneumatic duct. Usually, a fish expels spent air as it approaches the water's surface, captures and swallows a new gulp of fresh air, and descends again.

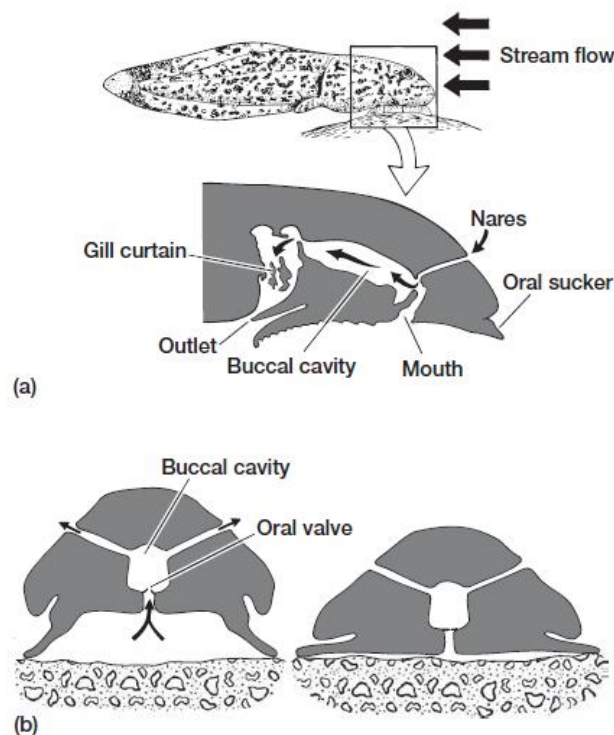


Amphibians

Amphibian Larvae

Salamander larvae typically have both internal and external gills. Pumping action of the throat irrigates the internal gills with a unidirectional stream of water across their surfaces. Feathery external gills are held out in the passing current, allowing water to flow across them. If there is no current or if water is stagnant, the larvae can wave their gills back and forth through the water to irrigate the capillary beds they carry. Larvae of anurans employ buccal and pharyngeal force pumps to produce a unidirectional flow of water across the gills and generate a food-bearing current. The basic mechanism of amphibian gill ventilation includes a buccal cavity and a pharyngeal cavity separated from each other by a valve, the velum. The buccal cavity is separated from the mouth by the **oral valve** and from the nares by an **internal narial valve**. Inhalation depresses the floor of the buccal cavity, which lowers the pressure within it. The velum closes temporarily to prevent entry of water into the pharyngeal cavity, but water fills the buccal cavity through the mouth and nares. Near the end of the inhalation stage, pharyngeal constriction causes a rise in pressure within the pharyngeal cavity relative to the buccal cavity.

This keeps the velum closed and pushes water across the gill curtain. The exhalation stage begins with elevation of the floor of the buccal cavity, raising the pressure within it and forcing the oral and narial valves closed.

