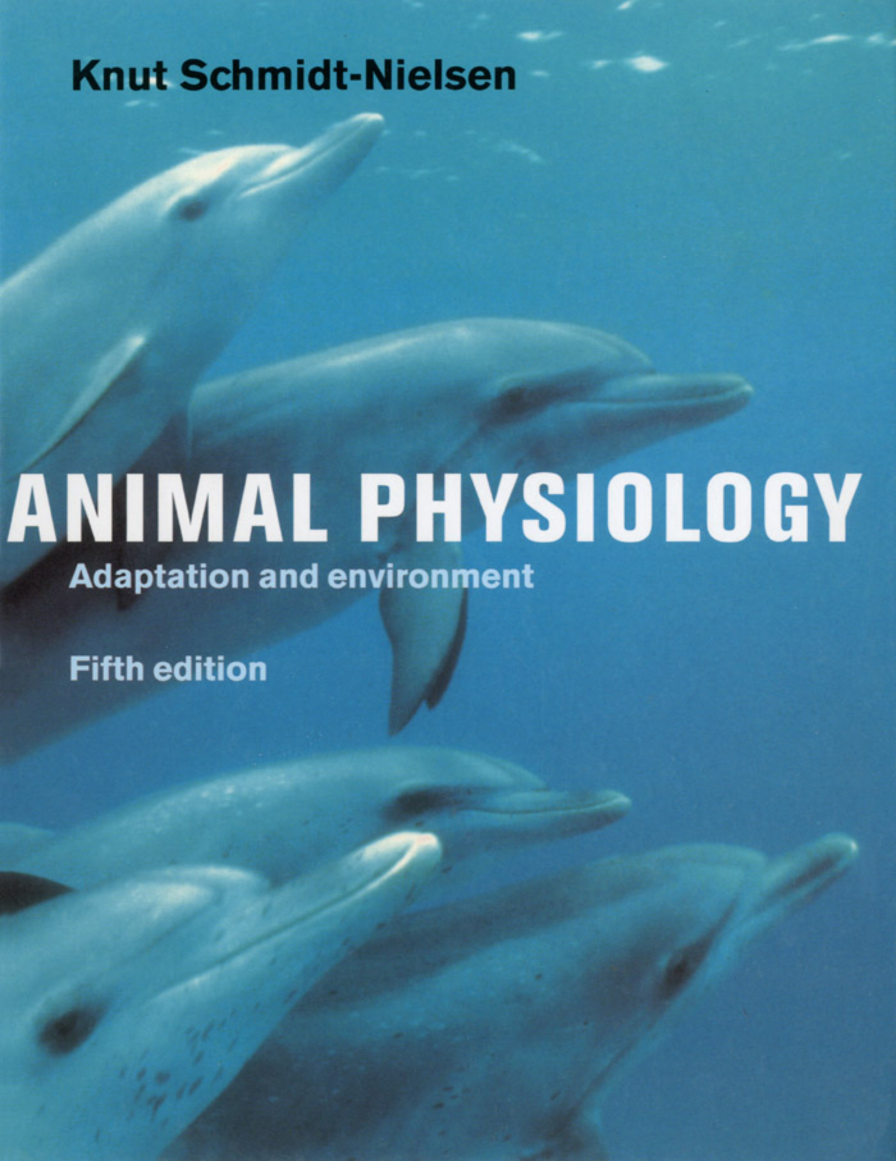
Knut Schmidt-Nielsen

ANIMAL PHYSIOLOGY

Adaptation and environment

Fifth edition



PHYSIOLOGY

Adaptation and environment

Fifth Edition

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ABOUT THIS BOOK

This book is about animals and how they function in their world. First of all it is about problems and their solutions. It is also about aspects of physiology that I myself happen to find particularly interesting. The book is aimed at students who want to know how things work, who want to know what animals do and how they do it.

The book deals with the familiar subjects of physiology: respiration, circulation, digestion, and so on. These subjects are arranged according to major environmental features: oxygen, food and energy, temperature, and water. This arrangement is important, for there is no way to be a good physiologist, or a good biologist for that matter, without understanding how living organisms function in their environment.

The book is elementary and the needed background is minimal. I have assumed that the student is familiar with a few simple concepts, no more than provided by a good high school text. I have, however, included in the text sufficient background information to make physiological principles understandable in terms of simple physics and chemistry.

The quantity and complexity of scientific information today are steadily increasing, and students are already overburdened with material to memorize. However, the mere recital of more facts does not signify understanding; we need a framework of principles on which to hang the facts. This book should help the student discover that many problems can be understood, once a few fundamental principles are familiar.

I also feel that clear concepts are more important than the learning of technical terms. However, because concepts cannot be conveyed without words, terminology is necessary. But terms are of no use unless they are clearly and accurately defined.

Much of this book explores how animals can live in environments that seem to place insurmountable obstacles in their way. The book discusses possible solutions. Animals with anatomical and physiological specializations often contribute much to our understanding of general principles. However, unless we look for these general principles, comparative physiology is apt to become a description of functions peculiar to uncommon animals – uncommon not because they are rare, but because they are outside our daily experience with other humans and with well known pets and laboratory animals such as dogs, cats, rats, and frogs. What we want is to place information into general concepts that help us understand how all animals function.

The text contains references to the scientific literature. These are arranged at the end of each chapter to help interested students satisfy their curiosity without having to search for information that is often hard to come by. The vast amount of scientific information made it necessary to be highly selective, and opinions about the proper selection will differ.

To bring more advanced information within the reach of the reader, I have arranged a list of Additional Readings for each chapter, placed after the list of text references. To spare the student from a feeling of helplessness, I have made these lists short. The titles vary from brief and simple essays to large, comprehensive treatises. Except for a few classical works, these lists contain reasonably recent and up-to-date material.

Like most authors I hope that friendly and perhaps less friendly readers will let me know about errors and what I could have done better.

PREFACE TO THE FIFTH EDITION

When I was revising an earlier edition of this book, a friend warned me against increasing its size. He reminded me of the dinosaur syndrome – when they got too big, they died out. I have therefore tried to make this book better without appreciably increasing its size.

