DOWNLOAD PDF GAS EXCHANGE AND RESPIRATORY ADAPTATION

Chapter 1 : Gas exchange - Wikipedia

Human respiratory system - Adaptations: Ascent from sea level to high altitude has well-known effects upon respiration. The progressive fall in barometric pressure is accompanied by a fall in the partial pressure of oxygen, both in the ambient air and in the alveolar spaces of the lung, and it is this fall that poses the major respiratory challenge to humans at high altitude.

Edit Gallery The avian respiratory system is physically distinct from the mammalian respiratory system, both in structure and in its ability to exchange gas as efficiently as possible. A breath of oxygen-rich inhaled air remains in the respiratory system for two complete inhalation and exhalation cycles before it is fully spent used and exhaled out the body. The inhaled air travels down each primary bronchus and then divides: Then, during the first exhalation, the fresh air in the posterior sacs enters the lungs and undergoes gas exchange. The spent air in the lungs is displaced by this incoming air and flows out the body through the trachea. During the second inhalation, fresh air again enters both the posterior sacs and the lungs. Spent air in the lungs is again displaced by incoming air, but it cannot exit through the trachea because fresh air is flowing inward. Instead, the spent air from the lungs enters anterior forward air sacs. Then, during the second exhalation, the spent air in the anterior sacs and in the lungs flows out through the trachea, and fresh air in the posterior sacs enters the lungs for gas exchange. This pattern of airflow through the respiratory system creates unidirectional one-way flow of fresh air over the gas exchange surfaces in the lungs. Furthermore, fresh air passes over the gas exchange surfaces during both inhalation and exhalation, resulting in a constant supply of fresh air enabling the bird to experience a near-continuous state of gas exchange within the lungs. This contrasts with mammalian lungs, which experience bidirectional airflow over the gas exchange surfaces. The efficiency of the avian respiratory system is owed in part to its unidirectional nature and the structure of its parabronchial system the smaller passages within the lungs. The air capillaries in the walls of the parabronchial system have a much larger overall surface area than that found in the mammalian respiratory system. The greater the surface area, the more oxygen and carbon dioxide can be passed between blood and tissues, which makes for more efficient breathing. This summary features contributions from Alex Uhrich. References Book Design in Nature: Avian lungs are small, compact, spongy structures molded among the ribs on either side of the spine in the chest cavity. The dense tissues of avian lungs weigh as much as the lungs of mammals of equal body weight but occupy only about half the volume. Healthy bird lungs are well vascularized and light pink in color. How do birds control the air so that it flows through their lungs when they can only inhale and exhale through one trachea? The solution is a surprising combination of unique anatomical features and the manipulation of airflow. Supplementing the lungs is an elaborate system of interconnected air sacs, not present in mammalsâ€¦Most birds inhale air through nostrils, or nares, at the base of the billâ€¦Inhaled air moves next down the trachea, or windpipe, which divides into two bronchi and in turn into many subdividing stems and branches in each lungâ€¦Most of the lung tissue comprises roughly smaller interconnecting tertiary bronchi. These bronchi lead into tiny air capillaries that intertwine with blood capillaries, where gases are exchanged. Most of the air inhaled in step 1 passes through the primary bronchi to the posterior air sacsâ€¦In step 2, the exhalation phase of this first breath, the inhaled air moves from the posterior air sacs into the lungs. There, oxygen and carbon dioxide CO2 exchange takes place as inhaled air flows through the air-capillary system. The next time that the bird inhales, step 3, the oxygen-depleted air moves from the lungs into the anterior air sacs. The second and final exhalation, step 4, expels CO2-rich air from the anterior air sacs, bronchi, and trachea back into the atmosphere. Most importantly, a bird replaces nearly all the air in its lungs with each breath. No residual air is left in the lungs during the ventilation cycle of birds, as it is in mammals. By transferring more air and air higher in oxygen content during each breath, birds achieve a more efficient rate of gas exchange than do mammalsâ€¦The air-sac system is an inconspicuous, but integral, part of the avian respiratory systemâ€¦Air sacs are thin-walled only one or two cell layers thick structures that extend into the body cavity and into the wing and leg bonesâ€¦The air sacs make possible the continuous, unidirectional, efficient flow of air through the lungs.

Chapter 2 : Air flow patterns facilitate efficient gas exchange : Birds - AskNature

(a) Adaptations for gas exchange allow an increase in body size. Small animals exchange gases across their general body surface. Comparison of amoeba, flatworm and earthworm.