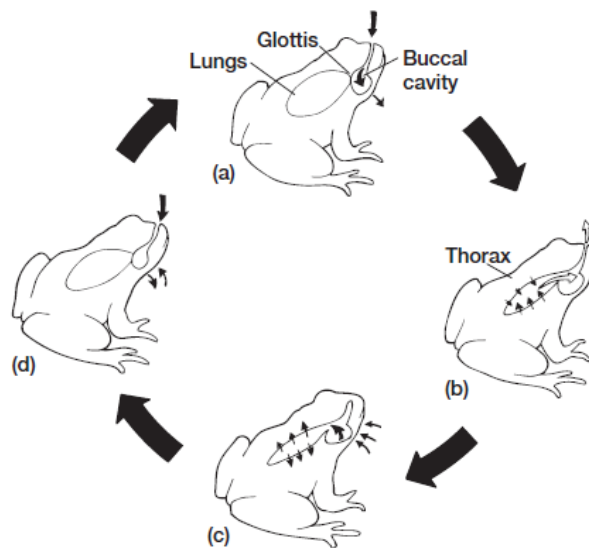


Amphibian Adults

When the amphibian larva undergoes metamorphosis into an adult, gills are lost. Cutaneous respiration continues to play an important role in meeting respiratory demands after metamorphosis, and lungs, if present, are ventilated by a buccal pump. The four stages of lung ventilation in frogs are best understood. In the first stage, the buccal cavity expands to draw fresh air in through the open nares. In the second stage, the glottis opens rapidly, releasing spent air from the elastic lungs. This air streams across the buccal cavity with little mixing and is vented through the open nares. In the third stage, the nares close, and the floor of the buccal cavity rises, forcing the fresh air held in this cavity into the lung through the open glottis. In the fourth stage, the glottis closes, retaining the air that has just filled the lungs, and the nares open again. Between cycles, the buccal cavity may oscillate repeatedly. This rapid oscillation was once thought to turn the lining of the mouth temporarily into an accessory breathing organ. However, experimental evidence refutes this. The capillaries lining the mouth do not serve in gas exchange. Instead, such Buccal oscillations between lung fillings serve mainly to flush the buccal cavity of any stray residue of expired air in the mouth following each ventilatory cycle.

The buccal pump, and hence the buccal cavity, in frogs is also deployed in producing vocalizations that play a key role in the social organization and breeding success of frogs. Evolutionary modifications of the buccal cavity consequently affect three significantly different functions.

In both groups, fresh air is pushed into the lungs against pressure. To some extent then, frogs have retained the basic pattern of lung filling deployed by lungfishes. However, all of this changes in reptiles, birds, and mammals. The mechanism of ventilation in these groups is the aspiration pump, a departure from that of amphibians and earlier air breathing fishes.



Reptiles

Pharyngeal furrows and occasionally pharyngeal slits appear during the early embryonic development of reptiles, but they never become functional after birth.

In some groups, supplemental cutaneous respiration is significant, but for the most part, paired lungs meet their respiratory needs.

The lungs of snakes and most lizards typically include a single central air chamber into which faveoli open. Like purse strings, cords of smooth muscle define and encircle the opening into each faveolus. The thin walls of each carry capillary beds and may be sub divided by even smaller internal septa. Sometimes the faveoli are reduced in the posterior part of the lung, leaving it as an on exchange region. In monitor lizards, turtles, and crocodiles, the single central air chamber itself is subdivided into numerous internal chambers that receive air from the trachea.

These internal chambers are ventilated by respiratory movements, whereas the exchange of gas between the faveoli and these chambers appears to occur by diffusion.

Filling of the lungs in all reptiles is based on an aspiration pump mechanism, although the anatomical parts that actually participate may differ. The aspiration pump acts on the walls of the lung to change its shape and induce airflow in or out. Ribs alter the shape of the body walls around the lungs, and intercostal muscles running between these ribs move them. In lizards, for instance, sets of intercostal muscles actively move the ribs forward and outward during inhalation.

The result is to enlarge the cavity around the lungs, decrease pressure within them, and draw air into the lungs. During active exhalation, different sets of intercostal muscles contract to fold the ribs back and inward, thus compressing the lungs within their cavity and expelling air. Occasionally, exhalation is passive. In this instance, muscle contraction is minimal, and gravity (and some elastic recoil) acts on the ribs, causing them to compress the lung cavity. Between breaths, the glottis is closed to prevent premature escape of air.

In snakes, the long, narrow lungs extend through most of the length of the body. In primitive snakes, as in other reptiles, the lungs are paired, but in many advanced snakes, the left lung is reduced and often lost entirely. In most snakes, faveoli are prominent anteriorly, but they decrease gradually and become absent posteriorly, producing two regions of the lung, an anterior respiratory portion (faveoli) and a posterior saccular portion (avascular). Ribs and associated muscles run the entire length of the thorax so that regional compression and expansion of the body wall expand or deflate the lung. Opening and closing of the glottis are synchronized with these movements. Gas exchange occurs in the respiratory portion of the lung. The saccular portion of the lung acts as a bellows when the anterior body is occupied with different functions and unavailable to compress or expand the lung. For instance, when a snake swallows prey, the body becomes distended as food passes slowly through the esophagus, yet ventilation of the lungs must continue.

Although the trachea, reinforced with semicircular rings of cartilage, stays open, the anterior body cannot act as the aspiration pump. Instead, the posterior body behind the prey expands and contracts, causing the saccular lung to fill and empty the lungs.

Ventilation in turtles represents a special problem in design. The shell around the lungs prevents changes in shape and precludes aspiration pumping using the ribs.

In soft-shelled turtles, movements of the hyoid apparatus draw water in and out of the pharynx. Oxygen is absorbed in the pharynx to sustain the turtle while it is submerged. In snapping turtles, the plastron is reduced, permitting deformations of the body wall that contribute to lung ventilation.

More commonly, in-and-out movements of the limb Salter pressure on the lungs, and special sheets of muscles within the shell change pulmonary pressure.

