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Respiratory system

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The system of organs involved in the acquisition of oxygen and the elimination of carbon dioxide by an organism. The lungs and gills are the two most important structures of vertebrates involved in the phase known as external respiration, or gaseous exchanges, between the blood and environment. Internal respiration refers to the gaseous exchanges which occur between the blood and cells. Certain other structures in some species of vertebrates serve as respiratory organs; among these are the integument or skin of fishes and amphibians. The moist, highly vascular skin of anuran amphibians is important in respiration. Certain species of fishes have a vascular rectum which is utilized as a respiratory structure, water being taken in and ejected regularly by the animal. Saclike cloacal structures occur in some aquatic species of turtles. These are vascular and are intermittently filled with, and emptied of, water. It is thought that they may function in respiration. During embryonic life, the yolk sac and allantois are important respiratory organs in certain vertebrates.

Structurally, respiratory organs usually present a vascular surface that is sufficiently extensive to provide an adequate area of absorption for gaseous exchange. This surface is moist and thin enough to allow for the passage of gases. This article treats the embryology and physiology of the gills; embryology, anatomy, and histology of the vertebrate lung; and vertebrate respiratory physiology. *See also:* Allantois (/content/allantois/023900); Hemoglobin (/content/hemoglobin/313800); Lung

(/content/lung/392100); Yolk sac (/content/yolk-sac/753600)

Gill Development and Anatomy

In the most primitive chordates, the Acrania, the gills are really part of the digestive, rather than the respiratory, system. However, in all these animals, except one genus, *Rhabdopleura*, there is a pharyngeal region in which there are one or more (usually many) paired visceral clefts with delicate intervening strands of tissue which constitute the primary bars or arches; these are greatly augmented in some cases by the down growth of tongues of tissue between them, which are termed secondary bars. There are also transverse connecting strands termed synapticulae in some species, such as *Branchiostoma*. The bars and synapticulae usually contain supporting gelatinous or chitinoid rods; in *Branchiostoma*, the primary bars contain prolongations of the dorsal coelom. Most important, blood circulates through the bars and synapticulae during respiration and is aerated by water drawn in through the oral opening by the ciliated endoderm and passed out through the interstices of the basketlike structure. This arrangement acts primarily as a strainer to retain food particles (**Fig. 1**).



Fig. 1 Branchiostoma lanceolatus. (a) Transverse section of the pharyngeal region. (b) Transverse section of the intestinal region. (After T. J. Parker and W. A. Haswell, A Textbook of Zoology, 6th ed., Macmillan, 1956)

The gills of chordates are located in the pharyngeal region. They are always related to the visceral arches and clefts. The latter structures are so defined because, in vertebrates that respire entirely with lungs, the arches and clefts, or incipient clefts, lack gills, which exist only in the embryo and disappear or are highly modified in the adult. They always arise by the outpushing of endodermal pouches, which are usually dorsoventrally elongated, through the mesoderm, which contact corresponding inpushings of ectoderm. Where these meet and break through, clefts are formed, and the intervening concentrations of mesoderm form the arches, which are covered internally by endoderm and externally by ectoderm. The number of clefts, the eventual content of the arches, and the extent to which the latter develop gills of one type or another are indicated in the following discussion.

Visceral arches in craniates

In this group, the typical number of paired visceral arches and pouches or clefts is six, including the mandibular and hyoid arches with the intervening spiracle. However, the number may be greater in some elasmobranchs and cyclostomes, and less in some animals where these structures occur only in the embryos. In the latter cases, the number of pouches which actually become clefts is usually very limited; for example, there are three pairs in the chick, one pair in the cow, and normally none in the pig and human, in which the number of arches is reduced to five, with the last vestigial. The blood vessels found in the arches in animals other than fish are of considerable phylogenetic interest. Thus, the vessels in the third visceral arches become the roots of the internal carotids; those of the fourth form a pair of aortae in amphibians and reptiles, or one of this pair forms an aorta in birds and mammals; and those in the fifth pair give rise to the pulmonary arteries. The pulmonary

arteries are really the sixth pair of aortic vessels because a vestigial fifth pair occurs, together with the sixth, in the fifth visceral arches.

In fishes, the aorta in each of the arches which bear gills, commonly the posterior four pairs, becomes altered and augmented to form the afferent and efferent vessels of the gills of that arch. The precise method of alteration and final condition vary somewhat in different groups of fishes.

In the elasmobranchs, the ventral two-thirds of the original aortic arch persists as the afferent vessel. This becomes disconnected from the dorsal third, from which two vessels grow ventrally. These and the dorsal third thus become the efferent aortic arteries and are connected with the afferent vessel through gill capillaries in a manner to be described below (**Fig. 2***b*). The more anterior of the two growing vessels drains the posterior half of the gill pouch preceding it, while the posterior half drains the anterior half of the gill pouch following. In each arch, the two efferent vessels have transverse connections midway between them, and all the efferent vessels on a side are eventually united by dorsal and ventral vessels. The teleost condition represents essentially the reverse of what occurs in the elasmobranchs with respect to the origin of the afferent vessel, whereas most of the original aortic arch forms the efferent vessel. Teleosts also have only one efferent vessel in each visceral arch (Fig. 2*d*). An intermediate form (Fig. 2*c*) with respect to the origins and character of these vessels occurs in *Acipenser, Amia*, and *Lepisosteus*, although in detail these forms are not precisely as shown in the diagram.



Fig. 2 Diagrams of the development of adult branchial vessels in various fishes. (*a*) Original continuous embryonic arch cross-lined. (*b*) Selachian. (*c*) Intermediate form, such as *Acipenser*. (*d*) Teleost: newly developed vessels, white. In *b*, *c*, and *d*, the original arch is interrupted. (*After E. S. Goodrich, Studies on the Structure and Development of Vertebrates, Macmillan, 1930*)

Branchial gills

The term branchial gills is used because there are other gills and structures functioning as gills, which are not in the pharyngeal region. There are generally considered to be two kinds of branchial gills, external and internal. Because the actinopterygian internal gill is apparently derived from the elasmobranch type, the elasmobranch gill is discussed first.

Elasmobranch gill

In these fishes, there develops within each branchial arch a delicate cartilaginous bar slightly proximal to the vessels, the median afferent and two lateral efferent vessels, which have already been described. The arches also become supplied by

branches of the ninth and tenth cranial nerves (the hyoid by the seventh) and acquire muscle fibers derived from the walls of coelomic extensions by which the arches are temporarily invaded. From the outer side of each arch, there grows along its dorsoventral extent a thickish sheet of tissue which develops along its border two indentations or clefts, tending to divide the single sheet into anterior, median, and posterior layers. The indentations never become very deep, however, so that these layers are essentially one. The middle layer or part of this sheet becomes the septum, consisting of connective tissue and a little muscle and covered, where it is free, with epithelium. The anterior and posterior layers on each side of the septum become half gills or hemibranchs, and the whole structure becomes a holobranch (**Fig. 3**).





Along the surface of each anterior and posterior layer, there arises a series of transverse folds of tissue extending outward from the arch (Fig. 4). These are the primary lamellae covered by an epithelium, flat for the most part but with some columnar or cuboidal secretory cells. Between the epithelial cells, there is connective tissue which contains, within each lamella, a loop from the afferent and adjacent efferent vessel of the arch. Another series of folds transverse to these lamellae develops next on the dorsal and ventral surface of each primary lamella. They are the secondary lamellae, whose internal surfaces are connected by numerous columnar cells which send out delicate protoplasmic strands beneath the epithelium of the folds. These cells are termed pilaster cells, and a network of capillaries runs among them connecting the afferent and efferent loops in the respective lamella (Fig. 5). A cartilaginous ray extends outward along the base of each primary lamella at the boundary between the posterior layer or hemibranch and the septum and helps to support the entire gill (Figs. 3 and 4c). In unhatched elasmobranchs, the primary lamellae of the posterior hemibranch grow outward as filaments beyond the external openings of the gill clefts (Fig. 3). These temporary filaments are therefore essentially external gills, although in both origin and structure they are unlike the "true" external gills, described below. Because they occur only in the unhatched fishes, where they float in the albuminous fluid of the egg, they are probably as much for absorption of food as respiration. The septum of each holobranch grows out beyond the gill in these fishes and turns posteriorly beneath the outer skin to the posterior edge of the following cleft, thus forming for the latter an individual cover analogous to the operculum. Each branchial arch develops an anterior and posterior row of papillae, sometimes covered with enamel, on its internal border. These are the gill rakers, which act as strainers to prevent the escape of food (Fig. 3). See also: Elasmobranchii (/content/elasmobranchii/214800)



Fig. 4 Diagrams of elasmobranch and teleost gill structure. (*a*) Gill arch and gill (hemibranch) from the right side of the head of an elasmobranch; posterior view. (*b*) Same view of teleost arch and gill. (*c*) Horizontal section along the length of a pair of primary lamellae and the septum of the holobranch of an elasmobranch. (*d*) Horizontal section through three tissue layers between primary lamellae of an elasmobranch. (*e*) Horizontal section along the length of a teleost holobranch. (*f*) Horizontal section between the filaments of a teleost holobranch, hence through the arch and remains of the septum only.



Fig. 5 Diagram of a section through a part of a secondary lamella of the gill of an elasmobranch fish, showing connection of the secondary lamella with a primary lamella.

Holocephalan gills

In the subclass Holocephali, the gills are similar to those in the elasmobranchs, although arranged slightly differently with respect to the arches, and are covered by an operculum.

