

The Comparative Physiology of Respiratory Organs¹

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Comparative physiology deals with animal functions, in relation to the very different and variable environments in which the animals live, and endeavours thereby to deepen our understanding of these functions.

When an eye is to produce sharp images of objects at varying distances it must possess a special mechanism for "accommodation". Comparative physiology shows that accommodation can be brought about in many different ways, down to the one found in jumping spiders (*Salpicus*) possessing two sets of eyes, of which one allows the animal to see its prey at some distance—provided it moves—while the other set gives a fairly sharp image when the distance is just right for a jump.

Comparative physiology is a young science, trying to cover a very extensive field. It is at the stage of collecting and recording facts and begins a tentative systematization, but the great goal, viz. to find out how all this has come about, remains very dim. In certain directions, e. g. the study of animal senses, mainly undertaken by v. FRISCH and his school, extraordinary progress has been made, and I shall in the following lines attempt to show that we also in regard to the comparative physiology of respiratory organs, in which I have been interested for many years, have gained a deeper insight and established some system.

The large majority of animal organisms require free oxygen to maintain their vital functions. The oxygen is used up in a kind of "combustion" and part of the energy liberated can be utilized by the organism. When oxygen is used up by the metabolic processes at a certain point in an organism the dissolved gas will diffuse towards this point from the surroundings, and the process may be maintained. This is the fundamental principle for the supply of oxygen, but although diffusion of oxygen (O_2), from regions with a higher to regions with a lower concentration, remains an important element in the respiration of all organisms, other transport mechanisms are as a rule necessary, and these become the main object for comparative physiological study.

The "Call for Oxygen" varies greatly from one animal to another. Very generally it can be stated that an increase in size means increased O_2 requirement, but there is no simple proportionality, the call for oxygen increasing definitely less than the weight and, for animals of similar build and habits, approximately with the square of the linear dimensions, while the weight increases with the cube. Many

other relations tend to modify this simple rule, and it is to be noted that muscular activity always increases the call for oxygen, which may rise even up to a hundredfold by maximal work in running, swimming and especially flying.

The access to oxygen shows large differences. In air the O_2 content is constant at about 21%, and only at high altitudes is significantly less oxygen available on account of the reduced total pressure, but in natural waters, inhabited by animals, the oxygen content may vary greatly. Fresh water saturated with air contains at 10° C about 8 ml dissolved O_2 per liter, decreasing with increasing temperature and also decreasing somewhat with increasing salt content. Sea water generally contains enough oxygen to supply the needs of the animals, but in fresh waters conditions differ greatly. The aquatic plants will often in light cause a supersaturation with O_2 which becomes liberated in numerous small bubbles, eagerly sought by certain animals, but where processes of decay are dominant—as in many tropical swamps—the oxygen content can become extremely low and force the animals to very peculiar measures of defence. In the deep layers of temperate lakes the water becomes stagnant and poor in O_2 during the summer, after being mixed from surface to bottom and practically saturated during the spring gales. In the bottom of fresh waters, where enormous numbers of animals find their living, much oxygen is used and the supply often a vital problem for the animals.

In air as well as in water oxygen is transported by currents (convection), but when the medium is stagnant transport must take place by diffusion which, being inversely proportional to the square of the distance, becomes a very slow process over larger distances, especially in water where the rate is only $1/300,000$ of that in air. In animal tissues diffusion is still slower. CO_2 diffuses more slowly than oxygen in air, but about 25 times more rapidly in water and tissues.

Calculations and observations go to show that many very small animals can obtain the necessary oxygen in all their tissues by diffusion through the body surface and need neither respiratory nor circulatory organs. This applies to the Protozoa, practically to all eggs, at least in the early stages of development, and also to many larvae and mature animals of sizes below 1 mm. Also a number of larger animals like Coelenterata and Actinia can exist without respiratory organs, because of their very low metabolic rate.

When, in somewhat larger forms, the diffusion distances become too long, diffusion is supplemented by a mechanical transport brought about by a fluid,

¹ Compiled from A. KROGH, Comparative Physiology of Respiratory Mechanisms, Philadelphia 1940.

blood, taking up oxygen at the surface and transporting it by circulation to the interior of the organism. In most cases the blood is specially adapted for O_2 transport as discussed below. A number of small animals, living in water or moist air, possess such an oxygen transport without having specialized respiratory organs, the oxygen absorption taking place through the undifferentiated surface, or part of it, into blood vessels running just below or in the skin. Such is the case in earthworms, leeches and many other worms, many larvæ of diverse groups and newly hatched fishes. Theoretical considerations show that animals possessing this type of respiration can attain a small size only, unless the skin remains very thin with increasing size. Even in moderately dry air such forms cannot exist, on account of the loss of water by evaporation.