Turtle lungs and other viscera reside in a single fixed cavity, so any change in volume alters pressure on the lungs.

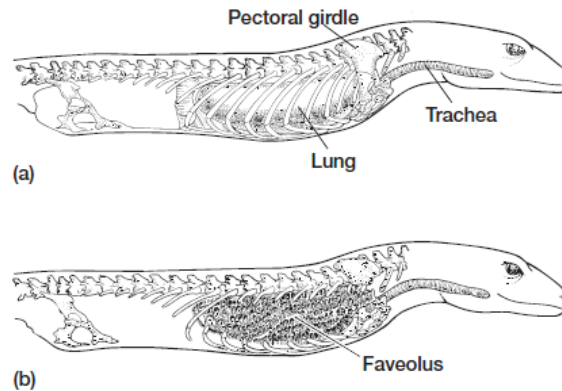


FIGURE 11.26 Lung ventilation in a lizard. (a) The lungs are located in the thorax, surrounded by ribs and connected to the trachea. Compression and expansion of the rib cage force air in or out of the lungs. (b) Cutaway view of the internal lining of the lungs showing numerous faveoli that collectively give the lining a honeycomb appearance. The internal faveoli of the lungs increase their respiratory surface area and function in gas exchange with capillaries lining their walls.

Mammals

An aspiration pump ventilates the lungs of mammals. Changes in the shape of the rib cage and piston like action of a muscularized **diaphragm** contribute to this pumping mechanism. The diaphragm consists of **crural**, **costal**, and **sterna** parts, all of which converge on a **central tendon**. Unlike the diaphragmatic muscles of crocodiles, which are located posterior to the liver, the diaphragm of mammals lies anterior to the liver, and acts directly on the **pleural cavities** in which the lungs reside. Intercostal muscles run between the ribs. The transverses abdomen is, serratus, and rectus abdomen is that are inserted on the ribs and originate outside the rib cage all aid in mammalian lung ventilation.

Ventilation

Mammalian **ventilation** is bidirectional and involves the rib cage and diaphragm. Upon inhalation, the external intercostal muscles contract to rotate the adjacent ribs and medial sternum forward. Because the ribs are bowed in shape, this rotation includes an outward as well as a forward swing of each arched rib. The result is to expand the space that the rib cage encloses around the lungs. Contraction of the dome-shaped diaphragm causes it to flatten, further enlarging the thoracic cavity. The elastic lungs expand to fill the enlarged thoracic cavity, and air is drawn in.

During active exhalation, internal intercostal muscle slant in the opposite direction of the relaxed external intercostals and pull the ribs back. Relaxation of the diaphragm causes it to recoil and resume its arched, dome shape. Rib retraction and diaphragm relaxation decrease chest volume, forcing air from the lungs. Elastic

energy stored in the lung and gravity acting to fold or collapse the rib cage may aid exhalation.

Although scientists agree on the muscles that control mammalian breathing, their precise functions have proved elusive, partly because of the surprisingly complex pattern of rib movement and partly because the rib cage and diaphragm are not equally involved in ventilation at all times. For example, during quiet breathing, only inhalatory muscles may show activity. At such times, exhalation muscles may not contract, and compression of the rib cage results from elastic and gravitational forces. As you can confirm for yourself, it is even possible to ventilate your lungs moving only the diaphragm and not the rib cage. When supporting vigorous ventilation during exercise, the rib cage, diaphragm, and most muscles are involved. To complicate the matter further, there appears to be a coupling of breathing cycles with loco motor cycles so that both are synchronized.

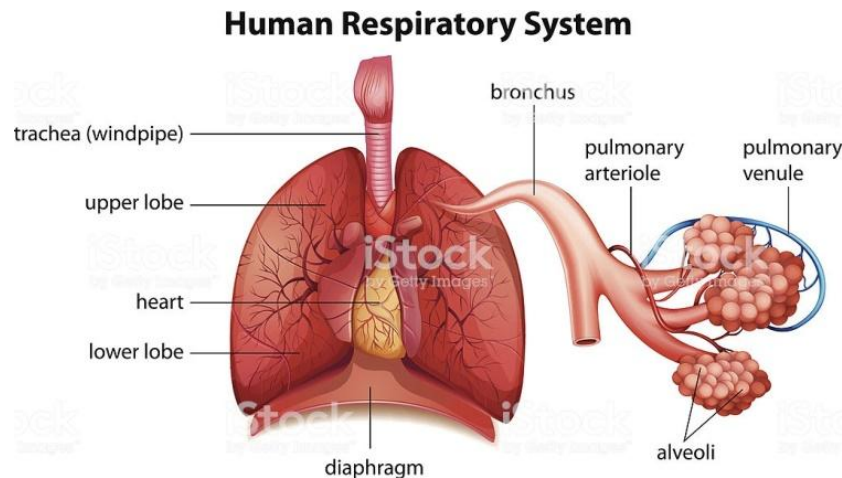
The mammalian diaphragm lies immediately posterior to the lungs and separates the thoracic cavity containing the lungs from the abdominal cavity containing other major viscera.