Indian moon moth Actias selene with some of the spiracles identified Scanning electron micrograph of a cricket spiracle valve Insects have spiracles on their exoskeletons to allow air to enter the trachea. The spiracles can be opened and closed in an efficient manner to reduce water loss. This is done by contracting closer muscles surrounding the spiracle. In order to open, the muscle relaxes. The closer muscle is controlled by the central nervous system but can also react to localized chemical stimuli. Several aquatic insects have similar or alternative closing methods to prevent water from entering the trachea. Spiracles may also be surrounded by hairs to minimize bulk air movement around the opening, and thus minimize water loss. The spiracles are located laterally along the thorax and abdomen of most insectsâ€"usually one pair of spiracles per body segment. Air flow is regulated by small muscles that operate one or two flap-like valves within each spiracleâ€"contracting to close the spiracle, or relaxing to open it. Structure of the tracheae[edit] After passing through a spiracle, air enters a longitudinal tracheal trunk, eventually diffusing throughout a complex, branching network of tracheal tubes that subdivides into smaller and smaller diameters and reaches every part of the body. At the end of each tracheal branch, a special cell the tracheole provides a thin, moist interface for the exchange of gasses between atmospheric air and a living cell. Oxygen in the tracheal tube first dissolves in the liquid of the tracheole and then diffuses across the cell membrane into the cytoplasm of an adjacent cell. At the same time, carbon dioxide, produced as a waste product of cellular respiration, diffuses out of the cell and, eventually, out of the body through the tracheal system. Each tracheal tube develops as an invagination of the ectoderm during embryonic development. To prevent its collapse under pressure, a thin, reinforcing "wire" of cuticle the taenidia winds spirally through the membranous wall. This design similar in structure to a heater hose on an automobile or an exhaust duct on a clothes dryer gives tracheal tubes the ability to flex and stretch without developing kinks that might restrict air flow. The absence of taenidia in certain parts of the tracheal system allows the formation of collapsible air sacs, balloon-like structures that may store a reserve of air. In dry terrestrial environments, this temporary air supply allows an insect to conserve water by closing its spiracles during periods of high evaporative stress. Aquatic insects consume the stored air while under water or use it to regulate buoyancy. During a molt, air sacs fill and enlarge as the insect breaks free of the old exoskeleton and expands a new one. Between molts, the air sacs provide room for new growthâ€"shrinking in volume as they are compressed by expansion of internal organs. Small insects rely almost exclusively on passive diffusion and physical activity for the movement of gasses within the tracheal system. However, larger insects may require active ventilation of the tracheal system especially when active or under heat stress. They accomplish this by opening some spiracles and closing others while using abdominal muscles to alternately expand and contract body volume. Although these pulsating movements flush air from one end of the body to the other through the longitudinal tracheal trunks, diffusion is still important for distributing oxygen to individual cells through the network of smaller tracheal tubes. In fact, the rate of gas diffusion is regarded as one of the main limiting factors along with weight of the exoskeleton that prevents real insects from growing as large as the ones we see in horror movies. Theoretical models[edit] Insects were once believed to exchange gases with the environment continuously by the simple diffusion of gases into the tracheal system. More recently, large variation in insect ventilatory patterns have been documented, suggesting that insect respiration is highly variable. Some small insects do demonstrate continuous respiration and may lack muscular control of the spiracles. Others, however, utilize muscular contraction of the abdomen along with coordinated spiracle contraction and relaxation to generate cyclical gas exchange patterns and to reduce water loss into the atmosphere. The most extreme form of these patterns is termed discontinuous gas exchange cycles DGC.

Chapter 3 : Respiratory System Adaptations to Exercise â€” PT Direct

Respiratory System Adaptations to Exercise This page highlights the specific adaptations made by the respiratory system in reponse to the types of training that place the greatest demand on this system.