In animals living in water the evolution is carried forward by the development of special appendages, usually called gills, with a large surface, thin walls and a copious blood supply. Gills can assume the most diverse forms and become very complicated. In some cases it can be shown that their development is directly conditioned by the access to oxygen. In Amphibia larvæ at a reduced O_2 pressure the external gills grow to a large size, while in oxygen saturated water they remain small (BABÁK, DRASTICH¹).

At the higher stages of development the gills are protected in a "gill cavity" through which a flow of water is maintained. The most perfect gills in fishes are arranged on "gill arches" as "filaments"

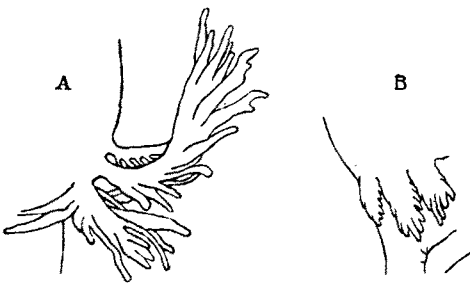


Fig. 1. Gills of Salamander larvæ. A from animal reared in water at 70 mm O_2 pressure; B at 760 mm O_2 pressure.

carrying an enormous number of leaf-like lamellæ. The flow of water has to pass the narrow spaces between these lamellæ, so that the distances to be traversed by diffusion are very small. VAN DAM² has shown further that a counter current principle is realized, the flow of blood inside the lamellæ being in the opposite direction to the water current. This makes it possible to utilize a very large proportion of the oxygen in the water and yet obtain a high final O_2 tension in the blood. Utilizations up to 80% have been measured. The oxygen in the blood has been

made to regulate the flow of water by causing more powerful respiratory movements when it falls off. In spite of the economies realized the amount of work necessary for ventilating the gills is responsible for a considerable fraction of the total metabolism of a fish. When for instance a trout is exposed to water with a low oxygen content the increased ventilation may raise the metabolism up to 70%. Certain fishes (mackerell) save the special respiratory work by swimming with the mouth open, increasing the water current through the gills in proportion to the speed, but this means that they have to keep on swimming to get oxygen, and they cannot be kept in ordinary aquaria.

It can be considered as proved that animal life was originally aquatic, and that the adaptations to life on land are secondary. These adaptations took place, mainly, in a very remote past, but nevertheless we can find even now many examples of transition from water to air breathing. Such examples are met with in the tidal zone of the ocean beaches and especially in tropical fresh-waters, where the oxygen content is often reduced below even very modest requirements. Ordinary gills are unsuitable for air breathing; while floating in water they collapse in air and present a greatly reduced surface. Several animals in the tidal zone have stiff gills, functioning in moist air as well as in water, and in the large pagurid *Birgus* which even climbs trees, special stiff gills for air breathing are present. They must be kept moist, and at intervals *Birgus* must enter the water for this purpose. Several tropical fresh water fishes can live for a time on land and show similar structures, but this is not the path leading to the evolution of higher vertebrates.

In other tropical swamp-fishes cavities have been developed which can be filled with air and, thanks to a dense capillary network in the walls, can act as lungs, and in the lung fishes (Dipnoi), relatives of the earliest Amphibia, the swim bladder is thus taken into the service of respiration. It is interesting to note that this line of evolution involves a very serious sacrifice in respiratory efficiency, which it has taken many millions of years fully to compensate. In the normal fishes the venous blood from all organs goes to the heart and is pumped directly through the gills to the organs, which all receive blood with as much O_2 as the gills have managed to absorb. When the gill function and the gills themselves become reduced and are replaced by the swim bladder, acting as a lung, the oxygenated blood from this organ is mixed with the venous blood from all the others, and the mixture is pumped out by the heart to all organs, including the lung. No single organ gets completely aerated blood, and the lung gets blood which is not properly desaturated, that is the respiratory efficiency is very seriously reduced.

In the lung breathing vertebrates, from the Dipnoi up, we find a series of the most complicated arrange-

¹ L. DRASTICH, Z. vgl. Physiol. 2, 632 (1925).

² L. VAN DAM, Diss., Groningen 1938.

ments to counteract this handicap, which among other things seriously affects the power of sustained muscular effort. In the Dipnoi there are separate pulmonary veins, carrying the oxygenated blood direct to the heart, and imperfect partitions within the heart, so that most of this blood is taken through the two first gill arches, supplying the head (and brain) which thus gets the best aerated blood. This arrangement is further developed in the Amphibia and reptiles, where the heart has two separate atria, for aerated and venous blood respectively, and such partitions in the common ventricle and the arterial trunks that a separation of increasing perfection is obtained, until we finally in the warmblooded find the heart completely divided, the right heart receiving blood from the body as a whole and sending it through the lungs to the left heart, which distributes completely aerated blood to all organs, as in the remote ancestors among the fishes.