When an animal is at rest, the muscularized diaphragm is the principal component in mammalian lung ventilation. However, during locomotion in quadrupedal mammals, the rib cage may receive ground reaction forces through the forelimbs that slightly change its shape. Further, the abdominal viscera, somewhat free to move within the body cavity, slide forward and backward in synchrony with the rhythm imposed on the body by the pattern of limb oscillation. The abdominal viscera act as a kind of “piston,” first pressing anteriorly on the thoracic cavity and then sliding posteriorly, releasing pressure on the lungs. A running mammal takes advantage of this rhythmic movement of the viscera, expelling air when the viscera press against the thorax and inhaling when they move away. Thus, in cursorial mammals, breathing patterns and loco motor gait are often coupled.

Gas Exchange

As we have seen in reptiles, faveoli along the interior walls of the lungs form the respiratory exchange surface. Air is drawn into the center core of the lung and diffuses outward into the faveoli. However, in mammals, the sites of respiratory exchange are reached via a different route. The respiratory passage way (including trachea, bronchi, bronchioles) repeatedly divides, producing smaller and smaller branches until they finally terminate in blind-ended compartments, the **alveoli**, which characterize the respiratory bronchioles and air sacs. The trachea, bronchi, and terminal bronchioles that transport gas to and from the alveoli are called the

respiratory tree in recognition of their branching pattern. No gas exchange occurs along the conducting passageway of the respiratory tree until air reaches the respiratory bronchioles and alveoli. In mammals, the total alveolar area is extensive, perhaps over ten times that of amphibians of similar mass. Such a large exchange area is essential in mammals to sustain the high rate of oxygen uptake required by an active endo therm. The nasal passages not only form part of this conducting system but serve to warm and moisten the entering air.



Birds

Cutaneous respiration is insignificant in birds. The almost exclusive respiratory organ is the lungs. Like mammals, birds have two lungs connected to a trachea and ventilated by an aspiration pump. Beyond this, however, the structural similarities are few. For example, there are no blind-ended alveoli in and out of which air moves. Instead, the conducting passages branch repeatedly and eventually form numerous tiny, one way passageways, the **para bronchi**, that permit air to flow through the lungs. Small **air capillaries** open off the walls of each para bronchus, and gas exchange with the blood actually occurs in the air capillaries. Further, nine avascular **air sacs** are connected to the lungs, although they are tucked in among the viscera and extend into the cores of most large bones. Thus, the bones of birds contain air, not marrow. From 6 (house sparrow) to 12 (shorebirds) air sacs may be present. Generally, the anterior air sacs include the single **inter clavicular sac** and the paired **cervical** and **anterior thoracic air sacs**. The posterior air sacs include the paired **posterior thoracic** and paired **abdominal air sacs**.

The trachea is divided into two **primary bronchi**, (meso bronchi) that do not enter the lung but extend posteriorly to reach the posterior air sacs. Along the way, the primary bronchi give rise to numerous branches, the most prominent of which include **latero**, **ventro**, and **dorso bronchias** well as **secondary bronchi**. These lead to the para bronchi. During passage through the para bronchus, gases diffuse