Carbon dioxide is also generated by cellular metabolism and must be removed from the cell. There must be an exchange of gases: Animals have organ systems involved in facilitating this exchange as well as the transport of gases to and from exchange areas. Bodies and Respiration Back to Top Single-celled organisms exchange gases directly across their cell membrane. However, the slow diffusion rate of oxygen relative to carbon dioxide limits the size of single-celled organisms. Simple animals that lack specialized exchange surfaces have flattened, tubular, or thin shaped body plans, which are the most efficient for gas exchange. However, these simple animals are rather small in size. Respiratory Surfaces Back to Top Large animals cannot maintain gas exchange by diffusion across their outer surface. They developed a variety of respiratory surfaces that all increase the surface area for exchange, thus allowing for larger bodies. A respiratory surface is covered with thin, moist epithelial cells that allow oxygen and carbon dioxide to exchange. Those gases can only cross cell membranes when they are dissolved in water or an aqueous solution, thus respiratory surfaces must be moist. Methods of Respiration Back to Top Sponges and jellyfish lack specialized organs for gas exchange and take in gases directly from the surrounding water. Flatworms and annelids use their outer surfaces as gas exchange surfaces. Arthropods, annelids, and fish use gills; terrestrial vertebrates utilize internal lungs. Gas exchange systems in several animals. Images from Purves et al. The Body Surface Flatworms and annelids use their outer surfaces as gas exchange surfaces. Earthworms have a series of thin-walled blood vessels known as capillaries. Gas exchange occurs at capillaries located throughout the body as well as those in the respiratory surface. Amphibians use their skin as a respiratory surface. Frogs eliminate carbon dioxide 2. Constraints of water loss dictate that terrestrial animals must develop more efficient lungs. Gills Gills greatly increase the surface area for gas exchange. They occur in a variety of animal groups including arthropods including some terrestrial crustaceans , annelids, fish, and amphibians. Gills typically are convoluted outgrowths containing blood vessels covered by a thin epithelial layer. Typically gills are organized into a series of plates and may be internal as in crabs and fish or external to the body as in some amphibians. Gills are very efficient at removing oxygen from water: Water flows over gills in one direction while blood flows in the opposite direction through gill capillaries. This countercurrent flow maximizes oxygen transfer. Countercurrent flow in a fish. Tracheal Systems Many terrestrial animals have their respiratory surfaces inside the body and connected to the outside by a series of tubes. Tracheae are these tubes that carry air directly to cells for gas exchange. Spiracles are openings at the body surface that lead to tracheae that branch into smaller tubes known as tracheoles. Body movements or contractions speed up the rate of diffusion of gases from tracheae into body cells. However, tracheae will not function well in animals whose body is longer than 5 cm. Respiratory system in an insect. Image from Purves et al. Lungs Lungs are ingrowths of the body wall and connect to the outside by as series of tubes and small openings. Lung breathing probably evolved about million years ago. Lungs are not entirely the sole property of vertebrates, some terrestrial snails have a gas exchange structures similar to those in frogs. Lungs in a bird top and amphibian bottom. Respiratory System Principles Back to Top Movement of an oxygen-containing medium so it contacts a moist membrane overlying blood vessels. Diffusion of oxygen from the medium into the blood. Transport of oxygen to the tissues and cells of the body. Diffusion of oxygen from the blood into cells. Carbon dioxide follows a reverse path. Functional unit of a mammalian lung. The Human Respiratory System Back to Top This system includes the lungs, pathways connecting them to the outside environment, and structures in the chest involved with moving air in and out of the lungs. The human respiratory system. Air enters the body through the nose, is warmed, filtered, and passed through the nasal cavity. Air passes the pharynx which has the epiglottis that prevents food from entering the trachea. The upper part of the trachea contains the larynx. The vocal cords are two bands of tissue that extend across the opening of the larynx. After passing the larynx, the air moves into the bronchi that carry air in and out of the lungs. The lungs and alveoli and their relationship to the diaphragm and capillaries. Bronchi are reinforced to prevent their collapse and are lined with ciliated epithelium and mucus-producing cells. Bronchi branch into smaller and smaller tubes known as bronchioles. Bronchioles terminate in grape-like sac clusters known as alveoli. Alveoli are surrounded by a network of thin-walled capillaries. Gas exchange across capillary and alveolus walls. The lungs are large, lobed, paired organs in the chest also known as the thoracic cavity. Thin sheets of epithelium pleura separate the inside of the chest cavity from the outer surface of the lungs. The bottom of the thoracic cavity is formed by the diaphragm. Ventilation is the mechanics of breathing in and out. When you inhale, muscles in the chest wall contract, lifting the ribs and pulling them, outward. The diaphragm at this time moves downward enlarging the chest cavity. Reduced air pressure in the lungs causes air to enter the lungs. Exhaling reverses theses steps. Diseases of the Respiratory System Back to Top The condition of the airways and the pressure difference between the lungs and atmosphere are important factors in the flow of air in and out of lungs. Many diseases affect the condition of the airways. Asthma narrows the airways by causing an allergy-induced spasms of surrounding muscles or by clogging the airways with mucus. Bronchitis is an inflammatory response that reduces airflow and is caused by long-term exposure to irritants such as cigarette smoke, air pollutants, or allergens. Cystic fibrosis is a genetic defect that causes excessive mucus production that clogs the airways. The Alveoli and Gas Exchange Back to Top Diffusion is the movement of materials from a higher to a lower concentration. The differences between oxygen and carbon dioxide concentrations are measured by partial pressures. The greater the difference in partial pressure the greater the rate of diffusion. Respiratory pigments increase the oxygen-carrying capacity of the blood. Humans have the red-colored pigment hemoglobin as their respiratory pigment. Hemoglobin increases the oxygen-carrying capacity of the blood between 65 and 70 times. Each red blood cell has about million hemoglobin molecules, and each milliliter of blood contains 1. Effectiveness of various oxygen carrying molecules. Carbon dioxide concentration in metabolically active cells is much greater than in capillaries, so carbon dioxide diffuses from the cells into the capillaries. Water in the blood combines with carbon dioxide to form bicarbonate. This removes the carbon dioxide from the blood so diffusion of even more carbon dioxide from the cells into the capillaries continues yet still manages to "package" the carbon dioxide for eventual passage out of the body. Details of gas exchange. In the alveoli capillaries, bicarbonate combines with a hydrogen ion proton to form carbonic acid, which breaks down into carbon dioxide and water. The carbon dioxide then diffuses into the alveoli and out of the body with the next exhalation. Control of Respiration Back to Top Muscular contraction and relaxation controls the rate of expansion and constriction of the lungs. These muscles are stimulated by nerves that carry messages from the part of the brain that controls breathing, the medulla. Two systems control breathing: Both are involved in holding your breath. Although the automatic breathing regulation system allows you to breathe while you sleep, it sometimes malfunctions. Apnea involves stoppage of breathing for as long as 10 seconds, in some individuals as often as times per night. This failure to respond to elevated blood levels of carbon dioxide may result from viral infections of the brain, tumors, or it may develop spontaneously. A malfunction of the breathing centers in newborns may result in SIDS sudden infant death syndrome. As altitude increases, atmospheric pressure decreases. Above 10, feet decreased oxygen pressures causes loading of oxygen into hemoglobin to drop off, leading to lowered oxygen levels in the blood. The result can be mountain sickness nausea and loss of appetite. Mountain sickness does not result from oxygen starvation but rather from the loss of carbon dioxide due to increased breathing in order to obtain more oxygen.

Chapter 4 : Chemistry for Biologists: Gas exchange

Gas exchange is the process by which oxygen and carbon dioxide (the respiratory gases) move in opposite directions across an organism's respiratory membranes, between the air or water of the external environment and the body fluids of the internal environment.