I have revised existing material and have added new information I thought essential, but the general outline of the book is unchanged. I have added new figures where recent information is helpful and I have deleted some old figures. Dozens of new references have been added, both as text references and for additional reading, and many old references have been deleted. The new references are selected with emphasis on recent developments, judiciously chosen from the burgeoning scientific literature. However, out of necessity, much important new information cannot be included. For those who teach physiology I should mention that I have increased the use of SI Units, but as in previous editions, always in parallel with the maintenance of traditional units.

Although the main outline of the book is unchanged, one chapter, Chapter 10, Movement, Muscle, Biomechanics, has been extensively revised and modified with the aid of my colleague, Hugh C. Crenshaw, who has made substantial changes and additions in this chapter. For this I am most grateful.

As before, I would appreciate hearing from any user of the book who may have comments or suggestions that would help increase its usefulness.

WHAT IS PHYSIOLOGY?

Physiology is about the functions of living organisms – how they eat, breathe, and move about, and what they do just to keep alive. To use more technical words, physiology is about food and feeding, digestion, respiration, transport of gases in the blood, circulation and function of the heart, excretion and kidney function, muscle and movements, and so on. The dead animal has the structures that carry out these functions; in the living animal the structures work.

Physiology is also about how the living organism adjusts to the adversities of the environment – obtains enough water to live or avoids too much water, escapes freezing to death or dying from excessive heat, moves about to find suitable surroundings, food, and mates – and how it obtains information about the environment through its senses. Finally, physiology is about the regulation of all these functions – how they are correlated and integrated into a smooth-functioning organism.

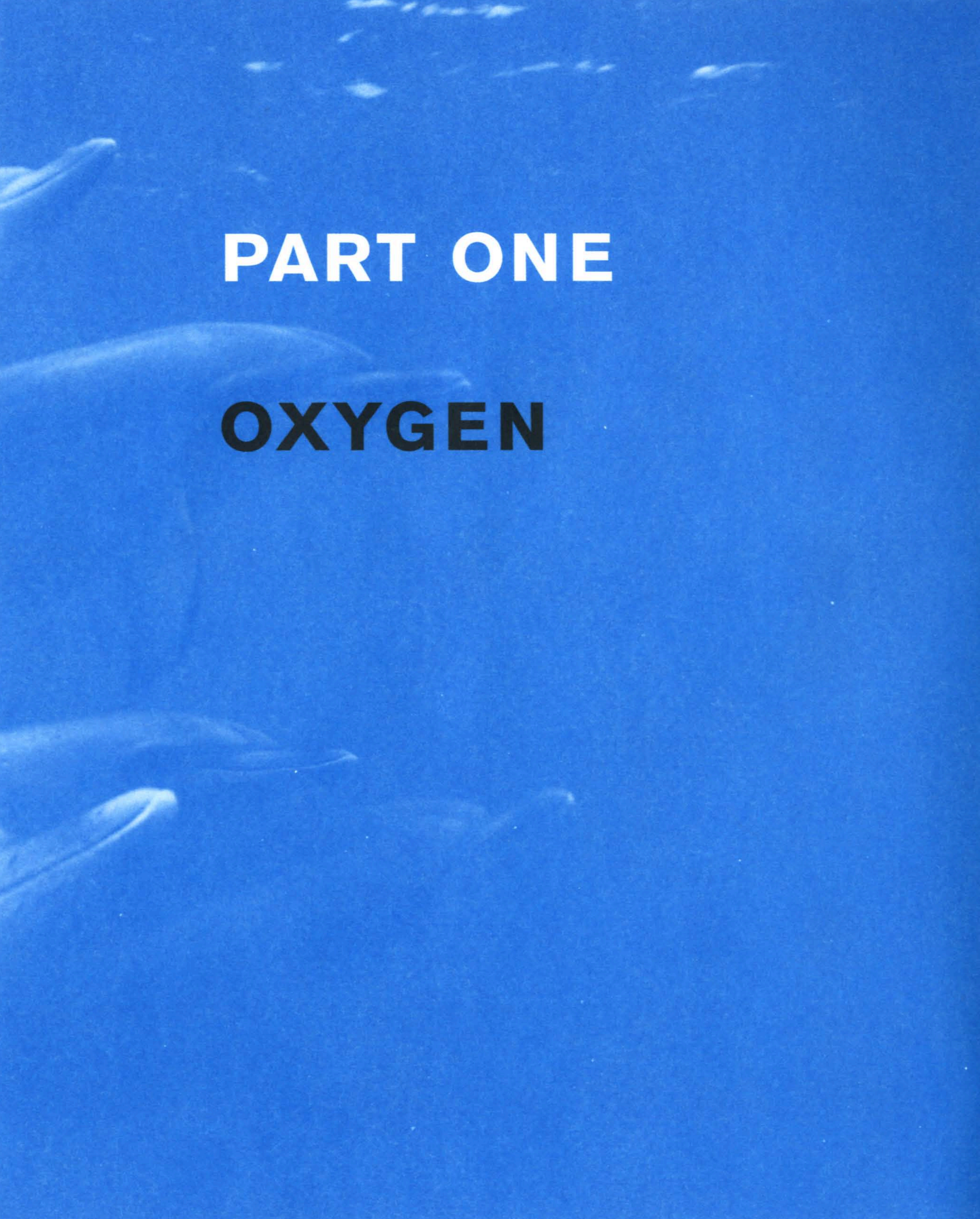
Physiology is not only a description of function; it also asks why and how. To understand how an animal functions, it is necessary to be familiar both with its structure and with some elementary physics and chemistry. For example, we cannot understand respiration unless we know about oxygen. Since ancient times breathing movements have been known as a sign of life or death, but the true meaning of respiration could not be understood until chemists had discovered oxygen.

The understanding of how living organisms function is helped enormously by using a comparative approach. By comparing different animals and examining how each has solved its problem of living within the constraints of the available environment, we gain insight into general principles that otherwise might remain obscure. No animal exists, or can exist, independently of an environment, and the animal that utilizes the resources of the environment must also be able to cope with the difficulties it presents. Thus, a comparative and environmental approach provides deeper insight into physiology.

Examining how an animal copes with its environment often tends to show what is good for the animal. This may bring us uncomfortably close to explanations that suggest evidence of purpose, or teleology, and many biologists consider this scientifically improper. However, we all do tend to ask, Why? What good is it for the animal? Anyway, the animal has to survive, and there is nothing improper or unscientific in finding out how and why it succeeds. If it did not arrive at solutions to the problem of survival, it would no longer be around to be studied. And the study of the living organism is what physiology is all about.