Cyclostome gill

Although this class is considered the most primitive of all the craniates, its consideration has been delayed because the gills present a highly specialized condition most easily described as a variant of the elasmobranch type. The early development is similar to that in elasmobranchs. The septa are soon drawn out, however, so that the clefts become elongated tubes that sometimes open separately, as in *Bdellostoma*, or unite to open through a single orifice, as in *Myxine*. The gills proper have primary and secondary lamellae, as in the elasmobranchs, and occur as hemibranchs on the sides of the septa near the pharynx where the tubes become enlarged into spherical pouches. The pouches open directly either to the pharynx or through very short ducts. The pharyngeal region becomes divided during development in the lampreys into a dorsal esophageal portion and a ventral respiratory tube with a blind posterior ending. It is this ventral portion which gives rise to the gill slits. The number of slits, eventually pouches and ducts, varies greatly in this class, ranging from 6 to 14 in different species of *Bdellostoma* (**Fig. 6**).



Fig. 6 Diagrams of head and gill region in (a) Bdellostoma, (b) Myxine, (c) a selachian, and (d) a teleost. Dorsal view partly dissected to show arrangement of gills. (After E. S. Goodrich, Studies on the Structure and Development of Vertebrates, Macmillan, 1930)

Actinopterygian gill

With a few exceptions to be noted below, it is possible to describe the gill situation in most bony fishes by indicating the ways in which it differs from that of the elasmobranchs. Although the holobranchs start to develop from the four branchial arches, as in the latter group, actinopterygians generally lack an open spiracle and the hemibranch related to it; instead, there is often a so-called pseudobranch which is probably glandular. Usually no temporary filamentous external gills occur. The septum grows out only a very short distance, and the anterior and posterior hemibranchs continue to grow out, not as sheets, but as numerous free filaments, corresponding to the primary lamellar folds (Fig. 4b, e, f). The secondary lamellae develop from these in the same way and with the same histological characters, as in elasmobranchs. Although there is only a single efferent artery in the arches of most bony fishes (Fig. 2d), the circulation in the filaments and secondary lamellae is similar to that in the primary lamellae of the former group. Another difference is that, instead of a single ray extending between each primary lamella of the posterior hemibranch and the septum, there is a ray in each pair of filaments of a holobranch (Fig. 4b, e). Lastly there is a single operculum on each side, attached anteriorly to the hyoid arch and covering all the gills. Each operculum is a sheet of tissue in which are embedded three flat bones, the operculars. Gill rakers are present in one or more (often two) rows, sometimes supported by ossifications (Fig. 6d).

There are a few exceptions to the situation just described. The gills of *Acipenser* are about halfway between those of elasmobranchs and typical actinopterygians, and the gill filaments of the lophobranchs consist of tufted processes. *See also:* **Actinopterygii** (/content/actinopterygii/009100)

Dipnoan gill

The Dipnoi may be considered as a sort of connecting link between the fishes and the amphibians. In Dipnoi, there are both internal and apparently true external gills. These latter gills exist in the embryos of all the Dipnoi, and vestiges of them persist in the adult where they are attached to the last three pairs of arches. The internal gills in this group are reduced in correlation with the accessory respiration furnished by the lung or lungs. The septa are somewhat diminished, causing the primary lamellae to become partly filamentous, but without rays. There may be hemibranchs on the hyoids, on the last pair of branchial arches, or on both; there are thus two to four pairs of holobranchs. *See also:* **Dipnoi (/content/dipnoi/198300)**

Other respiratory devices of fishes

In addition to pharyngeal gills of the types indicated, there are other aquatic respiratory mechanisms, which sometimes occur in quite different locations. One such organ, still associated with the pharynx, is found in *Anabas*, the climbing perch; in this fish, some of the pharyngeal bones are developed into folded plates covered with vascular epithelium, through which respiration can occur. This arrangement is covered by the operculum and can be kept moist for extended periods out of water. In one of the phyostomes, *Amphinous*, another pharyngeal derivative acting as a gill consists of vascular sacs opening out through the spiracles. Another peculiar structure used for respiration is the tail fin of an Indian Ocean fish which is immersed while the fish basks out of water. One of the Dipnoi, *Lepidosiren*, despite its lungs, apparently develops respiratory filaments on the paired fins. One of the siluroids employs rectal respiration by sucking in and expelling water from the anus.

Amphibian gills

Almost all amphibians have gills at some time during development and may retain them as adults. At least part of the time these are of the true external type as compared with the filamentous variety previously mentioned. Although some authorities consider that the differences between the internal gills and what are termed true external gills are not very significant, it seems that in this class of animals these differences are sufficient to demand some notice. Generally speaking, true external gills of amphibians may be distinguished from the gills, internal or external, already discussed in that they arise from the outer borders of the gill arches rather than from the sides and differ in certain details of structure. They are sometimes covered by an operculum.

Each gill of the type under consideration is composed of a rather heavy main stem, or rachis, which arises first. This is much thicker than the filaments of real internal gills and has been compared to the modified septum of such gills, which is otherwise entirely lacking in the variety being described. In those amphibians in which external gills are entirely larval, this rachis usually gives rise to rather blunt, short, fingerlike processes. The epithelium of such gills is ciliated, and within the rachis, at least, are muscle fibers so that the gills can be moved. The rachis also contains an arterial loop with extensions into each branch (**Fig. <u>7</u>**). Gills of this type, which are typically found in anurans, such as the frog, spring from the upper parts of the first three pairs of posthyoid branchial arches; those from the first pair are the most prominent, overlapping and concealing the other two pairs.

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Goodrich, Studies on the Structure and Development of Vertebrates, Macmillan, 1930)

These external gills in the anurans and many urodeles soon begin to be absorbed and are covered by back-growths of tissue from the hyoid arches which are continuous across the ventral side of the throat. This tissue contains no cartilaginous or bony plates and constitutes an operculum which fuses with the body wall everywhere posterior to the gill slits, except for one or two small openings termed spiracles through which water from the clefts leaves the branchial chamber. These spiracles are not homologous with those in fish previously mentioned.

Meanwhile, as the operculum is completed, the original external gills are absorbed, and in the Anura double rows of outgrowths on the borders of the first three pairs of branchial arches and a single row on the anterior border of the fourth are developed in their stead. These processes are quite similar to the processes which arose from the main rachis of the external gills, except they are shorter. They are sometimes termed internal gills, chiefly because they are covered by an operculum, but they are still not highly filamentous and lack any part of a septum. Hence, they may be regarded as reduced external gills which are covered (Fig. 7). There are, nevertheless, parts connected with these gills which appear to be closely related to similar parts of the internal gills of fish. The inner margins of the gill arches bear double rows of papillae which correspond, at least in function (that is, acting as strainers), to the gill rakers of the former group.

In certain of the urodeles, such as *Necturus*, the original gills are never covered or absorbed, but persist throughout life as actual external structures. In these cases, however, they differ somewhat from the larval external gills just described. The rachis is larger and heavier, and the secondary branches give rise to numerous fine, short, tertiary outgrowths, giving the whole structure a bushy effect (**Fig. 8**). Although apparently unnecessary, some of the clefts between these sets of gills remain open, for example, one pair in *Pseudobranchus*, two pairs in *Necturus*, and three in *Siren*. This retention of the gills and clefts in such forms has been regarded as an example of neoteny, that is, the persistence of larval characters in sexually mature animals. *See also:* **Amphibia (/content/amphibia/029600)**; **Neoteny (/content/neoteny/448400)**



Fig. 8 External gill form in adult urodeles. (a) Pseudobranchus striatus. (b) Siren lacertina. Drawn from living specimens about 6 in. (15 cm) total length. (After G. K. Noble, The Biology of the Amphibia, Dover, 1931)

Other amphibian respiratory devices

In the amphibians, as in fish, there are various peculiar structures which act as gills. Thus, in the marsupial frog, the two anterior pairs of gills are transformed into vascular wrappings which surround the body, whereas the balancers of some salamanders have been said to have a partly respiratory effect, although this is doubtful. The skin in amphibians certainly has a respiratory function, and that of *Cryptobranchus* is thrown into vascularized folds which are waved about. In the "hairy" frog, the skin of the breeding male develops filamentous processes which aid in respiration.

Gill ectoderm and endoderm

It has been claimed that the epithelium of internal gills is endodermal; but because the boundary between endoderm and ectoderm is indistinguishable by the time the gills arise, this is difficult to prove. It has also been stated that the ectoderm grows inward and covers the areas from which the gill lamellae and rakers develop, thus making the epithelium of these parts ectodermal. This would at least account for occasional rakers with enamel, a substance supposed to be derived only from ectoderm. The point of origin of gills designated as truly external marks their epithelium as clearly ectodermal; this is also probably true of the later internal gills of those amphibians which have them.

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Physiology of Gills

Gills are involved in many functions, including the exchange of oxygen, carbon dioxide, water, acid, inorganic ions, ammonia, and urea between the body and the surrounding water. Much of the transfer of these compounds is passive, but some ions are moved against an electrochemical gradient requiring the expenditure of energy. As a result, the gills are a metabolically active tissue; they consume up to 10–25% of the oxygen uptake of a resting fish.

Functionally, the gills can be considered as a large but thin, epithelial surface layer separating the inside (blood) of the animal from the water. In mammals and other air-breathing vertebrates, oxygen and carbon dioxide are transferred across a lung epithelium. The lung has a very different gross structure than gills and is ventilated in a different way. This is because gills are specialized for exchange of material in water, whereas lungs have evolved for gas exchange in air. Water is about 1000 times more dense and viscous than air and contains only 1/30th as much molecular oxygen; oxygen diffuses 10,000 times more slowly in water than air. To ensure adequate oxygen transfer from water into the animal, most aquatic animals maintain a continual, unidirectional flow of water over the gills, with only very small diffusion distances. The gills are essentially a fine sieve placed in the path of the water flow so that a thin layer of water passes over each region of the gill epithelium.