High altitudes Ascent from sea level to high altitude has well-known effects upon respiration. The progressive fall in barometric pressure is accompanied by a fall in the partial pressure of oxygen , both in the ambient air and in the alveolar spaces of the lung , and it is this fall that poses the major respiratory challenge to humans at high altitude. Humans and some other mammalian species, such as cattle , adjust to the fall in oxygen pressure through the reversible process of acclimatization , which, whether undertaken deliberately or not, commences from the time of exposure to high altitudes. Indigenous mountain species, such as the llama , exhibit an adaptation that is heritable and has a genetic basis. Respiratory acclimatization in humans is achieved through mechanisms that heighten the partial pressure of oxygen at all stages, from the alveolar spaces in the lung to the mitochondria in the cells , where oxygen is needed for the ultimate biochemical expression of respiration. The decline in the ambient partial pressure of oxygen is offset to some extent by greater ventilation, which takes the form of deeper breathing rather than a faster rate at rest. Diffusion of oxygen across the alveolar walls into the blood is facilitated , and in some experimental animal studies, the alveolar walls are thinner at altitude than at sea level. The scarcity of oxygen at high altitudes stimulates increased production of hemoglobin and red blood cells , which increases the amount of oxygen transported to the tissues. The extra oxygen is released by increased levels of inorganic phosphates in the red blood cells, such as 2,3-diphosphoglycerate 2,3-DPG. With a prolonged stay at altitude, the tissues develop more blood vessels , and, as capillary density is increased, the length of the diffusion path along which gases must pass is decreasedâ€”a factor augmenting gas exchange. In addition, the size of muscle fibres decreases, which also shortens the diffusion path of oxygen. The initial response of respiration to the fall of oxygen partial pressure in the blood on ascent to high altitude occurs in two small nodules, the carotid bodies , attached to the division of the carotid arteries on either side of the neck. As the oxygen deprivation persists, the carotid bodies enlarge but become less sensitive to the lack of oxygen. The low oxygen partial pressure in the lung is associated with thickening of the small blood vessels in pulmonary alveolar walls and a slight increase in pulmonary blood pressure , thought to enhance oxygen perfusion of the lung apices. Their hemoglobin has a high oxygen affinity , so that full saturation of the blood with oxygen occurs at a lower partial pressure of oxygen. In contrast to acclimatized humans, these indigenous adapted mountain species do not have increased levels of hemoglobin or of organic phosphates in the red cells; they do not develop small muscular blood vessels or an increased blood pressure in the lung; and their carotid bodies remain small. Native human highlanders are acclimatized rather than genetically adapted to the reduced oxygen pressure. After living many years at high altitude, some highlanders lose this acclimatization and develop chronic mountain sickness, sometimes called Monge disease, after the Peruvian physician who first described it. This disease is characterized by greater levels of hemoglobin. In Tibet some infants of Han origin never achieve satisfactory acclimatization on ascent to high altitude. A chemodectoma, or benign tumour , of the carotid bodies may develop in native highlanders in response to chronic exposure to low levels of oxygen.

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Chapter 5 : Human respiratory system - Adaptations | calendrierdelascience.com

Respiratory adaptation is the specific changes that the respiratory system undergoes in response to the demands of physical calendrierdelascience.come physical exertion, such as that involved in fitness training, places elevated demands on the respiratory system.

Gas exchange in simple terrestrial organisms: The Earthworm lives on land and keeps its thin skin moist by secreting mucus from the epidermis. Earthworms have no special organs for gas exchange hence gas exchange takes place by diffusion across the epidermis covering the whole body. This is possible because it has: A tubular, elongated shape. Lack of activity means it is difficult to maintain the concentration gradient for the diffusion of gases. Earthworms have a blood vascular system containing the pigment haemoglobin in solution. They also have blood vessels with multiple hearts. Pumping activity of the major blood vessels circulates blood and dissolved gases round the body and maintains steep diffusion gradients. Insects, fish, reptiles, birds and mammals. Have a greater demand for energy higher metabolic rate Have a smaller surface area: Have to evolve systems and organs to increase the available surface for gas exchange. In aquatic insects and fish the gas exchange surface takes form of the gills. Terrestrial animal groups such as birds, reptiles and mammals have developed lungs. These animal groups have also developed: An internal transport system- provided by a blood circulation system to move gases between the respiring cells and respiratory surface. A respiratory pigment in the blood- to increase its oxygen carrying capacity. Bony Fish large and active. Water is a dense medium with a low oxygen content, therefore to increase efficiency, water needs to be forced over the gill filaments by pressure differences. Compared with parallel flow, counter current flow increases efficiency because the diffusion gradient between the adjacent flows is maintained on the whole. The gills of fish have the following features to maximise the rate of diffusion: A large SA, extended by gill filaments and gill plates. A rich supply of blood vessels to transport gases to and from the surface. The surface area of each gill filament is further increased by having many gill plates or lamellae.

Chapter 6 : ANIMALS / TERRESTRIAL INSECTS -GAS EXCHANGE - Pathwayz

Gas exchange surfaces such as the gills of a fish, the alveoli in the lungs of a mammal, the trachae of an insect and the spongy mesophyll cells in the leaves of a plant are effective exchange surfaces.

Water is more dense than air and it takes more force to move it across the gas exchange surface, this is why fish require relatively large structures to ventilate their gas exchange surface. This increases the internal volume and lowers the internal water pressure within the mouth. The Opercula remain closed ensuring water enters through the mouth. During expiration the mouth closes and muscles raise the floor of the buccal cavity and push in the walls of the operculum. This reduces the internal volume and increases the internal water pressure within the mouth. The opercula open and water is pushed out over the gill surface. Alternatively some larger fish such as Tuna swim continuously with their mouth open to keep water flowing across their gill surface. The feeding behaviour of fish means that sand, shell fragments and other debris all enter the mouth. Because fish also use their buccal mouth cavity to ventilate their gills there is an increased risk of damage to the gill filaments from such debris. Gill rakers help to filter out this debris that would otherwise damage or stick to the gill filaments, reducing their surface area. Their shape and staggered arrangement gives them a large surface area. These filaments are the site of gas exchange and they contain many tiny blood vessels called capillaries this is what gives them a dark red appearance. Their staggered arrangement and the continuous flow of water across the filaments ensures that they do not stick together, maximising the surface area that is exposed for gas exchange. While fish are still subjected to the forces of gravity, they do not need extensive support structures because this flow of water the gas exchange medium itself helps keep the filaments in an open conformation supports the gas exchange surface. The primary lamellae gill filaments are covered in a large number of tiny folds known as secondary lamellae. These further increase the surface area available for gas exchange. In the lamellae, blood moves though tiny capillaries in the opposite direction to the flow of water. This transport system helps to ensure a concentration gradient is maintained across the gas exchange surface by replacing oxygen rich blood with oxygen poor blood. This is an adaptation to the oxygen poor, aquatic, environment in which fish are found. Lamellae primary and secondary give the gill a large surface area increasing the rte of diffusion and therefore gas exchange. Fish are able to extract a much higher proportion of oxygen from water than most animals can form air. This is essential for an aquatic lifestyle as water has a much lower oxygen content than air. Water flowing across the lamellae keeps them apart maximising the surface area available for gas exchange. On land they would stick together drastically reducing the surface area available for gas exchange. The gills would also dry out as fish have no need for systems to keep the gas exchange system moist.