PART ONE

OXYGEN



1 RESPIRATION

Why is oxygen important? It is because most animals satisfy their energy requirement by oxidation of food materials, in the process forming carbon dioxide and water.

The process of oxygen uptake and release of carbon dioxide is called *respiration*. Aquatic animals take up oxygen from the small amount of this gas dissolved in the water, terrestrial animals from the abundant oxygen in the air.

Many small animals can take up sufficient oxygen through the general body surface, but most animals need special respiratory organs for oxygen uptake. Carbon dioxide follows the opposite path, being released from the general body surface or from the respiratory organs. The water formed in the oxidation processes merely enters the general pool of water in the body and presents no special problems.

The most important, and sometimes the only physical process in the movement of oxygen from the external medium to the cells is *diffusion*, a process in which a substance moves from a higher to a lower concentration. The movement of carbon dioxide in the opposite direction also follows the concentration gradients.

Diffusion may be aided by *bulk movement*, such as the movement of air in and out of the lungs, but concentration gradients remain as the fundamental driving force for moving the respiratory gases. To understand respiration it is therefore necessary to know about the respiratory gases, their solubility, and the physics of diffusion processes.

Life presumably originated in the sea, and most animals (except insects) are marine. Large-scale evolutionary adaptation to air breathing has occurred only among arthropods and vertebrates. Some snails are well adapted to terrestrial life, and a small number of other invertebrates live in various terrestrial micro-habitats.

Easy access to oxygen in the atmosphere permits a high rate of metabolism and a high degree of organizational development. The greatest drawback to breathing in air is the evaporation of water.

THE ATMOSPHERE

Composition of dry atmospheric air

The physiologically most important gases are oxygen, carbon dioxide, and nitrogen. They are present in atmospheric air in the proportions shown in Table 1.1. In addition, the atmosphere contains water vapor in highly variable amounts.

Component	%
Oxygen	20.95
Carbon dioxide	0.03
Nitrogen	78.09
Argon	0.93
Total	100.00

Table 1.1 Composition of dry atmospheric air. All atmospheric air contains water vapor in highly variable amounts. The less common noble gases (helium, neon, krypton, and xenon) together make up only 0.002% of the total. There are also minute amounts of methane and a variety of pollutant gases.

What physiologists usually call nitrogen is actually a mixture of nitrogen with about 1% of the noble gases, and for accuracy these should be listed as well. However, in physiology it is customary to lump these gases with nitrogen, the main reason being that in most physiological processes, nitrogen and the noble gases are equally inert to the organism. Another reason is that the analysis of respiratory gases is usually carried out by determining oxygen and carbon dioxide values and calling the remainder "nitrogen". To the physiologist the amount of "nitrogen" in air is, therefore, 78.09 + 0.93%, or 79.02%.

The nearly 1% argon is of physiological interest only in some quite special circumstances: for example, in connection with the secretion of gases into the swimbladder of a fish. The complete analysis of all the gases in an air sample can be carried out with the aid of a mass spectrometer, an expensive and rather elaborate instrument that most physiologists have no access to.

The composition of the atmosphere remains extremely constant. Convection currents cause extensive mixing to a height of at least 100 km, and no discernible changes in the percentage composition have been demonstrated, although the pressure of the air is greatly reduced at high altitudes. The statement that the lighter gases, notably hydrogen and helium, are enriched in the outer reaches of the atmosphere applies to the very outermost layers, which are of no physiological interest whatsoever. For our purposes, the open atmosphere has a constant gas composition, except for its water vapor.

The composition of the air is maintained as a balance between the use of oxygen in oxidation processes (primarily oxidation of organic compounds to carbon dioxide) and the assimilation of carbon dioxide by plants, which in the process release oxygen.

The fear that our use of fossil fuels – oil, coal, and natural gas – may deplete the atmosphere of oxygen is probably unfounded. In 1910 an extremely accurate oxygen analysis showed the value of 20.948%, and during 1967 to 1970 repeated measurements gave a value of 20.946% ± 0.006. The investigators who made these analyses then calculated that if all known recoverable fossil fuel reserves were depleted, there would still be 20.8% oxygen left in the atmosphere (Machia and Hughes 1970). Physiologically this change would be of no consequence; it would be no more than the change in oxygen partial pressure we are exposed to when taking an elevator from the ground floor to the fifteenth floor of a tall building.

The greenhouse effect

The slight increase in carbon dioxide caused by the combustion of all the fuel would likewise have negligible physiological effects, but this is not to say it would be harmless. Even a slight change in carbon dioxide alters the absorption of solar radiation in the atmosphere and may have an unpredictable *greenhouse effect* that over the years may drastically change climatic conditions on the earth's surface.

The atmosphere is more transparent to incoming short-wave radiation than to the long-wave radiation emitted by the earth. The outgoing long-wave radia-

Temperature (°C)	Water vapor mm Hg	kPa	% of 1 atm	mg H_2O per liter air
0	4.6	0.61	0.6	4.8
10	9.2	1.23	1.2	9.4
20	17.5	2.34	2.3	17.3
30	31.7	4.24	4.2	30.3
40	55.1	7.38	7.3	51.1
50	92.3	12.33	12.2	83.2
100	760.0	101.33	100.0	598.0
37	46.9	6.28	6.2	43.9

Table 1.2 Water vapor over a free water surface at various temperatures.

tion is absorbed in the atmosphere mainly by carbon dioxide and water vapor. It is estimated that a doubling of the atmospheric carbon dioxide content would increase world temperature by 1.3 °C if atmospheric water remained constant.

This would cause extensive melting of the polar ice covers and a rise in the ocean level of 20 to 30 m or more, enough to submerge enormous areas of coastal lands and many of the world's major cities. In addition, at higher temperature the atmosphere can hold more water vapor, which enhances the blanketing effect and causes further temperature rise. However, increased water vapor in the atmosphere may augment formation of clouds, which in turn reflect more of the incoming solar radiation, thus having the opposite effect. The complexity of these relationships makes predictions about the greenhouse effect of increased carbon dioxide highly uncertain (Bolin et al. 1986; Dickinson and Cicerone 1986; Ramanathan 1988).