The exchange units of the gills of fishes are the lamellae, which are arranged in rows on filaments attached to gill arches (**Fig. 9**). Blood flows through the lamellae in the opposite direction to water flow, creating a countercurrent exchange system between blood and water across the gill epithelium. Oxygen is delivered to the gill surface by water flow, diffuses across the gill epithelium, and is carried away in the blood bound to hemoglobin. Oxygenated blood, because of the presence of hemoglobin, contains much more oxygen per unit volume than water. The flow of water over the gills is much greater than the flow of blood through the gills, but the volume flow times oxygen content of blood leaving and water entering the gills is about the same. See also: <u>Countercurrent exchange (biology) (/content/countercurrent-exchange-biology/165100)</u>



Gill ventilation

Water flow over the gills of fishes is maintained by the action of muscular pumps and unidirectional flap valves situated at the mouth and the opercular cleft in bony fishes, and the mouth and gill slits of elasmobranches. The valves are skin folds that permit flow in only one direction, into the mouth and out via the gill slit (**Fig. 10**). The mouth (buccal) cavity expands, drawing water into the mouth; at the same time, the postgill or opercular cavity expands with the outlet valve closed, drawing water over the gills; the opercular and buccal cavities then contract, forcing water out via the gill slit. The buccal force and opercular suction pumps operate at the same frequency but slightly out of phase so that, although water velocity over the gills varies with each breathing cycle, there is nearly always some water flow over the gills, with little or no backflow. The relative importance of the buccal versus the opercular pump differs among species.



Fig. 10 Diagram of the mechanism of generating water flow over the gills of a fish (a) with mouth open and (b) with mouth closed.

Fast-swimming fishes, for example, mackerel and tuna, swim forward with an open mouth so that water is forced over the gills by the forward motion of the fishes. This is referred to as ram ventilation: clearly there is no requirement for, nor are there any, buccal or opercular movements. If, however, the animal stops swimming, then the buccal and opercular pumps are used to generate gill water flow. Some fishes, for example, tuna, swim all their lives and maintain water flow by ram ventilation. The actual water flow rate depends on the swimming speed and is adjusted at any one speed by changing the size of the mouth gap.

Some amphibians have external gills, that is, the gills are not enclosed in a buccal cavity. These gills are not ventilated but are waved around in the water to ensure adequate oxygen delivery. Some other amphibians have neither gills nor lungs but obtain oxygen from the water simply by diffusion across the general body surface.

Low oxygen levels often occur in rivers and lakes and even in the sea. Under these conditions, many fish supplement their oxygen supply by breathing air. The air-breathing organ is usually the swim bladder or a buccal or gut cavity and not the gills, which are retained for gas transfer in water. Some fish are obligate air breathers and die if denied access to air. In this case, the gills are retained for excreting carbon dioxide into water and maintaining ionic balance. The air-breathing organ is for oxygen uptake. This is associated with changes in the circulatory system (**Fig. 11**) culminating in the completely divided circulation of mammals and birds. *See also:* **Swim bladder (/content/swim-bladder/672500)**



Fig. 11 Circulation of the African lungfish, *Protopterus*. Separation of oxygenated blood and deoxygenated blood is achieved by a septum which divides the atrial and ventricular chambers. Blood flows directly to the systemic circulation via the dorsal aorta. The blood is directed to the dorsal aorta or lungs depending on whether the fish is breathing in air or water. (*After D. Randall et al., eds., Eckert Animal Physiology, 4th ed., W. H. Freeman, New York, 1997*)

Blood supply

The fish heart is situated ventral to the gills. Blood, pumped through the gills by the heart, spreads into a thin sheet within the lamellae. Blood pressure within the gill lamellae is high, but the lamellae do not expand because the two sides of the structure are held parallel to each other by a number of cells that contain collagen fibers, called pillar cells. Their collagen fibers are extracellular but contained in lateral folds of the pillar cell and extend along the lateral face of the lamellae, enclosing and supporting the blood space and retaining its thin, sheetlike nature in the face of a high blood pressure. Such high pressures are required to drive blood around the body after it has left the gills.

Level of oxygen transfer

If oxygen levels in the water are low, fishes attempt to maintain oxygen supply by increasing water flow across the gills. If the oxygen requirements of the fishes increase (for example, during exercise), then both water flow and blood flow are increased. The blood is more evenly distributed throughout the gills, and the epithlium is stretched and thinned, enhancing the area and reducing the thickness of the gill epithelium. This increases the capacity of the gills to transfer gases. The fish can increase oxygen transfer across the gills by 10–15 times and so maintain high levels of aerobic exercise. There are oxygen receptors on the gills that respond to reduced oxygen levels in the water and in the blood. These receptors when activated result in an increase in gill water flow. They may also cause a slowing of the heart rate, but cardiac output is not much affected because stroke volume increases. It seems that fishes adjust water and blood flow in the gills to meet the oxygen requirements of the animal rather than to regulate the carbon dioxide excretion of the fishes.

CO₂ delivery to gills

The tissues of animals produce about the same amount (or a little less) of CO_2 as the amount of O_2 consumed. The exact ratio of CO_2 produced to oxygen utilized (the respiratory quotient) depends on whether fats, proteins, or carbohydrates are used as the metabolic substrate. Carbon dioxide is transferred more rapidly than oxygen in tissues and water; thus, if the respiratory system is set to deliver adequate supplies of oxygen from water to the tissues, there will be no problem excreting carbon dioxide in the reverse direction. The only problem concerns the fact that CO_2 reacts with water to form carbonic acid

which dissociates to form bicarbonate. At body pH, most of the CO_2 exists as bicarbonate, but membranes are much more permeable to CO_2 than bicarbonate. Thus, bicarbonate in tissues is converted to CO_2 , diffuses into blood, forms bicarbonate, and is carried to the gills, where it is converted to CO_2 to diffuse across the gills into water. The conversion of CO_2 to bicarbonate and the reverse reactions occur slowly unless catalyzed by the enzyme carbonic anhydrase. Teleost fish red blood cells and fish gills have high levels of this enzyme, but no activity is found in the plasma. Bicarbonate in plasma enters the red blood cell and is converted to CO_2 before diffusing across the gills. Carbonic anhydrase in the gill epithelium appears not to play an important role in CO_2 excretion, but rather couples CO_2 excretion to ion transfer (Fig. 5). Elasmobranchs have carbonic anhydrase activity in the plasma as well as the red blood cells and the gills.

lon transfer

Animals in freshwater lose NaCl across their body surfaces. This loss is counterbalanced by an uptake of NaCl in the gills. Influx of Na⁺ is coupled to H⁺ or NH₄⁺ excretion, whereas Cl⁻ is coupled to HCO_3^- excretion in a separate mechanism. The HCO_3^- excreted via this pathway represents only a small portion (perhaps 5–10%) of the total CO₂ excretion. Sodium uptake via a sodium channel is maintained by the activity of a proton ATPase on the apical membrane of the gill epithelium. The excretion of protons generates a potential across the apical membrane, the inside negative. This creates an electrochemical gradient for sodium and draws sodium into the cell (**Fig. 12**). The sodium is then transferred into the blood via a Na⁺/K⁺ ATPase on the basolateral border of the epithelium. Carbonic anhydrase catalyzes CO₂ hydration and supplies protons for the proton pump. The associated bicarbonate production is exchanged for chloride. Seawater fishes have evolved specialized chloride cells which remove excess NaCl from within the fishes (**Fig. 13**). *See also:* **Osmoregulatory mechanisms (/content /osmoregulatory-mechanisms/478300)**



Fig. 12 Model of gas, sodium, and proton transfer across the gill epithelium of a freshwater teleost. Shading indicates carbonic anhydrase activity. (*After H. Lin and D. Randall, Proton pumps in fish gills, in C. M. Wood and T. J. Shuttleworth, eds., Cellular and Molecular Approaches to Fish Ionic Regulation, Fish Physiology, vol. 14, pp. 229–255, Academic Press, New York, 1995*)



Fig. 13 Sodium chloride (NaCl) excretion in seawater fish occurs via the chloride cell found within the gill epithelium.

Fishes like the salmon that can tolerate a wide range of salinity increase the number of chloride cells within the gill epithelium as they migrate from rivers to the sea. An associated accessory cell develops alongside each chloride cell with loose connections forming a gap between the cells (paracellular channel). The chloride cell is much larger than the epithelial cells and extends from the outside across the gill epithelium. The epithelial cells and the chloride cells are tightly cemented together; the only open channel is between the chloride and accessory cell. The basal (blood) border of the chloride cell is infolded, and the membrane is associated with high levels of the enzyme Na⁺/K⁺ ATPase. This enzyme is associated with Na⁺ removal from the chloride cell into the blood. This creates a Na⁺ gradient from blood into the chloride cell. Na⁺ diffuses back into the chloride cell, involving a carrier that couples chloride movement to Na⁺ movement. In this way, chloride builds up in the cell and, because the cell is negatively charged, there is a large electrochemical gradient from the chloride cell into seawater results in the development of a positive potential across the gill, creating an electrochemical gradient for sodium, which diffuses from blood to seawater mainly via the paracellular channels. If a fish returns to freshwater, this paracellular channel closes, the accessory cells disappear, sodium loss is reduced, and chloride efflux also declines. Thus the gills of fishes are very much involved in maintaining internal NaCl levels.

Ammonia excretion

The main excretory end product of protein metabolism in fishes is ammonia (NH₃), but some urea is also produced. Ammonia and urea are both lost by passive diffusion across the gills. In elasmobranchs, the body surfaces are not so permeable to urea, which is retained at high levels along with trimethylamine oxide to create conditions in the body fluid which are iso-osmotic with seawater.