Aërial respiration. Air is a much more favourable medium for respiration than water. 1 liter water weighs 1 kg and contains from 5 to 10 ml O_2 , when saturated. 1 liter air weighs 1.4 g only and contains 210 ml O_2 . Diffusion can provide large quantities of O_2 over distances up to 1 cm, and mechanical ventilation requires but little energy. It is usually important for the air breathing organisms to reduce the evaporation loss of water, and this is best accomplished when the respiratory surfaces are enclosed within a cavity with a limited and regulated supply of air from outside. When oxygen is absorbed from the air in such a cavity the gas is replaced by a similar volume of CO_2 , diffusing out from the blood. The CO_2 tension within the organism must be slightly higher than in the pulmonary air to allow the CO_2 to diffuse out, and this

Only on the lowest stage of evolution or development are the lungs simple sacs (fig. 2); usually the surface is increased by folding (fig. 3—4).



Fig. 4. Lung of tortoise (Diagram).

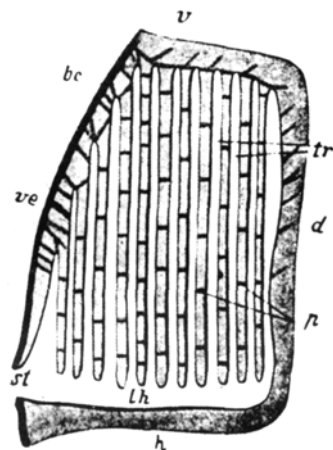


Fig. 5. Spider lung (about 1½ mm long).

Physiologically we distinguish between two types of lungs, viz. "diffusion lungs", in which the exchange between the lung surface and the outer atmosphere takes place by diffusion only, and "ventilation lungs", in which renewal of the air is provided by respiratory movements.

Diffusion lungs can only be efficient in comparatively small animals, because in large ones the diffusion distances become too long. They are quite common among air breathing invertebrates and, being independently developed even within rather small groups, are of very varying construction. Fig. 5 shows a section of a spider lung. The blood flows through the thin leaves of the "book". One group of spiders is characterized by having two pairs of such lungs. In another group one pair is made up of rather long, slightly branched tubes, resembling tracheæ. A mediterranean chilopod, *Scutigera*, has 7 small lungs along the dorsal midline each made up of about 600 slightly branched tubes ½ mm in length and opening into a common "vestibulum", connected with the atmosphere through a narrow spiracle. No ventilation movements have ever been observed in these types

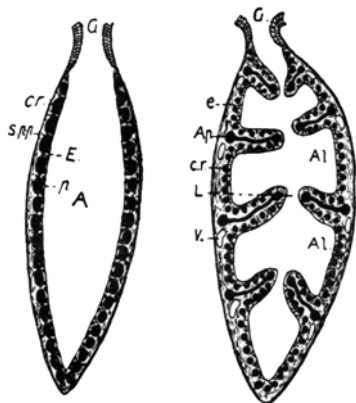


Fig. 2.
Lung of
Proteus
(Diagram).

Fig. 3.
Lung of
Siren
(Diagram).

fact sets a limit to the utilization of the oxygen, because CO_2 above a certain pressure becomes harmful. This limiting pressure often corresponds to about 6% CO_2 in the pulmonary air and therefore only about 6 out of the 21% O_2 in the air can be taken out before renewal must take place. In many air breathing animals the height of the CO_2 pressure is utilized to regulate the pulmonary ventilation.

of lung, and calculation shows that diffusion is amply sufficient.

Fairly simple conditions are seen in the pulmonate snails and slugs, and it is easy to observe the lung e. g. in the black *Arion* where the opening varies in diameter between 4 and 6 mm and the lung surface is about 6 cm². DAHR¹ calculated that an O₂ pressure difference of only 1/4% between the atmosphere and the lung surface is sufficient to provide the necessary oxygen by diffusion. Real ventilating movements are absent, although they have often been described in the literature during the period when they were assumed to be necessary.

Through the moist skin of these animals a fairly large fraction of the necessary oxygen can diffuse in, and the lung is often kept closed for rather long periods. Also in the Amphibia, for which a high degree of atmospheric moisture is essential, the skin is an accessory respiratory organ through which much CO₂ is eliminated and some O₂ absorbed.

Ventilation lungs have been developed only within the vertebrate phylum, and it can be safely stated that this type of respiratory organ is the only one, so far known, which will allow an air breathing animal to attain a high rate of metabolism and a really large size.