Chapter 7 : Respiratory System

In aquatic insects and fish the gas exchange surface takes form of the gills. Terrestrial animal groups such as birds, reptiles and mammals have developed lungs. All of these different mechanisms need a means of ventilation to supply the the respiratory surfaces with a fresh supply of oxygen and to maintain concentration gradients.

The oxygen is held on the hemoglobin by four ferrous iron -containing heme groups per hemoglobin molecule. The reaction is therefore catalyzed by carbonic anhydrase , an enzyme inside the red blood cells. A small amount of carbon dioxide is carried on the protein portion of the hemoglobin molecules as carbamino groups. The total concentration of carbon dioxide in the form of bicarbonate ions, dissolved CO_2, and carbamino groups in arterial blood i. Gills are specialised organs containing filaments , which further divide into lamellae. The lamellae contain capillaries that provide a large surface area and short diffusion distances, as their walls are extremely thin. Gills use a countercurrent flow system that increases the efficiency of oxygen-uptake and waste gas loss. This countercurrent maintains steep concentration gradients along the entire length of each capillary see the diagram in the "Interaction with circulatory systems" section above. Oxygen is able to continually diffuse down its gradient into the blood, and the carbon dioxide down its gradient into the water. The relative importance of these structures differs according to the age, the environment and species of the amphibian. The skin of amphibians and their larvae is highly vascularised, leading to relatively efficient gas exchange when the skin is moist. The larvae of amphibians, such as the pre-metamorphosis tadpole stage of frogs , also have external gills. The gills are absorbed into the body during metamorphosis , after which the lungs will then take over. The lungs are usually simpler than in the other land vertebrates , with few internal septa and larger alveoli; however, toads, which spend more time on land, have a larger alveolar surface with more developed lungs. To increase the rate of gas exchange by diffusion, amphibians maintain the concentration gradient across the respiratory surface using a process called buccal pumping. Reptiles[edit] All reptiles breathe using lungs. In squamates the lizards and snakes ventilation is driven by the axial musculature , but this musculature is also used during movement, so some squamates rely on buccal pumping to maintain gas exchange efficiency. Turtles and tortoises depend on muscle layers attached to their shells, which wrap around their lungs to fill and empty them. Inhalation-exhalation cycle in birds. A diagrammatic representation of the cross-current respiratory gas exchanger in the lungs of birds. Air is forced from the air sacs unidirectionally from right to left in the diagram through the parabronchi. The pulmonary capillaries surround the parabronchi in the manner shown blood flowing from below the parabronchus to above it in the diagram. Birds have lungs but no diaphragm. They rely mostly on air sacs for ventilation. These air sacs do not play a direct role in gas exchange, but help to move air unidirectionally across the gas exchange surfaces in the lungs. During inhalation, fresh air is taken from the trachea down into the posterior air sacs and into the parabronchi which lead from the posterior air sacs into the lung. The air that enters the lungs joins the air which is already in the lungs, and is drawn forward across the gas exchanger into anterior air sacs. During exhalation, the posterior air sacs force air into the same parabronchi of the lungs, flowing in the same direction as during inhalation, allowing continuous gas exchange irrespective of the breathing cycle. Air exiting the lungs during exhalation joins the air being expelled from the anterior air sacs both consisting of "spent air" that has passed through the gas exchanger entering the trachea to be exhaled Fig. The unidirectional airflow through the parabronchi exchanges respiratory gases with a crosscurrent blood flow Fig. The capillaries leaving the exchanger near the entrance of airflow take up more O_2 than capillaries leaving near the exit end of the parabronchi. CO_2 is the only carbon source for autotrophic growth by photosynthesis , and when a plant is actively photosynthesising in the light, it will be taking up carbon dioxide, and losing water vapor and oxygen. At night, plants respire , and gas exchange partly reverses: A stylised cross-section of a euphyllophyte plant leaf, showing the key plant organs involved in gas exchange Plant gas exchange occurs mostly through the leaves. Gases diffuse into and out of the intercellular spaces within the leaf through pores called stomata , which are typically found on the lower surface of the leaf. Gases enter into the photosynthetic tissue of the leaf through dissolution onto the moist surface of the palisade and spongy mesophyll cells. The spongy mesophyll cells are loosely packed, allowing for an increased surface area, and subsequently an increased rate of gas-exchange. Uptake of carbon dioxide necessarily results in some loss of water vapor, [37] because both molecules enter and leave by the same stomata, so plants experience a gas exchange dilemma: The size of a stoma is regulated by the opening and closing of its two guard cells: Plants showing crassulacean acid metabolism are drought-tolerant xerophytes and perform almost all their gas-exchange at night, because it is only during the night that these plants open their stomata. By opening the stomata only at night, the water vapor loss associated with carbon dioxide uptake is minimised. However, this comes at the cost of slow growth: High precision gas exchange measurements reveal important information on plant physiology Gas exchange measurements are important tools in plant science: If the environmental conditions humidity , CO 2 concentration, light and temperature are fully controlled, the measurements of CO 2 uptake and water release reveal important information about the CO 2 assimilation and transpiration rates. The intercellular CO 2 concentration reveals important information about the photosynthetic condition of the plants. Invertebrates[edit] The mechanism of gas exchange in invertebrates depends their size, feeding strategy, and habitat aquatic or terrestrial. Diagram representing the body structure of Porifera. The diagram shows the mechanism of water uptake for sponges. They obtain nutrients through the flow of water across their cells, and they exchange gases by simple diffusion across their cell membranes. Pores called ostia draw water into the sponge and the water is subsequently circulated through the sponge by cells called choanocytes which have hair-like structures that move the water through the sponge. Cnidarians are always found in aquatic environments, meaning that their gas exchange involves absorbing oxygen from water. The cnidarians include corals , sea anemones , jellyfish and hydras. These animals are always found in aquatic environments, ranging from fresh water to salt water. They do not have any dedicated respiratory organs ; instead, every cell in their body can absorb oxygen from the surrounding water, and release waste gases to it. One key disadvantage of this feature is that cnidarians can die in environments where water is stagnant , as they deplete the water of its oxygen supply. In this symbiosis , the coral provides shelter and the other organism provides nutrients to the coral, including oxygen. Cross section of a nematode. The roundworms Nematoda , flatworms Platyhelminthes , and many other small invertebrate animals living in aquatic or otherwise wet habitats do not have a dedicated gas-exchange surface or circulatory system. They instead rely on diffusion of CO 2 and O 2 directly across their cuticle. Other aquatic invertebrates such as most molluscs Mollusca and larger crustaceans Crustacea such as lobsters , have gills analogous to those of fish, which operate in a similar way. Photographic representation of spiracles. Unlike the invertebrates groups mentioned so far, insects are usually terrestrial, and exchange gases across a moist surface in direct contact with the atmosphere, rather than in contact with surrounding water. This respiratory system is separated from their circulatory system. Gases enter and leave the body through openings called spiracles , located laterally along the thorax and abdomen. Similar to plants, insects are able to control the opening and closing of these spiracles, but instead of relying on turgor pressure , they rely on muscle contractions. These branches terminate in specialised tracheole cells which provides a thin, moist surface for efficient gas exchange, directly with cells.