Most of the ammonia excreted can be accounted for by passive diffusion of ammonia gas. Membranes are very permeable to NH₃ but less so to ammonium ion, which is sometimes moved by a carrier molecule through membranes. Ammonia is toxic; and if levels in the water increase as a result, for example, of the deposition of biological waste, then fishes cannot excrete ammonia and it builds up in their bodies, and they die. Under some circumstances, fishes can excrete ammonium ions in exchange for sodium via a carrier-mediated process which may occur against a net ammonia gradient. Most ammonia excreted across the gills is produced in the liver, but some may be produced in the gills, which have the capacity to deaminate adenylates. The gill tissue also has the capacity to produce glutamine, but there is no evidence that ammonia is ever excreted as glutamine. *See also:* Ammonia (/content/ammonia/028600); Urea (/content/urea/722900)

pH regulation

Fish have difficulty excreting ammonia into alkaline waters or when air-exposed. Some fish have a complete ornithine urea cycle and can convert ammonia to urea for excretion. For example, the Lake Magadi (Kenya) tilapia, living in very alkaline conditions, can produce urea via the ornithine urea cycle at about the same rate as a rat. Other fish store ammonia as glutamine or other amino acids during air exposure and then convert the amino acids back to ammonia for excretion after returning to water. The gill epithelium also appears to transport hydrogen ions. Thus any acid produced by the fish could result in the movement of H⁺ across the gills into the water. The environment can be considered, therefore, as a very large H⁺ sink, ameliorating pH changes within the animal. When, however, the water is acidic, proton excretion is inhibited, and this in turn inhibits sodium uptake and sodium levels in the fish and the animal dies. As a result, acid waters are a danger to many fish. Calcium levels in the water are high. Industrial pollution in the form of acid rain quickly reduces the pH of soft-water rivers and lakes. These waters are poorly buffered and also have low Ca²⁺ levels; as a result, the fishes in these waters are very susceptible to acidification. Large numbers of lakes in North America and Europe no longer contain fishes because of acidification due to industrial pollution. *See also:* <u>Acid rain (/content/acid-rain/004760)</u>; <u>pH regulation (biology) (/content/ph-regulation-biology/504050)</u>

David J. Randall

Anatomy of the Lung

The shape and volume of the lung, because of its pliability, conforms almost completely to that of its cavity. The lungs are conical; each has an apex and a base, two surfaces, two borders, and a hilum.

Thoracic cavity

The apex extends into the superior limit of the thoracic cavity. The base is the diaphragmatic surface. The costal surface may show bulgings into the intercostal spaces. The medial surface has a part lying in the space beside the vertebral column and a part imprinted by the form of structures bulging outward beneath the mediastinal pleura (**Fig. 14**). The hilum and pulmonary ligament descending from it are notable. The cardiac impression is deeper on the left lung because of the position of the heart. The aorta arches over the left hilum, and the azygos vein arches over the right. Joining the right cardiac impression are the groove for the superior vena cava in front of the hilum and that for the inferior vena cava in front of the pulmonary ligament. Other impressions shown in the figures are those of the esophagus and trachea, the left subclavian artery, and brachiocephalic or innominate vein. The borders of the lung are pinched extensions between the pericardium and body of the sternum (anterior border) and between the diaphragm and body wall (inferior border). The inferior limit of the thoracic cavity on both sides is related to ribs 8, 10, and 12, whereas the lower borders of the lungs stop at ribs 6, 8, and 10, and the unoccupied space is the costodiaphragmatic recess on both sides. The cardiac notch is the absence of lung because of pressure from the heart. A similar, but smaller, notch is made in the underlying pleura, which gives rise to the left costomediastinal recess.



The oblique fissure cuts through the costal, diaphragmatic, and medial surfaces to the root of the lung. In the right lung, the horizontal fissure runs backward from the anterior border and meets the oblique fissure in the midlateral line. Thus, the right lung has three lobes, superior, middle, and inferior, whereas the left lung has two, the superior and inferior. The lingula, or anteroinferior part of the left upper lobe, and the cardiac notch above it correspond to the middle lobe of the right lung.

Bronchopulmonary segments

For convenience in exploration and study of the lung, it may be divided into anatomical areas. The bronchial tree branches mainly by dichotomy (**Fig. 15**). The ultimate generations, that is, the respiratory bronchioles, alveolar ducts, and alveoli constitute all of the respiratory portion of the lung. This respiratory portion (**Fig. 16**) consists of 10 segments in the right lung and 8 in the left, each of which is supplied by a tertiary branch of the bronchial tree (**Fig. 15**). Two or more of the segments make up a lung lobe. Further, the primary bronchi (from the trachea) divide as secondary bronchi, three on the right side and two on the left, corresponding to the lobes of the lung. Because the upper left lobe results from the fusion of two lobes, the prospective left upper and middle lobar bronchi become partially fused. As a result, the four segmental bronchi of the upper lobe are not tertiary, but bronchi of the fourth division of the tree. However, there is great similarity in the structure of the right and left bronchi.





Fig. 16 The 10 right and 8 left bronchopulmonary segments.

The trachea and extrapulmonary bronchi are kept open by C-shaped bars of hyaline cartilage. Within the lung, the bars are arcs staggered in the bronchial walls at different levels. When in their branching the bronchi and bronchioles are reduced to a diameter of 0.04 in. (1 mm) or less, they are then free of cartilage and are called terminal bronchioles. One of the terminal bronchioles enters the apex of a secondary lobule of the lung. These secondary lobules are anatomic units of the lung, whose hexagonal bases, 0.4–0.8 in. (10–20 mm) in diameter, rest on the pleura (Fig. 16) or next to a bronchiole or blood vessel, and whose apices point toward the hilum. Finer lines divide the bases of the secondary lobules into smaller areas (Fig. 17). These are the bases of primary lobules, each served by a respiratory bronchiole.



Fig. 17 Subdivisions of the lung.

Blood supply

The blood supply to the lung is provided by the pulmonary and the bronchial arteries. The right pulmonary artery runs dorsally between the bronchi of the right upper and middle lobes so that the upper bronchus arises 1 in. (25 mm) from the trachea. The left pulmonary artery and the arch of the aorta pass dorsally between the trachea and the bronchus of the left upper lobe bronchus, so that the latter is 2 in. (50 mm) from the trachea. Each pulmonary artery divides into 10 branches, which follow closely the posterosuperior walls of the segmental bronchi. They take the names of the 10 right segmental bronchi.

The bronchial arteries arise on the left side from the aorta, and on the right from either an intercostal or the left bronchial artery. They supply the walls of the bronchi, pulmonary vessels, and lymph nodes. They pass with the radicles of the pulmonary vein through the interlobular septa and supply the pulmonary pleura. Blood delivered to the lung by the bronchial arteries is returned by the radicles of the pulmonary veins, except that to the largest bronchi, which is returned by the bronchial by the bronchial veins to the azygos veins.

The pulmonary veins have 10 branches; their main stems run in the medial or inferior sides of the bronchi. Because their tributaries run intersegmentally and drain adjacent segments, and because the arteries may cross intersegmental boundaries, a bronchopulmonary segment would not be a morphologic bronchovascular unit. The upper and lower lobes of the left lung send an upper and a lower pulmonary vein, respectively, into the left side of the left atrium. The upper and middle right lobes provide the upper vein to the right side of the atrium.

Lymphatic channels are not found in interalveolar partitions but occur everywhere else in the lung, except in cartilage. There are two main sets of lung lymphatics, those in the pleura and those within the lung. The latter begin at the alveolar ducts and follow the bronchi and pulmonary vessels to the lymph nodes at the hilum. Those in the pleura form secondary and primary networks in the lobular septa and drain into the hilar lymph nodes.

Nerve supply

The nerves which supply the lung are branches of the vagus and of the thoracic sympathetic ganglia 2, 3, and 4. Efferent vagal fibers are bronchoconstrictor and secretory, whereas the afferents are part of the arc for the breathing reflex. Efferent sympathetic fibers are bronchodilators; hence, the use of adrenaline for relief of bronchial spasm resulting from asthma.

Histology of the Lung

Essential to lung function, histologically, are the respiratory passages, pleura, blood vessels, lymphatics, and respiratory surfaces proper.

Epithelium

Between the cartilage in the walls and the surface epithelium of the air passages are serous and mucous glands, which continuously pour their secretion through ducts to the surface of the epithelium. Also between the cartilage and epithelium below the trachea are smooth muscles which increase relatively in amount with decrease in size of the bronchioles. In the terminal bronchioles, which are free of cartilage, smooth muscle is the main constituent and may close the bronchiole, as in asthma. The epithelium is the respiratory type; that is, the cells are tall and capped by motile cilia. The cilia wave toward the throat, carrying along the secretions of the glands laden with inspired dust.

Pleura

The pleura lines the outer surface of the lung and the inner surface of the pleural cavity. It consists of a layer of flattened mesothelial cells and an underlying layer of collagenous and elastic fibers which support numerous blood and lymphatic capillaries, fibroblasts, and macrophages. The pleura continuously pours out a mucoid exudate, which lubricates the opposed surfaces. The pleura is pink in the newborn child.

Respiratory portion

This portion includes the respiratory bronchioles, which branch from the terminal bronchioles, the respiratory ducts, alveolar sacs, and alveoli. The respiratory ducts are similar to terminal bronchioles, except that they are smaller and have a few scattered alveoli protruding from their walls. Alveolar ducts, the next order of branching, have their walls studded with contiguous alveoli so that the openings of the alveoli occupy the greater area of the wall. Alveolar sacs are terminal dilations of the alveolar ducts. Alveolar ducts, among which are a few fibroblasts, dust cells or lung macrophages, and septal cells. The septal cells give rise to some of the macrophages, and others are carried in by the blood. Macrophages from both sources wander freely in the alveolar spaces. Two alveoli frequently have a single wall in common. The epithelial lining of the alveoli is so thin that it cannot be demonstrated with ordinary techniques. The greater volume of the lung is taken up by air space of the respiratory portion. Thus, the lung feels spongy and, when seen in sections, looks like fine lace.