Two essentially different types of ventilation lungs have come into existence. One is found in Amphibia, most reptiles and the mammals. In these animals the lungs are very elastic and freely suspended in the body cavity or in a special "pleural" cavity. They are alternately filled with air by inspiration and (partially) emptied by expiration. In the second type, found in the birds, the lungs are firmly attached to the ribs and almost immobile, while the ventilation is brought about by "air sacs" driving the respiratory air current back and forth through the lungs.

In the diagrams (figures 2—4) the increasing folding and surface development in the lungs of Amphibia and Reptilia is shown. In the mammals each lung is divided up into an enormous number of almost microscopic "alveoli", in the thin walls of which the blood flows through a very dense capillary network. The diffusion distances thus become extremely short and the surface very large. In man a somewhat uncertain calculation has given the figure 90 m² for a volume of 3 l.

The ventilation mechanism shows a characteristic evolution. In the Amphibia air is pressed into the lungs by a kind of swallowing, and, when opened to the atmosphere, they collapse completely. This mechanism is retained in some reptiles and is utilized by the *chamæleon* to blow up the lungs to an excep-

tionally large volume, but otherwise the normal type of respiration is similar to that in the mammals, viz. the lungs are suspended in a special pleural cavity in which the pressure is slightly below the atmospheric, so that the lungs can never collapse completely. When this cavity is dilated by inspiratory movements air will flow into the lungs.

In warmblooded animals the performance of the respiratory organs can become tremendous. In man at rest the ventilation amounts to a few liters per minute and the O₂ absorbed to about 1/4 l, but the ventilation can be increased to over 100 l, and over 4 l O₂/m can become absorbed during heavy work. Even with such violent breathing the work of ventilation does not represent more than 5% of the total. The ventilation is regulated by means of CO₂, acting through the blood on the "respiratory center" in the medulla. In muscular work the sensitivity of the center is increased in close relation to the severity of the work.

The respiratory system of the birds was probably evolved in analogy to that seen in a few reptiles, in which certain bronchi pass through the lungs into air sacs, but the connecting links between such forms and the birds are unknown, and it has proved extremely difficult to reach even an approximate understanding of the respiratory mechanism in birds. The decisive contribution was given in 1942 by ZEUTHEN¹.

The lungs of birds are rather small, firmly adherent to the ribs and only slightly distensible. The main bronchi pass through the lungs to air sacs (fig. 6),

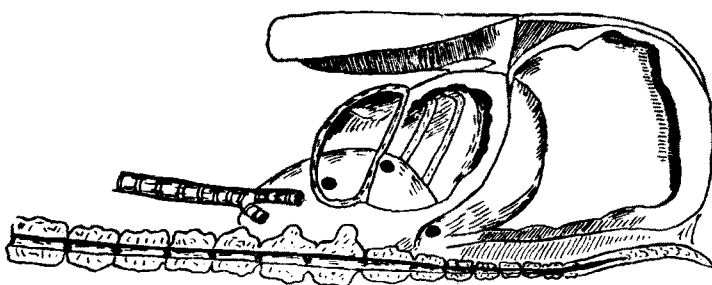


Fig. 6. Lung and air sacs in a duck. The bronchial openings into two thoracic and the abdominal air sac are shown.

of which the abdominal are by far the largest and most important. These are dilated by inspiration and compressed by expiration. From the anterior ends of the main bronchi a small number of "ventro-bronchi" take their origin, branching out along the ventral surface of the lung, and further on along the main bronchi the "dorsobronchi" branch out along the dorsal surface. These two sets of secondary bronchi are connected through a large number of "para-bronchi", less than 1/2 mm in diameter and, in a pigeon, a few mm long. Their walls are like a sieve, and the

¹ E. DAHR, Lund's Univ. Årsskr. 20, 10 (1924).

¹ E. ZEUTHEN, Danske vid. Selsk. biol. Medd. (1942).

holes lead into the air capillaries, filling up all inter-spaces between a very dense network of blood capillaries. In order to explain the passage of air through the narrow parabronchi the existence of special valves has been postulated, but nobody has been able to find such valves, and ZEUTHEN maintains that they are

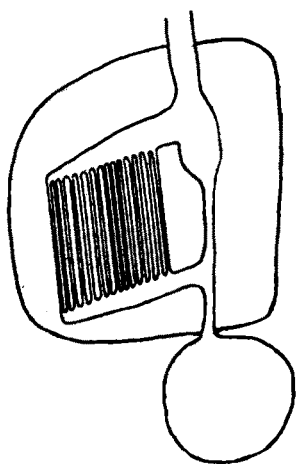


Fig. 7. Diagram of bird lung and one air sac.

superfluous. The air current will automatically be distributed, both during inspiration and expiration, between the two possible routes according to their respective resistance. The route through the small bronchi is certainly longer than the direct one, but its aggregate cross section is much larger. The exact distribution has still to be made out.