Having stressed the constancy of the atmospheric composition, we must add a few words about special cases. For example, microenvironments, such as burrows occupied by animals, have more variable air composition, with the oxygen as low as 15% or even less. The carbon dioxide content is increased, but not necessarily to the same extent. However, carbon dioxide may rise to above 5%, an amount that has considerable physiological effects (Kuhnen 1986).

The air contained in soil – in open spaces between the soil particles – is often low in oxygen. The reason is that the soil may contain oxidizable material that can severely deplete the oxygen. Not only organic matter, but also substances such as iron sulfide, can consume oxygen until practically all free oxygen has been removed. These oxidation processes depend on temperature, humidity, and other factors, as well as on the amount of exchange with the atmosphere. Rain, for example, may block the surface porosity of the soil and at the same time provide humidity for increased oxidation, and the microatmosphere may then change drastically.

Water vapor in air

The preceding information about the percentage composition of the atmosphere referred to dry air, and we must now turn to the water content of air. The pressure of water vapor over a free water surface changes with temperature (Table 1.2). At the freezing point the vapor pressure is 4.6 mm Hg (0.61 kPa).* It increases with increasing temperature, and reaches 760 mm Hg

---

* The unit millimeters of mercury (mm Hg) is traditionally used in physiology. It is derived from the use of mercury manometers, and 1 mm Hg at 0 °C is also known as 1 torr. In the International System of Units (the SI System) the pressure unit is the pascal (Pa), defined as 1 newton per square meter (N m^{-2}). Thus, 1 mm Hg = 133.3 Pa or 0.133 kPa; 1 atm or 760 mm Hg = 101.3 kPa. For further information on the SI system see Appendix A.

(101.33 kPa) at 100 °C. For this reason water boils at 100 °C if the atmospheric pressure is 760 mm Hg. If the atmospheric pressure is lower, water boils at a lower temperature; for example, if the pressure is reduced to 17.5 mm Hg (2.34 kPa) water boils at 20 °C.

Any mixture of gases, such as atmospheric air, that is in equilibrium with free water is said to be saturated with water vapor. It contains water vapor at a pressure corresponding to the temperature, and the fraction of the air sample that is made up of water vapor therefore increases with the temperature (column 4 of Table 1.2). At 37 °C, the usual body temperature of mammals, the water vapor pressure is about 47 mm Hg (6.28 kPa), and water vapor then makes up 6.2% of the air volume (see also Figure 8.10, page 324).

The lung air of humans and other air-breathing vertebrates is always saturated with water vapor at body temperature, but the outside atmospheric air usually is not. When air is saturated with water vapor, we say that the *relative humidity* (r.h.) is 100%. If the air contains less water vapor, the humidity can be expressed as a percent of the amount required for saturation at that temperature; for example, 50% relative humidity means that the air contains half the water it would contain if saturated with water vapor at that temperature.

For some purposes relative humidity is a convenient expression, but when we want to know the total *amount* of water vapor in the air, this can be expressed as milligrams of water per liter of air. Because cold air has a very low water vapor content, even at 100% r.h., the absolute amount of water in cold air is small. Therefore, if saturated outside air in winter enters our houses and is heated, the indoor relative humidity will be extremely low (although the absolute humidity of the air is unchanged), and we say that "the air is very dry". This dryness causes moist surfaces and mucous membranes to dry out, often to great discomfort of sensitive persons.

Altitude and atmospheric pressure

Climbing in high mountains or ascent to high altitude in nonpressurized aircraft has serious physiological effects. At an altitude of 3000 m humans begin to feel the effects of altitude as a reduction in physical performance, and at 6000 m (about 20 000 ft) most humans can just barely survive. This is because of lack of oxygen, although the air still contains the usual 20.95% oxygen.

At sea level, where atmospheric pressure is 760 mm Hg and 20.95% of this is oxygen, the *partial pressure* of oxygen in dry air is 159 mm Hg (21.2 kPa).* At 6000 m the atmospheric pressure is half that at sea level, or about 380 mm Hg (50.7 kPa). The partial pressure of oxygen is also half that at sea level, or about 80 mm Hg or 10.6 kPa (20.95% of 380 mm Hg or 50.7 kPa). It is this decrease in partial pressure of oxygen that produces such severe effects.

The relation between altitude and atmospheric pressure is shown in Figure 1.1. The lower scale of the abscissa shows the partial pressure of oxygen in inhaled air. The zero of this scale does not coincide with zero atmospheric pressure, but instead falls where atmospheric pressure is slightly less than 50 mm Hg (6.67 kPa). The reason is simple. At the body temperature of humans (37 °C) the water vapor pressure is 47 mm Hg (6.28 kPa). Therefore, if a person were placed at an atmospheric pressure of 47 mm Hg (19 000 m or 63 000 ft altitude), his lungs would be filled with water vapor and no air or oxygen could enter his lungs.

We shall later, at the end of Chapter 5, return to some of the effects of low oxygen partial pressure on animals at high altitude.

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* In a mixture of gases, the total pressure is the sum of the pressure each gas would exert if it were present alone. In dry atmospheric air at standard barometric pressure (760 mm Hg), the partial pressure of oxygen (P_{O_2}) is 159.2 mm Hg (20.95% of 760 mm Hg), of nitrogen (P_{N_2}) 600.6 mm Hg (79.02% of 760 mm Hg), and of carbon dioxide (P_{CO_2}) 0.2 mm Hg (0.03% of 760 mm Hg).

Atmospheric air is never completely dry, and its water vapor exerts a partial pressure (P_{H_2O}) corresponding to the water vapor content in the air. The partial pressure of the other gases is then reduced in exact proportion. If the air at 760 mm Hg contains 5% water vapor ($P_{H_2O} = 38$ mm Hg), the total pressure of the remaining gases is 722 mm Hg, and their individual partial pressures are in the proportion of their relative concentrations to make up the total of 722 mm Hg.