Chapter 8 : Adaptations for Gas exchange - Mr Lovat Biology

Energetics, thermodynamics and adaptation. This is a course in the physiology of animals, or, to use a common phrase, how animals work.

Because of the enormous number of alveoli approximately million in each human lung , the surface area of the lung is very large 75 m2. Having such a large surface area increases the amount of gas that can diffuse into and out of the lungs. Respiratory surfaces are also extremely thin typically only one cell thick , minimizing the distance gas must diffuse across the surface. Basic Principles of Gas Exchange Gas exchange during respiration occurs primarily through diffusion. Diffusion is a process in which transport is driven by a concentration gradient. Gas molecules move from a region of high concentration to a region of low concentration. Blood that is low in oxygen concentration and high in carbon dioxide concentration undergoes gas exchange with air in the lungs. The air in the lungs has a higher concentration of oxygen than that of oxygen-depleted blood and a lower concentration of carbon dioxide. This concentration gradient allows for gas exchange during respiration. Partial pressure is a measure of the concentration of the individual components in a mixture of gases. The total pressure exerted by the mixture is the sum of the partial pressures of the components in the mixture. The rate of diffusion of a gas is proportional to its partial pressure within the total gas mixture. Gas Pressure and Respiration The respiratory process can be better understood by examining the properties of gases. Gases move freely, but gas particles are constantly hitting the walls of their vessel, thereby producing gas pressure. Air is a mixture of gases, primarily nitrogen N_2; Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts, 0. The partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by: Therefore, the partial pressure of oxygen is: At high altitudes, Patm decreases but concentration does not change; the partial pressure decrease is due to the reduction in Patm. When the air mixture reaches the lung, it has been humidified. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure 47 mm Hg is subtracted from the atmospheric pressure: These pressures determine the gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system. To sum up the discussion of partial pressures above: Partial pressure is the pressure of a particular gas in a mixture of gasses, and is calculated by multiplying the fractional composition of the particular gas by the total air pressure in mm Hg The partial pressures of oxygen and carbon dioxide change as blood moves through the body. In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli result in the movement of carbon dioxide out of the blood into the lungs, and oxygen into the blood. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen. Stephen Childs Skin and Gills Earthworms and amphibians use their skin integument as a respiratory organ. A dense network of capillaries lies just below the skin and facilitates gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes. Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much smaller than that. Fish and many other aquatic organisms have evolved gills outgrowths of the body used for gas exchange to take up the dissolved oxygen from water. Gills are made of thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans. This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water high concentration to blood low concentration. Similarly, carbon dioxide molecules in the blood diffuse from the blood high concentration to water low concentration. As water flows over the gills, oxygen is transferred to blood via the veins. Insects have a highly specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body. The tubes in the tracheal system are made of a polymeric material called chitin. Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body and regulating the diffusion of CO2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements. Insects perform respiration via a tracheal system. Mammalian Systems In mammals, pulmonary ventilation occurs via inhalation breathing to bring air into the lungs infoldings of the throat or body surface that enclose respiratory surfaces. During inhalation, air enters the body through the nasal cavity located just inside the nose. As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system. Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle. The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The forced exhalation helps expel mucus when we cough. The trachea and bronchi are made of incomplete rings of cartilage. Bronchi and Alveoli The end of the trachea bifurcates divides to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes. The muscular diaphragm, which facilitates breathing, is inferior to below the lungs and marks the end of the thoracic cavity. The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes. In the lungs, air is diverted into smaller and smaller passages, or bronchi. Air enters the lungs through the two primary main bronchi singular: Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter bronchioles as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. In humans, bronchioles with a diameter smaller than 0. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

Chapter 9 : ANIMALS / FISH -GAS EXCHANGE - Pathwayz

Increasing the internal subdivision and hence the respiratory surface area of the lung occurs at a cost: in a compliant lung, narrow terminal gas exchange components demand more energy to dilate on ventilation and have a high propensity of collapsing.