When part of the air passes during inspiration direct to the air sacs these will contain air relatively rich in oxygen, and part of this passes through the parabronchi during expiration. The passage into the air capillaries must take place by diffusion.

During flight the uptake of oxygen must be enormous. ZEUTHEN calculates a 27 fold increase over the resting value in a pigeon flying at top speed. There are muscles in the walls of the parabronchi, and it is very likely, but so far not proved, that the relative resistances of the two routes for the air can be regulated.

A number of air breathing vertebrates from all classes have returned to live in water, but only the whales have become completely independent of land. This return and especially deep diving is connected with a series of adaptations, among which those affecting respiration are specially interesting. A reflex is developed causing complete closure of the nasal openings when touched by water. While in terrestrial vertebrates a small accumulation of CO_2 in the body compels respiration this is not the case in the aquatic forms. The diving animals carry a fairly large store of oxygen. This is not contained in the lungs which are rather small, but in a very large blood volume

with a high O_2 capacity (see p. 436) and often also in the muscles which are unusually rich in hæmoglobin.

Elaborate experiments on seals, carried out by SCHOLANDER¹, show that the oxygen store is insufficient and that a seal contracts a considerable "oxygen debt" during a prolonged dive. Also land animals, like man, can contract an oxygen debt in the muscles during work, while the brain must have its normal oxygen supply all the time. The diving animals have mechanisms for shunting blood from the muscles during the dive and securing the supply to the brain. In the seals the pulse rate is slowed down to a few beats per minute. The oxygen debt, which it is possible to incur, is related to the body size, and the large whales can stay under water for an hour or more.

The sperm whale is known to dive to depths of 900 m, corresponding to 90 atm. air pressure in the lungs. This should cause large amounts of nitrogen to become dissolved in the blood, and it has for long been an intriguing riddle how the whales could avoid the "diver's disease" which is well-known in human divers, coming up too rapidly from a depth of only 50 m, and is caused by bubbles of nitrogen liberated in their blood and tissues. SCHOLANDER made it probable that the air is driven out completely from the lungs of deep diving whales and stored in the trachea and bronchi.

The respiratory function of the blood. The transport of the respiratory gases between the body cells and the respiratory organs takes place by means of the blood stream, and the oxygen transport is bound up with several interesting adaptations. As stated above oxygen is only slightly soluble in water, and the O_2 transport takes place by means of special substances which combine reversibly with oxygen. 4 groups of such substances are known. They are pigments containing iron or copper and show colour changes, correlated with the oxygen content. The iron containing hæmoglobins are the best known, and these only will be dealt with here.

The simplest hæmoglobin is a compound of hæmatin, containing 1 iron atom, with a protein. The molecular weight is 17,250, and it is found dissolved in the body fluid of the red *Chironomus* larvæ. The hæmoglobins of vertebrates contain 4 such units in each molecule, and the hæmoglobins of several invertebrates many more. Each unit can combine with one molecule O_2 . Hæmoglobin is the O_2 carrying pigment in all vertebrates, but has been independently and apparently accidentally evolved in different invertebrates, most often in animals occasionally or normally exposed to serious oxygen lack. Its occurrence was altogether incomprehensible, until it was shown that substances nearly related to hæmatin are present in almost all

¹ P. F. SCHOLANDER, Norske vid. Akad. I (1940).

cells. Even with this information the evolution of hæmoglobins will be extremely difficult to make out.

The respiratory significance of a blood pigment is characterized by the "oxygen capacity" and the "oxygen dissociation curve" of the blood. The oxygen capacity is, traditionally, given in volumes per cent, viz. the number of ml O_2 maximally bound in 100 ml blood. The oxygen capacity of normal human blood is about 20, but in coldblooded and invertebrates much lower. In warmblooded at high altitudes it can become definitely higher.

The oxygen dissociation curve—or a set of such curves—expresses quantitatively the conditions under which the blood will take up or give off oxygen. When blood is exposed to mixtures of nitrogen and air with a varied O_2 content—which as a rule we express by the O_2 partial pressure, given in mm of mercury—we find the O_2 of the blood (in per cent of the capacity) depending upon the O_2 pressure in accordance with the O_2 dissociation curve. Fig. 8 shows a small number of such curves. It is seen that frog blood at $15^\circ C$ and human blood at $35^\circ C$ have very nearly the same curve, and further that at $15^\circ C$ human blood becomes a very poor respiratory medium, since it will scarcely begin to give off oxygen until the pressure is down to 5 mm—less than 1% of the atmospheric (7.6 mm). All O_2 dissociation curves are