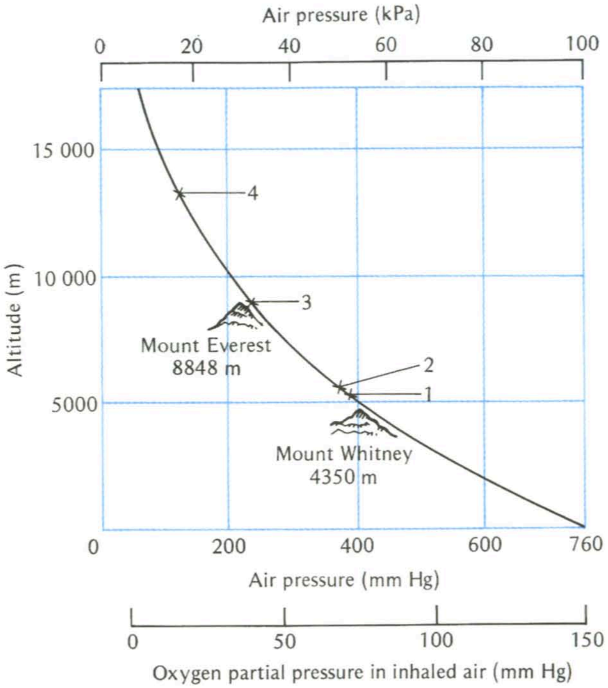

Figure 1.1 The relationship between altitude and atmospheric pressure. 1. Altitude where most unacclimatized persons will lose consciousness because of oxygen lack. 2. Highest permanent human habitation. 3. Highest altitude where acclimatized humans can survive for a few hours when breathing air. 4. Highest altitude possible for humans breathing pure oxygen. [Dejours 1966]

SOLUBILITY OF GASES

Gases are soluble in water. If a sample of pure water is brought into contact with a gas, some gas molecules enter the water and go into solution. This continues until an equilibrium has been established and an equal number of gas molecules enters and escapes from the water per unit time. The amount of gas that is then dissolved in the water depends on (1) the nature of the gas, for the solubility is not the same for all gases; (2) the pressure of the gas in the gas phase; (3) the temperature; and (4) the presence of other solutes. For an understanding of physiology it is necessary to be familiar with the fundamentals of these relationships.

Oxygen	34.1 ml O_2 per liter water
Nitrogen	16.9 ml N_2 per liter water
Carbon dioxide	1019.0 ml CO_2 per liter water

Table 1.3 Solubilities of gases in water at 15 °C when the gas is at 1 atm pressure.

The solubilities of different gases in water are very different; those of the physiologically most important gases are listed in Table 1.3. The *solubility coefficient*, α, is defined as the volume of gas dissolved in 1 liter of water, when the pressure of the gas itself, without the water vapor, is 1 atm. The amount of gas is expressed as the volume this gas would occupy if the dry gas were at 0 °C and 1 atm pressure; this is designated *standard temperature and pressure dry* (STPD).

We immediately see that nitrogen is only about half as soluble as oxygen, but carbon dioxide is roughly 30 times as soluble as oxygen or 60 times as soluble as nitrogen. This high solubility of carbon dioxide in water makes possible soda water or champagne. In an unopened bottle of soda water, which usually is at between 2 and 3 atm pressure, the small amount of gas at the top of the neck is under the pressure, and the remainder of the carbon dioxide is dissolved in the liquid. As we know, this must be a substantial amount, for large numbers of bubbles continue to rise to the surface for a long time. If nitrogen were dissolved at 3 atm pressure, only a few bubbles would be formed, for the amount of dissolved nitrogen would be only about 1/60 of the carbon dioxide.

Effects of pressure and temperature

The amount of gas dissolved in a given volume of water depends on the pressure of the gas. If the gas pressure is doubled, twice as much gas will be dissolved. The proportionality between gas pressure and the amount dissolved is known as *Henry's law* and can be expressed as follows:

$$V_g = \alpha \frac{P_g}{760} \cdot V_{H_2O}$$

α is the solubility coefficient (see Table 1.3), and the equation tells us the number of milliliters of the gas (V_g, at STPD) that is dissolved in the water at the pressure (P_g) given in millimeters of mercury.

The solubility of a mixture of gases depends on the partial pressure of each gas present in the gas phase. Any one of the gases is dissolved according to its own partial pressure in the gas phase, independently of the presence of other gases.

The solubility of gases decreases with increasing temperature. Most of us know this from our own experience. When we open a bottle of warm soda water or beer (Heaven forbid!), the drink has a much greater tendency to foam and overflow than if it is cold. Also, if we watch a pot of water being heated on a stove, small bubbles begin to form on its walls long before boiling begins; these bubbles consist of gas driven out of solution as temperature rises. The solubility of gases in water is thus exactly the reverse of the solubility of solids, which for the most part are more soluble in hot water than in cold (sugar, for example).

We can now examine the solubility of a gas in greater detail. As an example, the solubility of oxygen is given in Table 1.4. First, we must note that this table refers to the amount of oxygen dissolved in water in equilibrium with atmospheric air (not with 1 atm pure oxygen as in Table 1.3). We can see that the solubility of oxygen decreases to about half as the temperature is raised from the freezing point to 30 °C. This decreased solubility is quite important for many aquatic animals.

Table 1.4 also gives the solubility of atmospheric oxygen in sea water, which on the whole is some 20% lower than in fresh water. This is because salts reduce the solubility of gases. This reduction is a characteristic effect of dissolved solids, but does not apply to dissolved gases; gases do not affect the solubility of other gases under conditions with which we deal in physiology.

Temperature (°C)	Fresh water (ml O_2 liter^{-1} water)	Sea water (ml O_2 liter^{-1} water)
0	10.29	7.97
10	8.02	6.35
15	7.22	5.79
20	6.57	5.31
30	5.57	4.46

Table 1.4 The temperature effect on the amount of oxygen dissolved in fresh water and in sea water in equilibrium with atmospheric air. [Krogh 1941]

Partial pressure and tension

We have discussed the solubility of gases in terms of the amount of a gas that enters into solution when the gas has a certain pressure. Let us look at it the other way. Take a sample of water that has a certain gas dissolved in it; the amount of gas in the water sample must correspond to one specific gas pressure in the gas phase. This pressure is called the *tension* of this gas in the water sample.* If a water sample has several gases dissolved in it, the tension of each gas corresponds to the partial pressure of that particular gas in the atmosphere with which the water is equilibrated. The tension of a gas in solution is thus defined as the partial pressure of that gas in an atmosphere in equilibrium with the solution.

When the gas pressure over a water sample is reduced, gases tend to leave the solution. If we reduce the gas pressure to about half the original value, gas leaves the solution until equilibrium is reached when the amount of dissolved gas has reached half its original value.

If the gas pressure is reduced to zero, which is the same as exposing the water sample to a vacuum, all the gas leaves or is extracted from the water. Such vacuum extraction is one way of removing all dissolved gas from a liquid; in fact, it is a commonly used method in the analysis of the gas content of blood samples.