Embryology of the Lung

The lung is an organ adapted to respiratory exchange of gases between air and the blood of vertebrates. It ranges from the simple swim bladder of dipnoid fish to the large spongy, compound air sac of humans. The story of the lung includes the evolution of certain vital accessories to respiration, the diaphragm and thoracic wall. All lungs correspond in originating as a pocket from the pharynx near the level of the sixth aortic arches which furnish the blood supply; in innervation by the vagus nerve; and in their embryonic position in the abdomen. This position is retained in the adult of fish, amphibians, and reptiles and partially retained in birds, but in mammals the lung is segregated from the abdomen in fetal life into a new-formed thoracic cavity (**Fig. 18**). See also: **Pharynx (/content/pharynx/505100)**



Extrusion of lung

In the extrusion of the lung from the abdominal cavity, it first invaginates the cervical aponeurosis of the abdomen and in so

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doing enters the space being formed between the inner and middle layers of the body wall, the pleural cavity. These events bring the lung to an anterior, thoracic position, and also allow it to develop an apex, both important in respiration. In amphibians (**Fig. 19***a*), the lung comes to lie in the pleuroperitoneal cavity. It is infrapericardial, with both the root and apex in the same plane. Figure 19*b* represents the condition in birds in which an apex grows cranially beyond the root of the lung. Thus, the entire lung remains abdominal, because the apex carries forward the entire cervical aponeurosis. The human lung becomes supradiaphragmatic (Fig. 19*c*). The diaphragm is represented by only a thin layer of the aponeurosis that is carried forward (Gibson's fascia), and the remainder of the aponeurosis serves to close the passageway. Moreover, the root also is carried forward, and in humans it becomes closely bound to the pericardium (**Fig. 20**).





Fig. 20 Diagram showing closely bound connections of the diaphragm, pericardium, and root of the lung in a human.

The pericardial bond is of primary importance in humans and the great anthropoids because the pericardium is bound also to the central tendon and diaphragm (Fig. 20). The part of the lung above the pulmonary root is relatively large, and the apex, located at a fixed point at the level of the neck of the first rib, can expand when the diaphragm contracts and pulls the root and heart in a downward and forward direction (**Fig. 21**). Upon expiration, they move in the reverse direction. In the typical mammal, there is little or no contact of the diaphragm with the pericardium, and the part of the lung above the root is relatively small (**Fig. 22**). Here, the descent of the diaphragm has little effect on the movement of the heart and pulmonary roots. Instead, the azygos lobe expands between the esophagus and inferior vena cava into the subpericardial space beside the pericardial mesentery.



Fig. 21 Diagram showing movements of the diaphragm, pericardium, and root of the lung during respiration in higher mammals. Broken lines show position of thorax and viscera during inspiration.



Fig. 22 Diagram showing discontinuity of the diaphragm with the pericardium and hilum of the lung in the typical mammal (rabbit).

The body wall becomes an inspiratory mechanism in reptiles as a result of the ribs, sternum, and intercostal muscles which evolve in the middle layer of the wall. In phylogeny, the first intermuscular septum to extend completely to the median ventral line is that behind the seventh segment of the rectus abdominis in the amphibian *Necturus maculatus*. In this septum, the first

Amphibia

The amphibian lung is bifid, and each half projects into the abdomen above the pericardium and liver (**Fig. 23**). The inner surface of the lung presents folds and ridges which increase respiratory surfaces. Air is pumped into the lung by pharyngeal muscles and in the absence of ribs is forced out by abdominal muscles.



Reptilia

The collapsed lung of *Iguana* (**Fig. 24**) extends forward to the cervical aponeurosis. The 8th to 14th ribs are complete, and three cervical ribs can both expand and compress the apex of the lung. The sternum is a strong fulcrum for the costal cartilages. The cervical part of the trunk is increased in length, so that the head and pharynx are carried away from the heart. Whereas in amphibians the swallowing of air tends to force pulmonary blood out of the lungs, in the lizard the negative pressure produced by its costal mechanism draws both air and blood into the lungs.



Birds

Lungs in adult birds are extra-abdominal, except the posterior ends, which are dilated to form abdominal air sacs. However, the avian lungs have grown through the cervical aponeurosis of the abdomen into a new space in the body wall, the pleural cavities (**Fig. 25**). Air sacs develop in this aponeurosis, and the septum is divided by these into two layers, the dorsal or pulmonary and ventral or abdominal (<u>Fig. 25</u>). If these lungs were removed from the thorax and the avian septum were replaced against the dorsal wall, the three-layered body wall of the amphibian would be restored. Although the lungs are in the thorax, the air sacs remain in the abdomen.



Human embryo

The lung in the 5-week human embryo lies in the abdomen. The septum transversum in humans consists of a ventral part (**Fig. 26***b*, *c*) representing the entire septum of amphibians (Fig. 19*a*) and a dorsal part representing a fusion of the amphibian cervical aponeurosis with the dorsal wall of the pericardium. The common cardinal vein (Fig. 26*b*, *c*) runs in the anterior part of the septum next to the wall of the pericardium. The lung lies medial to the Wolffian fold, which is attached to the mesonephros dorsally, the liver ventrally, and the septum in front, with its free border facing backward. In the amphibians, the lungs grow backward in the abdomen and are attached to the mesentery between the aorta and esophagus above and liver and stomach below. In the human embryo, they advance medially to the septum (Fig. 26*b*, *c*), and then evaginate laterally into the dorsal part of the septum between its anterior part, which contains the common cardinal vein next to the pericardial roof, and the posterior part, which develops to become the pleuroperitoneal membrane.



Fig. 26 Human embryo. (*a, b*) Diagram of embryo of 5 weeks showing initial process of lung extrusion. (*c*) Embryo of about 7 weeks showing extrusion into the cervical aponeurosis.

After this extrusion of the human lung from the abdominal cavity, the lung lies next to the medial surface of the middle layer of the body wall. Upon removal of the body wall, the lungs are exposed. The lungs can grow in a forward or backward direction and ventrally between the inner and middle layers of the body wall at equal rates, as these open up. The site of extrusion (pleuroperitoneal opening) has only to close, and the lung will occupy new, completely enclosed, pleural cavities.

Leo P. Clements

Physiology of the Lung

Simple molecular diffusion of gases underlies respiratory exchange in all animals. The lungs of air-breathing vertebrates require mechanical ventilation to sustain this diffusion. The molecular characteristics of respiratory gases (**Table 1**), the physical properties of atmosphere (**Table 2**) and of body fluids (**Table 3**), the physiological limitations on lung structure and location, and the large requirement of the active animal for O_2 uptake and CO_2 removal (**Table 4**) all restrict the effectiveness of diffusion respiration alone. Diffusion suffices only within a few millimeters of those membranes across which interchange of O_2 and CO_2 can occur. Refinements in ventilation respiration intervene as continuing speciation involves increased O_2 requirements. The functional as well as structural changes follow recognizable evolutionary trends. *See also:* **Metabolism** (/content/metabolism/417500); **Respiration** (/content/respiration/583400)

	v	Vater	Atmosphere (N ₂)		
Variable	Ocean	Fresh	Sea level	6000-m altitude	
Temperature, [°] C	-2.0 to 30.0	2.0-32.0	0.7-15.7	-28.1 to -15.1	
Pressure, total mmHg	760-760,000	760-20,000	760	347.5 to 360.2	
Density, g/liter	1027* (20°C)	1000* (4 °C)	1.223-1.290	0.649-0.659	
pН	7.5-8.4	3.2-10.6			
Concentration, vol %					
H ₂ O	94-97	97-99	1.00 [†]	1.00 [†]	
N ₂	1.03" (15 °C)	1.33* (15°C)	78.03 (STP)	78.03 (STP)	
CO ₂	0.02" (15 °C)	0.03° (15°C)	0.03 (STP)	0.03 (STP)	
O ₂	0.58" (15°C)	0.72* (15°C)	20.99 (STP)	20.99 (STP)	
Salts	3.46*	0.18"			
Inert gases	Trace	Trace	0.95 (STP)	0.95 (STP)	
Partial pressure (tension), mmHg					
H ₂ O	12.79 (15°C)	6.10 (4°C)	6.40 [‡] (15 °C)	0.72 [‡] (-15°C)	
N ₂	593.02 (STP)	593.02 (STP)	593.02 (STP)	281.06 (STP)	
CO ₂	0.23° (STP)	0.23* (STP)	0.23 (STP)	0.11 (STP)	
O ₂	159.52° (STP)	159.52° (STP)	159.52 (STP)	75.61 (STP)	
Inert gases	7.46 (STP)	7.46 (STP)	7.46 (STP)	3.42 (STP)	
Total pressure	760.00	760.00	760.00	360.20	
Diffusion coefficient, ml/(min)(cm ²)(cm), at 760 mmHg, 20°C					
H ₂ O					
N ₂		0.000018 (0.53)*			
CO ₂		0.000785 (23.1)			
O2		0.000034 (1.0) ⁶	11.0		

Туре	Weight (O = 16)	Diameter, [†] cm \times 10 ⁻⁸	Density, g/liter	Mean free path, cm × 10 ⁻⁶ (750 mmHg)	Collision frequency (20 °C)	Average velocity, cm/s	Water solubility		Vol 0/
							STP	20°C	(40°C)
N ₂	28.02	3.15-3.53	1.251	8.50	5070	45,400	2.35	1.54	1.18
H ₂ O	18.02	3.0-5.0	0.0005-0.030‡			56,600			
CO ₂	44.01	3.34-3.40	1.977	5.56	6120	36,200	171.3	87.8	53.0
02	32.00	2.92-2.98	1.429	9.05	4430	42,500	4.89	3.10	2.3