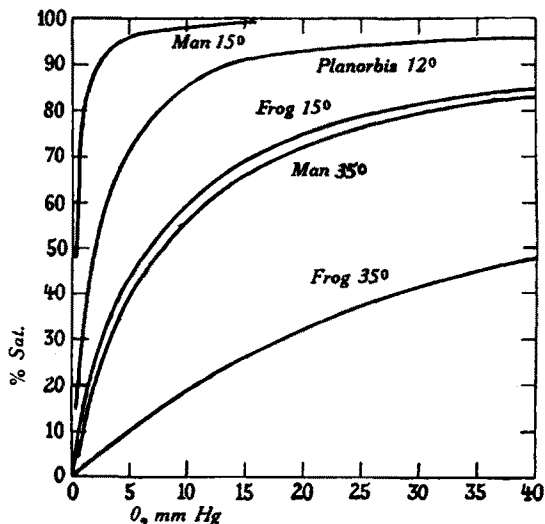


Fig. 8. Oxygen dissociation curves for man, frog and *Planorbis* at different temperatures.

strongly influenced by temperature and show that oxygen becomes more firmly bound with decreasing temperature.

Fig. 9 shows another important relation, also universal, but showing very large quantitative differences, namely to the simultaneous pressure of carbon dioxide. These curves illustrate how at low O_2 pressures CO_2 drives out oxygen from the hæmoglobin and that, therefore, the CO_2 coming from the tissues facilitates the transfer of oxygen to them.

For purposes of biological comparison it is often sufficient to know the "loading" and "unloading" tensions of the blood, which means the O_2 pressures at which the blood will bind respectively 95% and 50% of its capacity. In fig. 9 the loading tensions

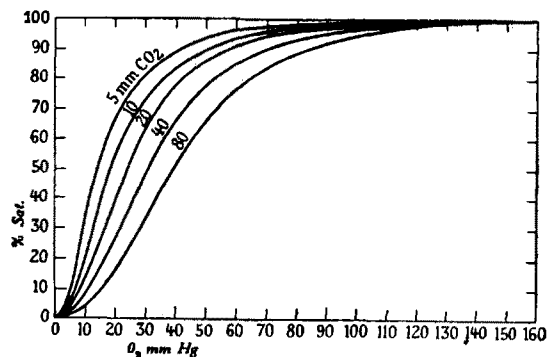


Fig. 9. Oxygen dissociation curves for dog's blood at increasing CO_2 tensions.

for the curves drawn vary from about 60 to about 100 mm and the unloading tensions from 15 to 40 mm. Generally it is to the interest of the organism to have a high tension of unloading, because it facilitates the transfer of O_2 to the tissues, and on the other hand a loading tension low enough to allow practically complete saturation of the blood with oxygen in the respiratory organs. As the two tensions are interdependent the result must be a compromise, but hæmoglobins can be adapted to very different conditions as illustrated in the following examples.

There is a very definite adaptation to the normal temperature range of the organism, as illustrated in fig. 8 for man and the frog, and further an adaptation to the special respiratory conditions of the habitat can usually be demonstrated.

In the sea and in rapid streams the O_2 tension is generally high and almost constant and the CO_2 tension very low (both being approximately in equilibrium with the atmosphere) and most fishes living there have a high loading tension and also a fairly high unloading tension at the summer temperatures to which they are exposed. Both tensions are strongly affected by CO_2 , which is of no consequence for the loading, but definitely facilitates the unloading. Fresh water fishes in lakes and ponds, in which the O_2 tension often becomes very low and CO_2 is sometimes accumulated, have a much lower loading tension, only slightly affected by moderate CO_2 tensions, while the tension of unloading is considerably increased by CO_2 . *Cyprinus carpio* for instance shows a loading tension of only 10 mm. At the atmospheric CO_2 pressure the unloading tension is only 3 mm, but a CO_2 pressure of 16 mm raises it to 15 mm.

Certain invertebrates, having a very low unloading tension, utilize their hæmoglobin only when the oxygen content of the water becomes minimal, and this is

characteristic especially for the red larvæ of the mosquito *Chironomus*, living in the bottom of deep lakes, where the oxygen gets very low in the course of the summer. They manage to survive, but their growth is definitely retarded.

In the free atmosphere the O_2 and CO_2 contents are constant, but in the lungs of vertebrates the concentrations of these gases can vary considerably from one species to another. The most usual conditions in mammals are illustrated by the curves in fig. 9.

Special conditions obtain at high altitudes. The Lama, normally living high up in the mountains, has a definitely lower loading tension than mammals at low levels and also a somewhat lower unloading tension, but a greatly increased oxygen capacity and also much hæmoglobin in the muscles. Human beings cannot change their oxygen dissociation curve, even by a prolonged sojourn at great heights, but the O_2 capacity becomes greatly increased. Considerable acclimatization is possible, but the ability to do muscular work remains lowered to such an extent that it appears impossible ever to reach the summit of Mount Everest by climbing. Dogs reared at high altitude produce much muscle hæmoglobin, but it is improbable that such a production can be induced in the adult organism.