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* Physiologists often refer to the *tension* of a gas in a liquid, rather than its partial pressure, and define tension of a gas in solution as the pressure of this gas in an atmosphere with which that particular liquid sample is in equilibrium. The major reason for using the word *tension* is that a dissolved gas as such exerts no measurable pressure, and the term *partial pressure* is therefore conceptually somewhat misleading. However, we frequently find the two terms used interchangeably.

Because the gas dissolved in a liquid is in equilibrium with a given partial pressure in the gas phase, we can say that the gas in the liquid is under that particular partial pressure. If we have a container of water that has been equilibrated with atmospheric air, and we introduce a tiny bubble of, for example, pure nitrogen into the water, oxygen (as well as carbon dioxide) will diffuse from the water into the bubble, equilibrium being reached when the bubble contains 20.95% oxygen. Some nitrogen will initially dissolve into the water, for the initial nitrogen pressure in the bubble is 1 atm and the tension in the water only 0.79 atm. However, as oxygen enters, the loss of nitrogen subsides, and the final concentrations within the bubble are those of the initial equilibration atmosphere. (This argument depends on the bubble's volume being so small, relative to the volume of water, that it does not materially influence the gas concentration in the water.)

Solubility of carbon dioxide

The solubility of carbon dioxide in water is some 30 times as high as that of oxygen (see Table 1.3). However, because the amount of carbon dioxide in the atmosphere is very small (0.03%), the total quantity dissolved in water is very small. The amount can be calculated from the solubility coefficient and the fractional concentration of carbon dioxide in the atmosphere as follows:

$$\text{volume dissolved } CO_2 = \frac{1019 \times 0.03}{100}$$
$$= 0.3 \text{ ml } CO_2 \text{ per liter water}$$

The solubility of carbon dioxide in water is complicated by the reaction of water with carbon dioxide to form carbonic acid:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons 2H^+ + CO_3^{2-}$$

This reaction is sometimes called the carbonate, or bicarbonate, reaction and is of great importance in many physiological processes. The result is that carbon dioxide, when dissolved in water, does not persist strictly as molecular carbon dioxide, rather some portion of the carbon dioxide reacts with water to become bicarbonate or carbonate, with a release of one or two protons.

In addition to bicarbonate and carbonate formed by this reaction, natural waters contain variable amounts of carbonate and bicarbonate due to both biological and geological processes. The total amount of carbon dioxide present in water in nature therefore can be quite high and varies with the cations present. Hard water, for example, contains large amounts of dissolved calcium bicarbonate, $Ca(HCO_3)_2$, which adds to the total amount of carbon dioxide.

In sea water, which is slightly alkaline (pH = ca 8.2), the total amount of carbon dioxide may range between 34 and 56 ml CO_2 per liter sea water (Nicol 1960), yet the amount of carbon dioxide present as dissolved gas is still that which is in equilibrium with the atmosphere, about 0.3 ml CO_2 per liter; the remainder is primarily in the form of bicarbonate ion. Thus, in spite of the carbon dioxide *content* of sea water (and many other natural waters), oceanic sea water still has a carbon dioxide tension close to that in the atmosphere, 0.23 mm Hg (0.031 kPa).

In an isolated body of water the concentrations of oxygen and carbon dioxide can change appreciably. The two major processes are (1) that oxygen is formed in photosynthesis by plants and (2) that plants as well as animals use oxygen and produce carbon dioxide. In the day-time photosynthesis will usually dominate so that the oxygen content increases substantially in the water, which becomes supersaturated. At night, on the other hand, both animals and plants use oxygen and produce carbon dioxide, almost totally depleting all available oxygen.

These two opposing biological processes can lead to extreme conditions. Measurements made in an isolated rock tidal pool are recorded in Figure 1.2. When the pool was isolated from the sea during the day, the P_{O_2} increased from the normal level of sea water to as much as 555 mm Hg by midafternoon. The carbon dioxide used for photosynthesis was taken from the sea water, but as the amount dissolved is small, most of the CO_2