		Inspired air		VENTILATIO	N Alveolar air®		Expired air	rð	
	Compo-	Partial	-	Compo-	F	Partial	Compo-	Partial	
	sition,	pressure	θ,	sition,	pr	essure,	sition,	pressure	
Gas	vol % ^b	mmHgʻ	2	vol %	m	nmHg₫	vol % ^b	mmHg ^d	
H₂O	0.00	5.7		00.0		47	00.0	47	
N ₂	79.02	596.0		80.4		573	79.2	565	
02 CO2	20.95	158.0		14.0		40	4.5	32	
102	0.00	0.0		TRANSDORT	.e	10	-110		
	Arterial		Capil	lary	Tis	sue fluid	Venous	mmHg	
Sas	vol %	mmHg	vol %	mmHg	vol %	mmHg	vol %	mmHg	
H ₂ O	83 (81-86)	47 8	83 (81-86)	47	83 (81-86)	47	83 (81-86)	47	
N ₂	0.975	573 (0.975	573	0.975	573	0.975	573	
D ₂	19.6 (17.3-22.3)	94	1-22.3'	1-94'	0.185	30'	12.9 (11.0-16.1) ^g	40	
O2	48.2 (44.6-50.4)	40 4	44.6-57.7'	40-50'	3.046'	50'	54.8 (51.0-57.7) ^o	46	
^o Dry ar, p ^c Ambient ^d Physiolo ^a Values in ^f Variable, ^g Internal j	paraal pressure in miming — o tar (slight variations exist), in ogical air, normal temperature n parentheses are ranges, , depending on blood flow, tis jugular.	(37°C) and standard pre- sue activity, and relation	760 (Dalton's lan ssure (760 mmH of sample to cap	v). g). illary length or field					
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[™] Dry alt, p CAmbiend ^d Physiolo [®] Variable, ^g Internal j	paroai pressure in miming — (iar (slight variations exist), in ogical air, normal temperature n parentheses are ranges. , depending on blood flow, tie jugular.	TABLE 4. C in pigeon, i sacs and la Category	Combined I Sombined I duck, and ung	w). g). illary length or field measuremet chicken to c Volume, 6 of total	nts of respir compare role 	atory values es of various aposition CO ₂ %			
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Other vital requirements

Besides exchange of O₂ and CO₂, there are other vital requirements for breathing processes in air. Among these are (1) limitation of the evaporation of water in general and control of the dissipation of heat in birds and mammals in particular; (2) ventilation of the olfactory membrane; (3) production of high intrapulmonary pressure for such acts as coughing, defecation, and parturition; and low intrapulmonary pressure for regurgitation; (4) provision for large pulmonary volume in such acts as sneezing, yawning, and phonation; and (5) allowance for control of buoyancy in aquatic animals. All these ancillary processes involve corresponding variations in the respiratory mechanisms. As animals are compared, differences are found in buccopharyngeal, pulmonary interstitial, and diaphragmatic musculature for inducing and directing movement of air in valvular muscle of nares, glottis, and pulmonary ducts or apertures for controlling flow and pressure; in accessory air sacs to increase capacity for ventilation itself, or for phonation; in heart for adequate pulmonary blood supply and in circulation, for efficient perfusion; in brain and peripheral nerve patterns for initiation, maintenance, and adjustment of ventilatory processes, control of circulation, and regulation of ancillary functions; and in skeletal and connecting structures. A brief review of comparative respiration can only delineate the basic trends in phylogeny of respiration. Certain general features of the breathing process must be considered before comparisons among species can be made. *See also:* **Speech (/content/speech/642900)**

Breathing

The act of breathing induces mass flow of air in and out of the respiratory organs. This inspiration and expiration mechanically ventilates the entire lung of those animals, such as lungfish, salamander, and frog, in which the organ is a simple sac. Here, the inner lining or pulmonary epithelium, where diffusion itself occurs, is directly exposed to the tidal airflow caused by breathing. In these animals, breathing is intermittent or periodic; that is, cycles of inspiration and expiration occur in groups after many minutes of nonbreathing or apnea. The periods of apnea may exceed those of ventilating. The lung is normally closed from the atmosphere by a valve (glottal valve) at the opening into the trachea supplemented by valves (nasal valves) at the nares. The lung, however, does not remain a simple sac. Beginning with toads and climaxing in birds and mammals, more elaborate secondary and tertiary sacculations, the alveoli and the alveolar or air sacs, evolve. This evolution increases the diffusion surfaces tremendously and also removes these surfaces from direct exposure to ventilatory airflow. Thus, a uniform gaseous exchange medium comes to prevail at the respiratory membranes of birds and mammals, the breathing cycles become continuous and shallow (eupneic), and the lung remains normally open to the atmosphere. Nasal valves are usually absent in animals above reptiles, and the glottis closes only for such occasional acts as swallowing and coughing.

Breathing in vertebrates

Breathing induces air movement resulting from a mechanically imposed difference in pressure between a compressible cavity and the atmosphere. In mammals and reptiles, this cavity is the lung itself. In birds and amphibians, however, secondary cavities are responsible, namely, special air sacs in the former and the mouth (buccopharyngeal cavity) in the latter. These secondary cavities communicate with both the lung and the atmosphere and accommodate the bellowslike action. Two basic processes of air breathing reflect the structural differences. The more primitive type, buccopharyngeal breathing, is found in lungfish and amphibians. It involves the same basic neuromuscular elements of mouth and throat as water breathing in fishes. The more specialized type, thoracoabdominal breathing (in humans, for example), involves trunk musculature to supply pulmonary ventilation in all reptiles, birds, and mammals. A rather continuous buccopharyngeal ventilation, not always involving pulmonary ventilation itself, is characteristic of amphibians (**Table 5**) and persists in lizards, turtles, and other reptiles. In amphibians, therefore, buccopharyngeal activity subserves both breathing and olfaction; in reptiles, it subserves only the olfactory sense (smell).

	Weight, kg	Breathing rate,† cycles		Tidal	Minimum	O2 con-	Intrapleural	Com- pliance
Animal*		Vent./min	Comp./h	ml	liter/min	sumption, mm ³ /(g)(h)	cm H ₂ O	H ₂ O
Frog (Rana fusca)		41	17 (26°C)			210.0 (20 °C)		0.001
Turtle (Malaclemys centrata)		3.7 (24 °C)		14.0	0.051	35.0 (24°C)		
Alligator (Alligator mississippiensis)						8.9 (22 °C)		
Canary (Serinus canarius)		108				2900.0		
Chicken (Gallus domesticus)		17		45.0		497.0		
Duck (Anas sp.)		42		36.5		800.0		
Rat (Rattus norvegicus)	0.273	60	26	1.4	0.074	770.0	-2 to -8	0.001
Dog (Canis familiaris)	20	17	5	302.0	5.30	580.0	-5.4 to -13.5	0.09
Horse (Equus caballus)	696	12		9060.0	107.0	250.0	-8.0 to -22.0	0.80
Human (Homo sapiens)	66	14	3	372.0	5.04	220.0	-3.8 to -9.3	0.20

Buccopharyngeal breathing

Buccopharyngeal breathing is indirect, when compared with thoracoabdominal. It involves two distinct stages: ventilation of the mouth and ventilation of the lungs. The necessary pressure gradients between mouth and atmosphere and between mouth and lungs are generated by muscles which raise and lower the hyoid apparatus and floor of mouth and throat; the

same mechanism is used for water breathing in fishes. Pulmonary inspiration in buccopharyngeal breathing is more descriptively an injection or adspiration. The volume of air inspired or expired per breathing cycle is called tidal volume.

In the frog, movement of air between mouth and atmosphere requires only about 3–5 mm of water (H₂O) pressure; that between mouth and lungs reaches 25–35 mm H₂O pressure during the peak of pulmonary inspiration. A gradient is directed toward the lung of about 20 mm on inspiration, because a volume of gas (functional residual volume) remains in the lung from the preceding expiration under about 10 mm H₂O pressure. The glottis closes at the end of inspiration, and a positive intrapulmonary pressure persists during apnea, of about 20 mm H₂O, as a result of elastic recoil and muscular tonus in the lung itself and in the body wall. These forces also cause expiration when the glottis opens. Whether buccal ventilation alone or pulmonary ventilation or a combination of these occurs depends upon neuroregulatory processes which determine the relationship of nasal and glottal valves with each other and with the breathing musculature. Thus, a frog's lungs and body can be distended greatly beyond normal dimensions by successive inspirations alone.

Vital capacity

The excess capacity of any animal to inspire beyond normal tidal volume is called inspiratory reserve volume, and the total breathing capacity of the lungs as measured by the volume which can be completely expired after maximum filling is the vital capacity. Included in this is an amount, called expiratory reserve volume, which can be expired from the functional residual volume. Total expiration might completely empty the simple lungs of some amphibians. However, as the lungs of animals elaborate with alveolar development, it is not possible to expire all lung contents. The remainder after limit of vital capacity is reached is called residual air, and its presence at metamorphosis, hatching, or birth always indicates that breathing has started. The various volumes and pressures of ventilation have not been measured in most species. Some representative values are given in <u>Table 5</u>.

Dead space

Buccopharyngeal ventilation continues in reptiles, but this mechanism no longer provides for pulmonary ventilation. It remains an important adjunct to breathing, however, because it serves to reduce the dead-space volume. Dead-space average normal volume for an adult human, for example, is about 150 ml and tidal volume is about 500 ml, which means an actual ventilatory volume of about 350 ml. In a few air-breathing animals which occupy an aquatic habitat, respiration is apparently supplemented by buccopharyngeal breathing of water. Such a process has been described for a few species of turtles which have an especially vascular pharynx, but whether an important amount of O_2 is thus derived has not yet been ascertained. This ventilation with water may actually subserve olfactory and gustatory senses.

Thoracoabdominal breathing

Pulmonary ventilation in reptiles utilizes a more familiar process than buccopharyngeal breathing; that is, it depends upon an aspiration or sucking inspiration, such as in birds and humans. This involves development of a movable rib basket and elaboration of the intercostal musculature which, by enlargement of the body cavity, produces on inspiration a negative pressure in the lungs (intrapulmonary) with reference to the atmosphere. The abdominal muscles and myoelastic tissue of the lungs and air sacs remain, as in amphibians, important in expiration, but these are augmented by striated muscular membranes which form diaphragms and also ensheath the lungs in some turtles.