Tracheal Respiration, as found in a number of arthropods and highly developed in the insects, represents a solution of the oxygen supply problem which differs in principle from the one depending on circulation of blood. The air penetrates through richly branched chitinous tubes from the surface to all points in the body and right into the cells. Blood circulation is superfluous from the point of view of oxygen supply, but exists and fills other functions. In an insect larva the whole tracheal system can be injected with highly coloured lipoids and thereupon all the tissues removed by artificial digestion, so that a measuring study of the tracheæ becomes possible (KROGH¹). Bushes of tracheæ spring from two series of openings, called spiracles, one on each side of the body, and elaborate measurements on a *Cossus* larva 6 cm long and weighing 3.4 g showed an average length of the tracheæ of 6 mm with an aggregate cross section not less than 6.7 mm². Calculations showed that the oxygen required for the animals metabolism would be made to diffuse in through the whole length of the tracheæ by an O_2 pressure difference of only 11 mm, corresponding to 1½ %. If we assume the larva magnified 10 times, to a length of 60 cm and a weight of 3.4 kg, its metabolism would increase, probably about 300 fold, but diffusion would only be able to supply 10 times as much as in the actual larva, since the total cross section of the tracheæ would be increased 100 times, but their length 10 times.

On the other hand conditions would be greatly improved in an animal $\frac{1}{10}$ the length of the *Cossus* larva, which is much nearer to the average size of insects.

The oxygen uptake by diffusion in the tracheal system of insects is regulated in two different ways. HAZELHOFF¹ showed by observations on large insects that the mechanism for closing spiracles is activated by the concentration of CO_2 . They are almost completely closed in CO_2 free air and wide open at a concentration of 3%. When the animals are at rest the spiracles are nearly closed, but muscular effort causes them to open through the increased production of CO_2 . The significance of this mechanism, the respiratory effect of which during rest is to impede the diffusion

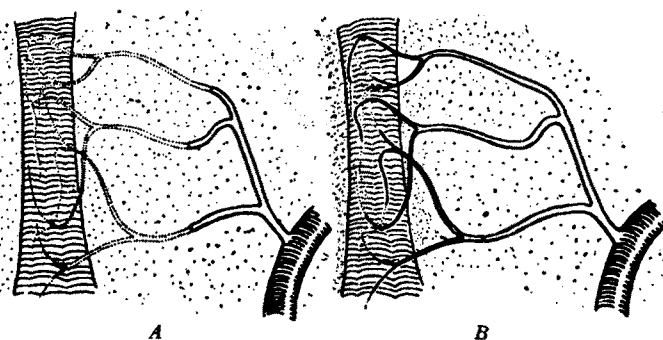


Fig. 10. Diagram of tracheoles to a muscle fibre. *A* at rest with tracheoles filled with fluid; *B* exhausted by repeated contractions.

of oxygen by necessitating a higher pressure difference, has been shown to lie in the fact that it reduces the loss of water vapour from the tracheal system.

The second mechanism, demonstrated by WIGGLESWORTH², can greatly increase the supply of oxygen to working organs. The exchange between the tissues and the tracheal air does not take place in the directly visible tracheæ, which have chitinous walls offering a high resistance to diffusion, but in a richly branched system of "tracheolæ" with diameters below 1 μ . These tracheolæ are in the resting animal almost filled with fluid and invisible, even at the highest magnifications, but when a muscle works substances are produced which cause a retraction of the fluid in the tracheolæ and thereby improve the conditions for diffusion.

In many insects of medium and large size—from bees upwards—the diffusion is insufficient, especially during flight, when metabolism can be raised more than a hundred times. Diffusion is then supplemented by mechanical ventilation of special tracheæ or parts of tracheæ, which are either elliptical in cross section or made up as thin-walled sacs. These organs are highly elastic and are compressed by active expiratory movements. Even in these insects the major part of the tracheal system consists of chitinous tubes with

¹ A. KROGH, Pfl. Arch. 179, 95, 113 (1920).

¹ E. H. HAZELHOFF, Proefschrift, Utrecht 1926.

² V. B. WIGGLESWORTH, Proc. roy. Soc. B. 106, 230 (1930).

a circular cross section which are almost incompressible, and the oxygen must diffuse along relatively considerable distances from the ventilation tracheæ to the organs. A size limit is therefore present even for insects having mechanical ventilation, and there is reason to believe that the 30 cm *Meganeura* of the Carbon period reached this limit.

The tracheal respiration would appear to be very closely tied up with life on land and in the air, but nevertheless many insect larvæ and some imagines live in fresh waters and show the most diverse adaptations, which may even make them completely independent of the surface.