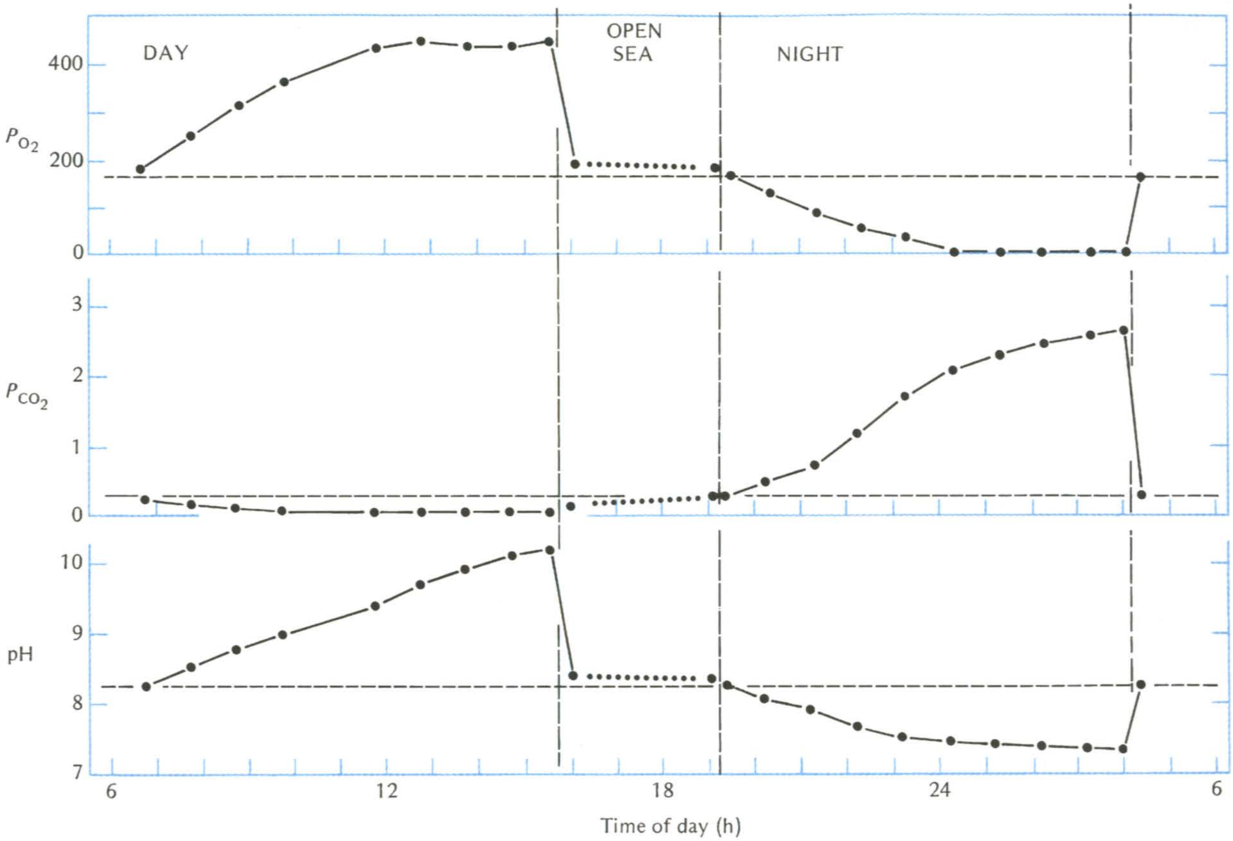

Figure 1.2 The water in a tidal rock pool undergoes great variations in gas tensions when it is isolated from the sea at low tide. These records were made in a rock pool on the coast of Brittany (France). Gas tensions, Po_2 and Pco_2, are in millimeters of mercury. The normal value for each variable in sea water is indicated by a broken line. [Dejours 1981]

was removed from the bicarbonate in the sea water. This resulted in a tremendous shift in the pH of the sea water, which became highly alkaline, reaching a pH of 10.1, while the P_{CO_2}, decreased to 10^{-4} mm Hg.

When, at high tide in the late afternoon, the rock pool was connected to the open sea, the values immediately approached those in normal sea water. At night, when the pool again was isolated, the respiring organisms, both animals and plants, rapidly removed oxygen, which fell to values as low as 1.6 mm Hg. The pH then fell to 7.3, a whole pH unit below that in normal sea water, and the P_{CO_2} increased to 2.7 mm Hg. The reason that the P_{CO_2} increased by only a few millimeters of mercury is that most of the CO_2 again entered into the bicarbonate.

Similar variations in the gas tensions have been reported for fresh water. The magnitude of the changes depends on local conditions, on the composition of the water, and on the amounts of plants and animals in the water. The general rule is that the oxygen tension tends to increase in the day-time, in particular in strong sunlight, and may fall substantially and approach zero at night.

Gas diffusion

In the respiratory organs of animals (e.g., gills, lungs) gases diffuse between the environment and the organism; oxygen enters and carbon dioxide leaves the animal. It is therefore of interest to know how fast the gases diffuse, their *rate of diffusion* (see Appendix B). This subject needs special attention, for many biologists have been led to believe that carbon dioxide diffuses much faster than oxygen. This is not so.

The rate of diffusion of a gas is inversely proportional to the square root of its molecular weight; carbon dioxide is heavier than oxygen and therefore diffuses more slowly. The molecular weight of carbon dioxide is 44 and that of oxygen 32; the square roots of these numbers are 6.6 and 5.7. Because the diffusion rates are inversely proportional to the square roots, the diffusion rates of carbon dioxide and oxygen are in the proportion of 5.7/6.6, or 0.86. In other words, carbon dioxide diffuses at a rate which is 0.86 that of oxygen.

When carbon dioxide diffuses between air and water, its high solubility in water makes carbon dioxide appear to diffuse faster. The situation can be explained by reference to Figure 1.3. Let us assume we have a gas mixture that contains oxygen at 100 mm Hg and carbon dioxide at 100 mm Hg pressure (i.e., the partial pressures, or concentrations, of the two gases are equal). Each gas dissolves in the surface water independently of the other, in proportion to its concentration in the gas phase and the solubility coefficient. The amount of the two gases dissolved at the surface is therefore 4.5 ml O_2 per liter and 134 ml CO_2 per liter (at 15 °C). In other words, at the surface the concentration of carbon dioxide in solution is 30 times as high as that of oxygen (29.8 times, to be exact), although in the gas phase their concentrations are equal.

Carbon dioxide and oxygen now diffuse from the surface into the body of water. The amount of carbon dioxide dissolved at the surface is much higher, and more carbon dioxide therefore diffuses into the water. The carbon dioxide molecules as such diffuse at a rate 0.86 times that of the oxygen molecules, and the amount of carbon dioxide diffusing, relative to oxygen, is $29.8 \times 0.86 = 25.6$.

We now understand that, when carbon dioxide and oxygen diffuse from equal concentrations in air into water, the total amount of carbon dioxide diffusing is about 25 times higher. Likewise, if the carbon dioxide and oxygen tensions in the water are equal (in our case, 100 mm Hg at the surface of the water), diffusion into the atmosphere is also higher for carbon dioxide. It is important to note that this apparently faster diffusion of carbon dioxide is applicable only when diffusion takes place in water or between gas and water, and we refer to *the tension or partial pressure of the gases rather than to their molar concentrations.* This fast diffusion is attributable to the higher solubility of carbon dioxide; as a molecular species carbon dioxide still diffuses according to the laws of physics (i.e., somewhat slower than oxygen).*

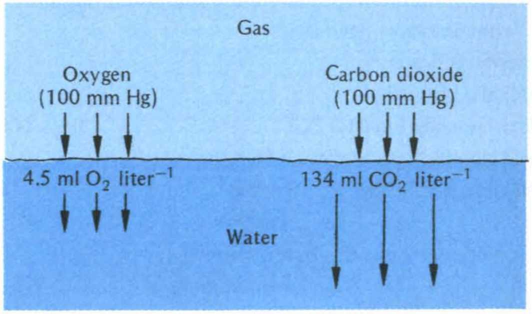

Figure 1.3 Diffusion between air and water of oxygen and carbon dioxide. The amount of carbon dioxide dissolved at the surface of water (at 15 °C) is 29.8 times as high as the amount of oxygen when the two gases are at the same partial pressure in the gas phase. Carbon dioxide molecules diffuse more slowly (at a rate 0.86 times the rate for oxygen), but because of their higher concentration in the surface layer, the amount of carbon dioxide diffusing from the same pressure in the gas phase into the water is 25.6 times the amount of oxygen ($29.8 \times 0.86 = 25.6$).