Turtles are exceptional among reptiles and air breathers generally because the ribs are fused into a shell which prohibits expansion of the body wall for inspiration. In these animals, muscular membranes which enclose the viscera and others which form diaphragms at the leg pockets in the shell produce expiratory and inspiratory force, respectively.

Reptiles

In reptiles generally, when at rest, breathing cycles occur in groups which are interspersed among long intervals of apnea. During apnea, the glottis is closed, the lung air is under a few millimeters of mercury positive pressure, and buccopharyngeal ventilation waxes and wanes to a degree associated at least in part with the extent of sensory disturbance. This buccopharyngeal activity resembles olfactory sniffing, as seen in dogs. The reptilian cycle of pulmonary inspiration and expiration is much simpler than the frog's, because the glottis and nares remain open while breathing movements occur, and air moves freely between lung and atmosphere in direct response to the action of breathing muscles in trunk and viscera. These muscles act alternately to enlarge and reduce the body cavity, exerting changes in pressure through tissue fluids directly on the lung air itself. Inspiration is clearly by suction. This is in contrast to the injection action of the buccopharyngeal muscles in amphibians. Like amphibians, however, the breathing remains periodic, and the glottis is normally closed.

Birds and mammals

Birds and mammals utilize strictly thoracoabdominal breathing to ventilate both nasal and pharyngeal cavities and lungs. The same structures used in reptiles continue to operate, namely, trunk musculature and diaphragms. The glottis does not close the lung from atmosphere normally, however; nasal valves are absent, and buccopharyngeal movements cease. Because the lung and airway are greatly elaborated over those in previously considered classes of animals, certain central regions develop more critical and specific control than glottal valves over airflow and diffusion. Such control regions involve, in mammals, the conducting bronchi and bronchioles and the valvelike sphincters at alveolar sac openings; and in birds, the corresponding ducts and orifices, including parabronchi and air capillaries. Also, other discrete structures develop as bellows, to change breathing forces into ventilation pressures. These structures are the extrapulmonary air sacs in birds (air sacs also occur in some reptiles) and the distal ducts and alveolar sacs in mammals. The alveolus becomes more strictly a diffusion exchange unit. As a result of all these specializations, great stability of physical conditions at diffusion surfaces is achieved in a system which, at the same time, accommodates high and variable rates of exchange.

The muscles of bronchioles, like those of arterioles in the circulatory system, are strategically situated to modify the distribution of inspired air in lungs by affecting duct caliber. However, not only distribution but also direction of airflow is altered in the bronchi of birds, a fact long obscured by emphasis on the simple, uniform mammalian tidal pattern.

It is now well established for breathing in birds that the tidal flow of air in and out of the conducting airways between atmosphere and air sacs is interrupted in certain bronchi leading to the lung itself; the flow is changed from tidal to unidirectional before reaching most air capillaries. A detailed explanation of this change of flow is still obscure, but the advantages of the change are apparent, namely, (1) continual exposure of respiratory surfaces to atmospheric air and the highest available O_2 concentration; concomitant with (2) optimum conditions for diffusion control of H_2O and CO_2 in pulmonary fluids. Birds thus surpass mammals in physiological access to oxygen.

There are other elements of breathing besides respiratory exchange which require control of the air movement itself as a mass flow along pressure differentials, as distinguished from control of movement in molecular migration along diffusion gradients. For example, whenever panting or phonation affects breathing, or when pulmonary pathology occurs, the amount of air going to different parts of the lung might greatly affect underlying respiratory exchange and disrupt diffusion control. But homeostasis requires a stable gaseous composition within alveoli and a minimal evaporation of water from alveolar surfaces; and diseased or injured lung regions require immobilization. Consequently, panting thermoregulation depends primarily on conduction and evaporation only from the upper air passages, and also from peripheral air sacs in birds. The cooling fluid is provided mainly through controlled secretion from serous membranes or glands, such as salivary glands in dogs. The membranes of passages and air sacs are not adapted for respiratory exchange, and insignificant amounts of O₂ or CO₂ diffuse across them. Phonation likewise uses the segregated air capacity of the ducts and sacs to move large volumes and

produce sounds without affecting gaseous molecular exchange.

The structural differences between the respiratory units of bird and mammal are subordinate to their common functional characteristics. The alveolus of mammals is usually a terminal membranous pouch with a porelike orifice (the postmortem diameter is about 70 micrometers in the rabbit) into an alveolar sac; occasionally they are appendant on a respiratory bronchiole. The corresponding structure in birds, called an air capillary or cylindrical alveolus, is an appendant membranous tubule with an orifice (diameter about 50 μ m in the chicken) into a tubular parabronchus. These alveolar structures frequently interconnect, via pores in mammals and anastomoses in birds. They both provide, in the aggregate, a reservoir with tremendous surface area (at least 50 m² in humans) which sequesters a mechanically stable intra-alveolar atmosphere based on nitrogen. It is through this medium that large quantities of oxygen, carbon dioxide, and water vapor molecules diffuse according to pressure gradients established, as in all vertebrates, on one hand by ventilation and on the other by pulmonary circulation. This intrapulmonary atmosphere, made up of the slightly varying composition among millions of alveoli, is often called alveolar air. It stays remarkably uniform in total composition despite ten- to twentyfold variations in oxygen and carbon dioxide exchange, such as occur during exercise. Some standard resting values for ventilation and diffusion in respiratory exchange of humans are shown in Tables 3–5.

The microscopic size of alveoli exaggerates a persistent tendency of all such bubblelike or balloonlike structures to collapse. This tendency in alveoli is partly the result of the surface tension of a fluid film which bathes their gas-exposed surface and partly the result of the elasticity of stretched fibers widely distributed within pulmonary tissues. Actual collapse (atelectasis) will occur at once as a result of these forces, for example, if much gas (pneumothorax) or fluid (hydrothorax) accidentally enters the pleural cavity.

A lipoprotein material is secreted onto the alveolar surface, a material characterized as surfactant, which reduces the surface tension at the gas-liquid interphase where respiratory exchange begins. This action lowers the alveolar rate of shrinkage and consequently helps to maintain an effective area of respiratory surface.

Alveolar size and effective surface area are further supported by periodic deep inspirations which are an integral part of the respiratory patterns of mammals, with the possible exception of a few very large representatives like the horse. These are called complementary cycles, or sighs, in humans, and they arise from sensory monitoring and nervous control of the functional residual volume of alveolar air. These cycles occur about nine times per hour in humans; in other animals, they occur more or less frequently, depending on the characteristic size of the adult (<u>Table 5</u>).

F. Harold McCutcheon

Avian respiration

The respiratory system of birds has a unique and complex structure. The lungs are relatively rigid and do not change volume significantly during ventilation; air passes through them and into a group of usually nine air sacs. There is no diaphragm separating the thoracic and abdominal cavities, and both phases of ventilation are active, even in birds at rest.

Structure

The primary bronchus originates from the trachea, runs along the entire length of the lung, and divides into two groups of secondary bronchi (**Fig. 27***a*). As the two groups of secondary bronchi enter the lung, they divide into four branches that spread across the medial and ventral surface of the lung. The primary bronchus also forms branches that extend along the lateral and dorsal surface and join the secondary bronchi by means of straight tubes (tertiary bronchi).



Fig. 27 Overall structure of the lung of birds (a) without and (b) with the neopulmo system (tertiary bronchi), showing the connections to the air sacs. (After H.-R. Duncker, Structure of the avian respiratory tract, Respir. Physiol., 22:1–19, 1974)

This network system of secondary and tertiary bronchi is known as the paleopulmo system, and it is present in all birds (Fig. <u>27</u>*a*). In the penguins and emus, it is the only system; whereas in all other birds, there is also a tertiary bronchial network between the lateral side of the primary bronchus, the laterobronchi, and the posterior air sacs. This network system is known as the neopulmo system (Fig. <u>27</u>*b*). A meshwork of fine air capillaries, which intertwine with equally fine blood capillaries, radiates from the lumen of each tertiary bronchus. These blood capillaries arise from arterioles and form collecting venules near the tertiary bronchial lumen. Gas exchange occurs in the air capillaries leading from the tertiary bronchi.

The cervical air sacs arise from the first medioventral bronchus of each lung, and the (single) clavicular air sac is joined to the first, second, and third medioventral bronchi of both lungs, whereas the cranial thoracic sacs connect predominantly to the third medioventral bronchus of each lung. These form the cranial (anterior) group of air sacs. The second lateroventral bronchi of each lung form large connections to the caudal thoracic air sac, and the primary bronchi continue to the caudal edge of each lung and empty into the abdominal air sacs. These latter two pairs of air sacs form the caudal (posterior) group.

Pathway of air

Airflow through the tertiary bronchi of the paleopulmo system is in the same direction during both phases of ventilation (**Fig.** <u>28</u>). During inspiration, some air travels through the primary and tertiary bronchi of the neopulmo system to the posterior group of air sacs, while the remaining air travels through the mediodorsal secondary bronchi and the tertiary bronchi of the paleopulmo system to the anterior group of air sacs. During expiration, the gas in the posterior air sacs travels again through the tertiary bronchi of the neopulmo system, then into the mediodorsal secondary bronchi, through the tertiary bronchi of the paleopulmo system, and into the medioventral secondary bronchi where, together with gas from the anterior group of air sacs, it enters the primary bronchus and trachea.

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show features essential to aerodynamic valving in geese, Respir. Physiol., 84:295-309, 1991)

There is no evidence of any mechanical valves in the airways, and the unidirectional airflow through the tertiary bronchi of the paleopulmo system is thought to result from the aerodynamic conditions in the lung. During inspiration, the velocity of airflow is important; the greater the velocity, the more likely is the inspired gas to flow pass the medioventral bronchi and continue along the primary bronchus. There are indications that the diameter of the primary bronchus decreases close to its junction with the first medioventral bronchus. This region is called the segmentum accelerans because it causes an increase in the velocity of airflow at that point.