Bring fact-checked results to the top of your browser search. Abnormal gas exchange Lung disease can lead to severe abnormalities in blood gas composition. Because of the differences in oxygen and carbon dioxide transport, impaired oxygen exchange is far more common than impaired carbon dioxide exchange. Mechanisms of abnormal gas exchange are grouped into four categoriesâ€" hypoventilation , shunting, ventilationâ€"blood flow imbalance, and limitations of diffusion. If the quantity of inspired air entering the lungs is less than is needed to maintain normal exchangeâ€"a condition known as hypoventilationâ€"the alveolar partial pressure of carbon dioxide rises and the partial pressure of oxygen falls almost reciprocally. Similar changes occur in arterial blood partial pressures because the composition of alveolar gas determines gas partial pressures in blood perfusing the lungs. This abnormality leads to parallel changes in both gas and blood and is the only abnormality in gas exchange that does not cause an increase in the normally small difference between arterial and alveolar partial pressures of oxygen. In shunting, venous blood enters the bloodstream without passing through functioning lung tissue. Shunting of blood may result from abnormal vascular blood vessel communications or from blood flowing through unventilated portions of the lung e. A reduction in arterial blood oxygenation is seen with shunting, but the level of carbon dioxide in arterial blood is not elevated even though the shunted blood contains more carbon dioxide than arterial blood. The differing effects of shunting on oxygen and carbon dioxide partial pressures are the result of the different configurations of the blood-dissociation curves of the two gases. As noted above, the oxygen-dissociation curve is S-shaped and plateaus near the normal alveolar oxygen partial pressure, but the carbon dioxide-dissociation curve is steeper and does not plateau as the partial pressure of carbon dioxide increases. When blood perfusing the collapsed, unventilated area of the lung leaves the lung without exchanging oxygen or carbon dioxide, the content of carbon dioxide is greater than the normal carbon dioxide content. The remaining healthy portion of the lung receives both its usual ventilation and the ventilation that normally would be directed to the abnormal lung. This lowers the partial pressure of carbon dioxide in the alveoli of the normal area of the lung. As a result, blood leaving the healthy portion of the lung has a lower carbon dioxide content than normal. The lower carbon dioxide content in this blood counteracts the addition of blood with a higher carbon dioxide content from the abnormal area, and the composite arterial blood carbon dioxide content remains normal. This compensatory mechanism is less efficient than normal carbon dioxide exchange and requires a modest increase in overall ventilation, which is usually achieved without difficulty. Because the carbon dioxide-dissociation curve is steep and relatively linear, compensation for decreased carbon dioxide exchange in one portion of the lung can be counterbalanced by increased excretion of carbon dioxide in another area of the lung. In contrast, shunting of venous blood has a substantial effect on arterial blood oxygen content and partial pressure. Blood leaving an unventilated area of the lung has an oxygen content that is less than the normal content indicated by the square. In the healthy area of the lung, the increase in ventilation above normal raises the partial pressure of oxygen in the alveolar gas and, therefore, in the arterial blood. The oxygen-dissociation curve, however, reaches a plateau at the normal alveolar partial pressure, and an increase in blood partial pressure results in a negligible increase in oxygen content. Mixture of blood from this healthy portion of the lung with normal oxygen content and blood from the abnormal area of the lung with decreased oxygen content produces a composite arterial oxygen content that is less than the normal level. Thus, an area of healthy lung cannot counterbalance the effect of an abnormal portion of the lung on blood oxygenation because the oxygen-dissociation curve reaches a plateau at a normal alveolar partial pressure of oxygen. This effect on blood oxygenation is seen not only in shunting but in any abnormality that results in a localized reduction in blood oxygen content. Mismatching of ventilation and blood flow is by far the most common cause of a decrease in partial pressure of oxygen in blood. There are minimal changes in blood carbon dioxide content unless the degree of mismatch is extremely severe. Inspired air and blood flow normally are distributed uniformly, and each alveolus receives approximately equal quantities of both. As matching of inspired air and blood flow deviates from the normal ratio of 1 to 1, alveoli become either overventilated or underventilated in relation to their blood flow. In alveoli that are overventilated, the amount of carbon dioxide eliminated is increased, which counteracts the fact that there is less carbon dioxide eliminated in the alveoli that are relatively underventilated. Overventilated alveoli, however, cannot compensate in terms of greater oxygenation for underventilated alveoli because, as is shown in the oxygen-dissociation curve, a plateau is reached at the alveolar partial pressure of oxygen, and increased ventilation will not increase blood oxygen content. In healthy lungs there is a narrow distribution of the ratio of ventilation to blood flow throughout the lung that is centred around a ratio of 1 to 1. In disease, this distribution can broaden substantially so that individual alveoli can have ratios that markedly deviate from the ratio of 1 to 1. Any deviation from the usual clustering around the ratio of 1 to 1 leads to decreased blood oxygenationâ€"the more disparate the deviation, the greater the reduction in blood oxygenation. Carbon dioxide exchange, on the other hand, is not affected by an abnormal ratio of ventilation and blood flow as long as the increase in ventilation that is required to maintain carbon dioxide excretion in overventilated alveoli can be achieved. A fourth category of abnormal gas exchange involves limitation of diffusion of gases across the thin membrane separating the alveoli from the pulmonary capillaries. A variety of processes can interfere with this orderly exchange; for oxygen, these include increased thickness of the alveolarâ€"capillary membrane, loss of surface area available for diffusion of oxygen, a reduction in the alveolar partial pressure of oxygen required for diffusion, and decreased time available for exchange due to increased velocity of flow. There is no diffusion limitation of the exchange of carbon dioxide because this gas is more soluble than oxygen in the alveolarâ€"capillary membrane, which facilitates carbon dioxide exchange. The complex reactions involved in carbon dioxide transport proceed with sufficient rapidity to avoid being a significant limiting factor in exchange. Interplay of respiration, circulation , and metabolism The interplay of respiration, circulation, and metabolism is the key to the functioning of the respiratory system as a whole. Cells set the demand for oxygen uptake and carbon dioxide discharge, that is, for gas exchange in the lungs. The circulation of the blood links the sites of oxygen utilization and uptake. The proper