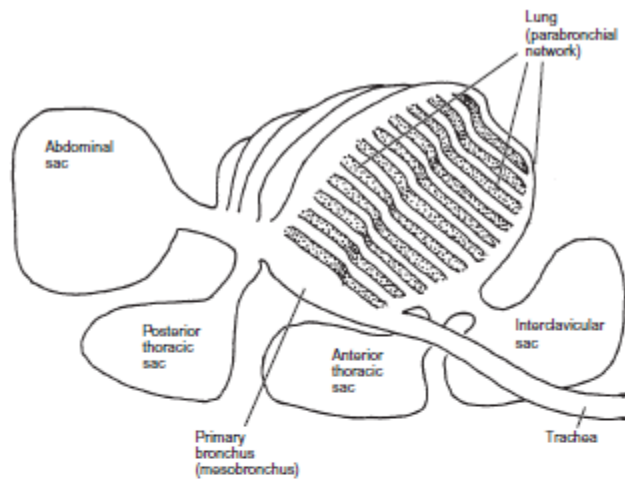
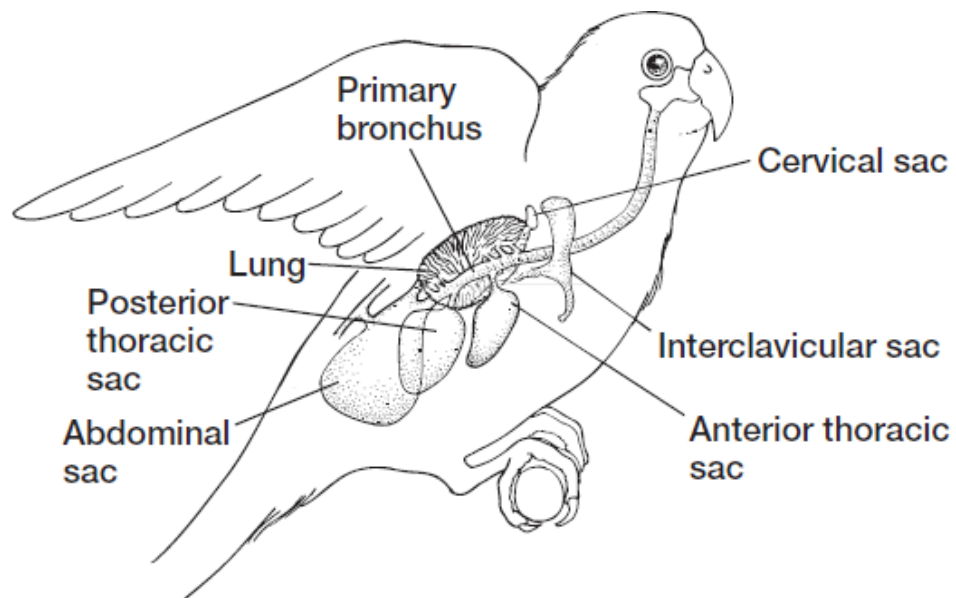
between the lumen of the para bronchus and the connecting, blind-ended air capillaries.

Oxygen diffuses in turn from the air capillaries into the adjacent blood capillaries that give up carbon dioxide to the air capillaries. Thus, the walls of air and blood capillaries constitute the sites of gas exchange.

Within this vast system of connecting passageways, there are no valves to suggest what the pattern of airflow might be. This has led to much speculation about the roles played by the different parts of the respiratory system. Without giving it much thought, some have proposed that air sacs function to lighten the bird like helium balloons. But because air in the sacs has the same density as air outside the bird, the air sacs provide no lift. Adding air sacs does not make the bird lighter.

Others propose that air sacs serve to cool hot testes, but female birds have similar sacs. Certainly, air sacs are not a prerequisite for flight, because bats, who have typical mammalian lungs, are good fliers and can even, on occasion, migrate long distances.

Recent research suggests another possibility—air sacs act as bellows. Details of this mechanism are still debated, but some aspects are understood. If we follow a single breath, its passage through the sacs and lungs includes two complete cycles of inhalation and exhalation. During the first inhalation, air enters the trachea, passes along the primary bronchi, and then is divided: Some air passes directly to the lungs, and the rest fills the posterior air sacs (posterior thoracic and abdominal air sacs). Upon the first exhalation, air from these posterior air sacs now flows through the lungs, displacing the spent air that exits via the trachea. As the second inhalation begins, the entering air again divides, some refilling the posterior air sacs and the rest flowing through the lungs, pushing the remainder of the spent air of the previous cycle out and temporarily into the anterior air sacs (anterior thoracic and inter clavicular air sacs). With the second exhalation, air in these anterior sacs now exits along with air from the lungs, replaced by air from the posterior air sacs, which now flows through the lungs. Thus, this pattern of ventilation produces a nearly continuous, unidirectional flow of fresh air across the lungs. Speculating further, such a unidirectional flow may also establish a crosscurrent exchange within the lung, with air flowing from posterior to anterior air sacs as circulating blood flows next to it in the opposite direction.



(a)