Disregarding a number of small forms, which have given up tracheal respiration altogether (*Chironomus* and *Corethra* larvæ), the simplest cases (e. g. *Culex*) are those in which the larvæ spend most of their time hanging at the surface from which O₂ diffuses through the whole length of the body.

The larvæ of the big water beetles (*Dytiscus*) must come to the surface at intervals to fill by means of a few deep respirations their ventilation tracheæ, which stretch along the whole length of the body and act as air reservoirs during the dive.

A number of forms (*Notonecta* etc.) carry air stores held by hydrophobe hairs on the integument, and these act as a kind of gills, oxygen diffusing in from the water and CO₂ diffusing out.

A few larvæ from different orders of insects have "discovered" the air in the submersed tissues of plants and introduced their thornshaped spiracles into this air from which they are supplied by diffusion.

A number of forms have evolved "tracheal gills" making them completely independent of the surface. The most perfect are those of the dragon fly larvæ,

carefully studied by H. KOCH¹. These gills are made up of a system of thin leaves in the rectum, in which the water is renewed by pumping movements. In each leaf there is a richly branched network of tracheæ, exchanging gases with the water by diffusion. The oxygen must diffuse from these gills through very wide tracheal tubes, running the whole length of the body. The larger forms of dragon fly larvæ (*Aeschna* and *Libellula*, about 5 cm long) can only live in well aerated water and come very close to the size limit for this type of respiration apparatus.

Zusammenfassung

Es wird in diesem Artikel versucht, die Evolution der Atemmechanismen in verschiedenen Entwicklungsrichtungen darzustellen und die Korrelation, welche zwischen Tiergröße und Leistung besteht, aufzuweisen.

Die einfachsten Atemeinrichtungen lassen nur geringe Körpergröße und niedrigen Stoffwechsel zu.

Kiemen, wie sie bei Wasserorganismen ausgebildet sind, können eine hohe Wirksamkeit entwickeln und erlauben eine gesteigerte Körpergröße.

Der Übergang zum Luftleben, wie er in der Geschichte der Vertebraten wirklich vor sich gegangen ist, brachte eine ganz erhebliche Herabsetzung der respiratorischen Wirksamkeit des Kreislaufs mit sich, die erst bei den warmblütigen Säugetieren und Vögeln vollständig überwunden werden konnte.

Die Vogellungen, die einen Luftstrom vor- und rückwärts durch die Luftkapillaren treiben, sind sogar wirksamer als diejenigen der Säugetiere.

Die Atempigmente im Blute vieler Tierformen zeigen interessante Anpassungen an den Sauerstoff- und Kohlensäuredruck, dem die Tiere ausgesetzt sind.

Tracheenatmung, die hauptsächlich durch Diffusion von Sauerstoff durch ein System starrer Röhren hervorgebracht wird, setzt der möglichen Größe der Tracheaten eine feste Grenze, aber sie läßt innerhalb dieser Grenze eine große Mannigfaltigkeit zu.

¹ H. Koch, Mem. Acad. roy. Belg. Cl. Sci. 16, 1 (1936).

Die Sinneswelt der Fledermäuse

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Unter den nächtlich lebenden Tieren zeichnen sich die Fledermäuse durch ihre Eigenart aus und bieten dem Zoologen eine Fülle interessanter Probleme. Eine Reihe von Forschern hat sich mit ihnen beschäftigt; die Ergebnisse sind mehrfach zusammengefaßt worden^{2,3,4}. Aus diesen Darstellungen ergibt sich, daß über die Sinnesfähigkeiten der Fledermäuse im Gegensatz zu anderen Fragen verhältnismäßig wenig bekannt ist. In den letzten Jahren ist nun auf diesem Gebiet

ein wichtiger Fortschritt erzielt worden, indem ein altes Problem aus dem nächtlichen Leben der Fledermäuse seiner Lösung zugeführt werden konnte. Wir wollen uns im folgenden zunächst mit dieser Frage und ihren älteren und neueren Lösungsversuchen beschäftigen. Im Anschluß daran soll die Bedeutung der einzelnen Sinne im Leben der Fledermäuse kurz erörtert werden.

Das Spallanzanische Fledermausproblem

Die Sicherheit, mit der Fledermäuse im Dunkeln umherzufliegen wissen, ohne irgendwo anzustoßen, hat schon früh die Aufmerksamkeit erregt. Durch die

¹ Zoologisches Institut der Universität Groningen.

² C. KOCH, Jb. Ver. Naturk. Nassau 17/18, 261-593 (1862/63).

³ M. EISENTRAUT, Die deutschen Fledermäuse. Leipzig 1937.

⁴ G. M. ALLEN, Bats. Cambridge 1939.