functioning of the respiratory system depends on both the ability of the system to make functional adjustments to varying needs and the design features of the sequence of structures involved, which set the limit for respiration. The main purpose of respiration is to provide oxygen to the cells at a rate adequate to satisfy their metabolic needs. This involves transport of oxygen from the lung to the tissues by means of the circulation of blood. Modern cell biology has unveiled the truth behind the metaphor. Each cell maintains a set of furnaces, the mitochondria , where, through the oxidation of foodstuffs such as glucose , the energetic needs of the cells are supplied. The precise object of respiration therefore is the supply of oxygen to the mitochondria. Cell metabolism depends on energy derived from high-energy phosphates such as adenosine triphosphate ATP , whose third phosphate bond can release a quantum of energy to fuel many cell processes, such as the contraction of muscle fibre proteins or the synthesis of protein molecules. To recharge the molecule by adding the third phosphate group requires energy derived from the breakdown of foodstuffs, or substrates. Two pathways are available: The anaerobic pathway leads to acid waste products and is wasteful of resources: The breakdown of one molecule of glucose generates only two molecules of ATP. For any sustained high-level cell activity, the aerobic metabolic pathway is therefore preferable. Since oxidative phosphorylation occurs only in mitochondria, and since each cell must produce its own ATP it cannot be imported , the number of mitochondria in a cell reflects its capacity for aerobic metabolism, or its need for oxygen. The supply of oxygen to the mitochondria at an adequate rate is a critical function of the respiratory system, because the cells maintain only a limited store of high-energy phosphates and of oxygen, whereas they usually have a reasonable supply of substrates in stock. If oxygen supply is interrupted for a few minutes, many cells, or even the organism, will die. Oxygen is collected from environmental air, transferred to blood in the lungs, and transported by blood flow to the periphery of the cells where it is discharged to reach the mitochondria by diffusion. The transfer of oxygen to the mitochondria involves several structures and different modes of transports. It begins with ventilation of the lung, which is achieved by convection or mass flow of air through an ingeniously branched system of airways. In the most peripheral airways, ventilation of alveoli is completed by diffusion of oxygen through the air to the alveolar surface. The transfer of oxygen from alveolar air into the capillary blood occurs by diffusion across the tissue barrier; it is driven by the oxygen partial pressure difference between alveolar air and capillary blood and depends on the thickness about 0. Convective transport by the blood depends on the blood flow rate cardiac output and on the oxygen capacity of the blood, which is determined by its content of hemoglobin in red blood cells. The last step is the diffusive discharge of oxygen from the capillaries into the tissue and cells, which is driven by the oxygen partial pressure difference and depends on the quantity of capillary blood in the tissue. In this process the blood plays a central role and affects all transport steps: Blood also serves as carrier for both respiratory gases: Metabolism, or, more accurately, the metabolic rate of the cells, sets the demand for oxygen. At rest a human consumes about ml about 15 cubic inches of oxygen each minute. With exercise this rate can be increased more than fold in a normal healthy individual, but a highly trained athlete may achieve a more than fold increase. As more and more muscle cells become engaged in doing work, the demand for ATP and oxygen increases linearly with work rate. This is accompanied by an increased cardiac output , essentially due to a higher heart rate, and by increased ventilation of the lungs; as a consequence, the oxygen partial pressure difference across the airâ€”blood barrier increases and oxygen transfer by diffusion is augmented. This range of possible oxidative metabolism from rest to maximal exercise is called the aerobic scope. The upper limit to oxygen consumption is not conferred by the ability of muscles to do work, but rather by the limited ability of the respiratory system to provide or utilize oxygen at a higher rate. Muscle can do more work, but beyond the aerobic scope they must revert to anaerobic metabolism, with the result that waste products, mainly lactic acid , accumulate and limit the duration of work. The limit to oxidative metabolism is therefore set by some features of the respiratory system, from the lung to the mitochondria. Knowing precisely what sets the limit is important for understanding respiration as a key vital process, but it is not straightforward, because of the complexity of the system. Much has been learned from comparative physiology and morphology , based on observations that oxygen consumption rates differ significantly among species. For example, the athletic species in nature, such as dogs or horses , have an aerobic scope more than twofold greater than that of other animals of the same size; this is called adaptive variation. Then, oxygen consumption per unit body mass increases as animals become smaller, so that a mouse consumes six times as much oxygen per gram of body mass as a cow , a feature called allometric variation. Furthermore, the aerobic scope can be increased by training in an individual, but this induced variation achieves at best a 50 percent difference between the untrained and the trained state, well below interspecies differences. Within the aerobic scope the adjustments are due to functional variation. For example, cardiac output is augmented by increasing heart rate. Mounting evidence indicates that the limit to oxidative metabolism is related to structural design features of the system. The total amount of mitochondria in skeletal muscle is strictly proportional to maximal oxygen consumption, in all types of variation. In training, the mitochondria increase in proportion to the augmented aerobic scope. Mitochondria set the demand for oxygen, and they seem to be able to consume up to 5 ml 0. If energy ATP needs to be produced at a higher rate, the muscle cells make more mitochondria. It is thus possible that oxygen consumption is limited at the periphery, at the last step of aerobic metabolism. But it is also possible that more central parts of the respiratory system may set the limit to oxygen transport, mainly the heart, whose capacity to pump blood reaches a limit, both in terms of rate and of the size of the ventricles, which determines the volume of blood that can be pumped with each stroke. The issue of peripheral versus central limitation is still under debate. It appears, however, that the lung as a gas-exchanging organ has sufficient redundancy that it does not limit aerobic metabolism at the site of oxygen uptake. But, whereas the mitochondria, the blood, the blood vessels , and the heart can increase in number, rate, or volume to augment their capacity when energy needs increase, such as in training, the lung lacks this capacity to adapt. If this proves true, the lung may well constitute the ultimate limit for the respiratory system, beyond which oxidative metabolism cannot be increased by training.