Functional implications

Bulk airflow through the tertiary bronchi of the paleopulmo system is in the same direction during both phases of ventilation, and it has been demonstrated that bulk blood flow through the arterioles in the peritertiary bronchial tissue is at right angles to the bulk airflow. This is known as a cross-current arrangement, and it is more effective at exchanging gases (CO₂, in particular) than is the mammalian lung. It has been suggested that the unique structure of the avian lung is an adaptation to the high oxygen requirements of flight and an explanation of the better ability of birds to tolerate the hypoxia of high altitude compared with mammals. However, the typically mammalian lungs of bats have equally high mass-related oxygen consumptions during flight; and although there are indications that the lungs of birds confer some advantage during hypoxia compared to that of mammals, this decreases at the highest altitudes. *See also:* Hypoxia (/content/hypoxia/334750)

P. J. Butler

Mammalian respiration

Ventilation in mammals is more nearly like that in reptiles than in birds. In mammals, alveoli are terminal sacculations in a serial arrangement of ventilatory ducts and sacs, rather than appendant tubules along a parallel duct arrangement as in birds. The only nondiffusion regions of mammalian lungs are the major airways down through the terminal bronchioles; there are no

ventilatory sacs in the pulmonary system. However, the alveolar sacs of mammals may be considered the ventilatory analogs of the air sacs of birds, whereas the alveoli themselves incorporate most of the functionally specialized exchange surface. Alveolar sacs histologically are diffusion structures, unlike avian air sacs; however, the size and structural location relative to the alveoli indicate that they and not the alveoli accommodate much of the lung volume change during eupnea. Thus, enlargement of the lung during inspiration brings air down to the mouths of alveoli, including a small remainder of expiratory air in the ducts from the preceding breath. This unavoidable dilution of inspired air is like that found in the neopulmo of birds. But unlike the bird, there is no counterpart of a paleopulmo system to provide undiluted atmosphere to any part of the exchange surface. Consequently, the pulmonary system of mammals has H₂O and CO₂ diffusion control like birds, but it lacks the O_2 supply efficiency. The important question of the specific intrapulmonary distribution of air in mammals is under intensive study by histological as well as physiological techniques. A major organ of ventilation found only in mammals is the muscular diaphragm which divides thorax and abdomen. Because it lies as a dome with its convex face toward the thorax, when it contracts and flattens it augments thoracic muscles in increasing the capacity of the thoracic cavity. The abdominal wall relaxes at the same time to accommodate viscera which are displaced by the diaphragm. As a result of these movements, air under pressure differential of a few millimeters of mercury (for example, -1.5 mmHg in the nasal cavity of the horse) passes into the pulmonary system. The abdominal muscles cannot contribute directly to inspiration in mammals or any other vertebrates except turtles, in which a special arrangement is associated with the shell as previously mentioned.

Breathing mechanism

It is in the nature of muscular membranes that they must be oriented as the mammalian diaphragm is; that is, they must insert along their periphery into a resistant structure and bulge into the cavity if contraction is to produce negative pressure in the cavity. A positive expiratory force is a different matter, however, and abdominal muscles contribute such force in all vertebrates. The extent varies with the degree of ventilation, having a much greater contribution in exercise than at rest; with the species; and even with the sex. In the human female during eupneic breathing, for example, costal movement predominates and expiration results largely from the passive recoil of lung and chest; whereas in males, there is somewhat more abdominal involvement. In mammals generally, abdominal muscles are more involved in expiration than is true for humans; and in the larger quadrupeds, the work of displacing heavy pendant viscera requires their continuous activity. Forced breathing (hyperpnea) with increased amplitude, as during exercise; labored breathing (dyspnea), as during strenuous exercise or at high altitude; and compressatory acts all require the abdominal muscles. These supplement the internal intercostal muscles which pull the ribs to resting position. On the other hand, they are little involved in panting (polypnea) or sniffing.

Myoelastic fibers

Myoelastic fibers of the lung itself not only provide a passive component of expiration, but also account for collapse of the lung if the chest cavity is opened to the atmosphere. Because from the first filling at birth these fibers are stretched during the entire life of the animal, the surface of the lung always tends to recoil from adjacent structures. This recoil is limited in birds because the lung is structurally attached; but in mammals and all other animals, the lung surface is free from attachment. The visceral pleura of mammals, a covering membrane, adheres to the lungs, but this is in turn separated from all adjacent structures, which are covered by a parietal pleura, only by a film of mucoid fluid. Measurement of the elastic pulling force exerted by the lung against the surface tension of this fluid reveals the equivalent of a pressure which is negative with respect to atmosphere, when the animal is at rest or during eupnea. It is negative with respect to intrapulmonic pressure at all times. This is called intrapleural pressure (Table 5).

Pressure change and ventilation

The relationships between various pressure changes and ventilation activity in mammalian breathing are illustrated in Fig. 29.

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Here are shown tracings from instruments which recorded abdominal movements in a horse during one breathing cycle, along with concomitant pressure changes in the designated areas. The shapes of such graphs vary in detail among different species of mammals, as can be expected from a comparison of some ventilation parameters for a few animals (<u>Table 5</u>). The forces of respiratory exchange are apparent from such measurements as those in <u>Table 3</u>, made on air and blood entering, within, and leaving the lungs of humans.



Vertebrate respiratory regulation

Ventilation and circulation through the lungs are controlled and adjusted to maintain an efficient exchange of gases in relationship to the needs of the animal and to the suitability of the environment. Sensory units (tension receptors) for pressure or distension occur in lung and breathing elements and in related circulatory organs. These signal the medulla oblongata of the brain, from which the breathing rhythm itself originates, as well as other parts of the brain, and breathing is adjusted to physiological changes and physical conditions. Other receptors, especially in certain major blood vessels near the heart and in the medulla itself, signal the respiratory areas of the brain about blood chemical conditions, in particular, about oxygen, carbon dioxide, and acidity. Signals from other parts of the brain determines how breathing will proceed: whether to speed up, stop, cough, or to do whatever is appropriate. Oxygen tension in blood is a basic regulatory element for ventilation rate in lower vertebrates, but it becomes secondary to carbon dioxide in birds and mammals. Because carbon dioxide is a major factor in blood acidity, ventilation also comes to play a major role in critical regulation of hydrogen ion concentration (blood acidity) in higher animals. *See also:* **Brain (/content/brain/093200); Carotid body (/content/carotid-body/110700)**

Respiration in aquatic animals

The critical need for oxygen in amounts available only by continuous air breathing becomes more pronounced the higher an animal is in the evolutionary scale. This reflects the increasing energy requirements of such biological advantages as rapid sustained locomotion and critical continuous neuroregulatory activity. Through such attributes animals gain increasing independence from environmental limitations. Because there is about 30 times less oxygen in an aquatic environment, volume for volume, than in the atmosphere above it, no air-breathing animal except a few fish and most amphibians can maintain vital processes with oxygen gained by aquatic respiration. In amphibians, the skin is free from such protective

structures as scales, corneum, and hair; thus, diffusion is much less restricted than in other animals, and the skin is an important respiratory organ in water as well as in air. Permeability to respiratory gases includes permeability to water, however, and this restricts even terrestrial amphibians, such as toads, to a very humid atmosphere. Some aquatic amphibians, such as the mud puppy (*Necturus*), possess lungs as well as gills, but no such animals are capable of the high energy output which characterizes each of the strictly terrestrial and air-breathing vertebrate classes: the reptiles, birds, and mammals. Even these classes do include some species which are partly and some strictly aquatic in habitat. All the aquatic species remain strictly air-breathing, but they have modified respiratory and circulatory processes which accommodate diving and underwater activity during long suspension of breathing.

Suspension of breathing

In aquatic reptiles, such as snapping turtles and alligators, breathing suspension for dives is simply a special instance of the apnea which characterizes normal periodic breathing of reptiles on land. In diving birds and mammals, however, the suspension is a departure from the eupneic pattern, for eupnea is normally interrupted only at rest by an occasional deep breath and a pause of about 5 s duration, such as the sigh in humans. A dive of more than 2–3 min duration in birds and mammals requires special adaptations, because no animal has means of storing oxygen to last more than a few minutes; however, seals may submerge for 15–25 min and whales for 1 h or more. Important means of submergence in such animals include (1) restriction of blood flow from the bulk of the muscles, thus sequestering lactic acid and building up a debt for oxygen to be paid on access to air; (2) higher tolerance for carbon dioxide, which is always toxic in excess, and which must accumulate until breathing is resumed; (3) conservation of movement while submerged; (4) reflexes around nostrils which stop breathing on contact with water; and (5) great reduction in lung volume when the high pressure of great depths is involved, which reduces diffusion area of the lung. The last of these does not concern respiration itself; rather it serves to limit nitrogen buildup in tissues, with its attendant hazard of bubble formation, or bends. Such bubbles may form on too rapid ascent from depths, and they can cause immobilization and death. Also, lungs and air sacs may serve as buoyancy organs for swimming and diving, because their contents can be altered in volume to change the displacement of the animal.

Adaptations in terrestrial animals

The adaptations for diving in birds and mammals have been found in counterpart among some nonaquatic animals such as rabbits, which may become immobile and suppress breathing under certain conditions, for example, in evading predators. For active locomotion in air and for highest brain activity, however, oxygen is the most urgently needed of all substances required from the environment; therefore, essentially continuous ventilation is a necessity for strictly terrestrial animals such as the chicken, cat, and human. Such animals survive without actual ventilation only before the time of birth, or hatching, although nonrespiratory periodic breathing movements do occur in the egg or uterus as appropriate structures develop. Early respiration utilizes special diffusion respiratory structures, such as the allantois and placenta. In birds, an actual pulmonary ventilation, utilizing the air chamber of the egg, begins shortly before hatching. In mammals, it can begin only when the fetus gains direct access to air at birth. *See also:* Placentation (/content/placentation/520700); Respiratory system disorders/583700)

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