COMPARING WATER AND AIR

The differences between water and air are extremely important for animals and their supply of oxygen. We can illustrate these differences by comparing some of

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* In a gas the molar concentrations are directly proportional to the pressures and no confusion can arise as to the rate of diffusion.

	Water	Air	Ratio: water/air
O_2 concentration (liter/liter)	0.007	0.209	~1:30
Density, p (kg/liter)	1.000	0.0013	~800:1
Dynamic viscosity, (cP)	1	0.02	50:1
Heat capacity (cal/liter °C)	1000	0.31	~3000:1
Heat conductivity (cal/s cm °C)	0.0014	0.000 057	~25:1
Diffusion coefficient, D_{O_2} (cm^2/s)	0.000 025	0.198	~1:8000
D_{CO_2} (cm^2/s)	0.000 018	0.155	~1:9000
Diffusion constant, K_{O_2} (cm^2/atm min)	34×10^{-6}	11	~1:300 000
K_{CO_2} (cm^2/atm min)	850×10^{-6}	9.4	~1:11 000
Liters of medium per liter O_2	143	4.8	~30:1
Kilograms of medium per liter O_2	143	0.0062	~23 000:1

Table 1.5 Comparison of air and water as respiratory medium.

the physical properties of water and air, as listed in Table 1.5.

For example, let us compare how much oxygen is available in water and in air. Water in equilibrium with atmospheric air at 15 °C contains 7 ml O_2 per liter (1000 ml). This 7 ml O_2 weighs 0.01 g, and this amount is found in a weight of water 100 000 times as great. To obtain a given amount of oxygen, we must therefore move 100 000 times its weight* of water over the respiratory organs.

In contrast, 1 liter of air contains 209 ml O_2, which weighs 280 mg. The remainder of the air, 791 ml N_2, weighs 910 mg. To obtain the oxygen, we must move only 3.5 times its mass of inert gas. This difference is illustrated in Figure 1.4.

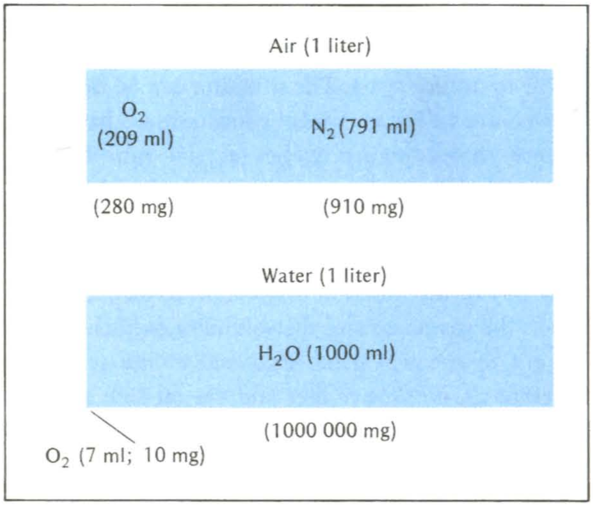

Figure 1.4 Air has a high oxygen content (21%) and contains inert gas (nitrogen) in an amount weighing only 3.5 times as much as the weight of the oxygen. Water, in contrast, contains only 0.7% of its volume as dissolved oxygen (at 15 °C, P_{O_2} 159 mm Hg). In this case the weight of inert medium is 100 000 times as great as the weight of oxygen.

This tremendous difference in the *mass* of the inert medium has one important consequence: In aquatic respiratory systems the movement of water is almost always unidirectional. If the flow of water were in and out or back and forth, a large mass of water would have to be accelerated, then stopped, and again accelerated in the opposite direction. A high expenditure of energy would be required for the continuous changes in kinetic energy of the water. For respiratory organs that use air, such as the lung, an in-and-out flow is not very expensive, for the inert mass will be only a few times more than the mass of oxygen used. However, air-breathing animals may use a unidirectional flow of air, as we shall see later in this chapter when we discuss bird and insect respiration.

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* More correctly, mass. Because in daily speech we say that we weigh an object when we determine its mass, it is very common to say weight when we should say mass. See footnote on page 29.

In addition to the mass of the respiratory medium, another factor contributes to the amount of work required to move it. Water has a higher viscosity than air, and this increases the work required to pump the fluid, for the driving pressure must be increased in proportion to the higher viscosity. Because the energy required for moving the fluid increases in direct proportion to the pressure, it also increases in direct proportion to the viscosity.

The *viscosity* of water at 20 °C is 1 cP (centipoise), and the viscosity of air is 0.02 cP (i.e., water is about 50 times as viscous as air). The work required for pumping increases accordingly.

Another advantage of air respiration is the high rate of *diffusion* of oxygen in air, which, at the same partial pressure or tension, is some 10 000 times as rapid as in water (see Appendix B). This fast diffusion in air permits very different dimensions in the respiratory organs. The distances over which a gas can diffuse, for example in a lung, may be several millimeters, but the diffusion distance in the fish gill is a minute fraction of a millimeter.

To prevent undue *evaporation* from the respiratory surfaces, these should not be freely accessible to the outside air. The gas-exchange surfaces are usually located in specialized respiratory cavities (lungs), and this greatly limits the access of air. The renewal of air in the cavity is often very carefully regulated, being no greater than dictated by the requirement for oxygen.

Gas exchange across the general body surface is usually possible only in a moist habitat. Earthworms, for example, in which the entire respiratory gas exchange takes place through the body surface, are very susceptible to water loss. They live in moist habitats, and if they remain exposed on the surface of the earth they rapidly dry out and die.

With regard to water and the need for gas exchange, plants are really in a much worse situation than animals. Plants need carbon dioxide for photosynthesis, and they must obtain this gas from the air, which, as we have seen, contains only 0.03% CO_2 (0.23 mm Hg or 0.031 kPa). The diffusion gradient for carbon dioxide into the plant is therefore extremely small. Even if the plant can maintain a zero concentration of carbon dioxide inside its tissues, the driving force for carbon dioxide diffusion is no more than 0.23 mm Hg. The water vapor pressure of plant tissues varies with temperature; at 25 °C it is 24 mm Hg (3.2 kPa). The driving force for diffusion of water from the plant to dry air is, therefore, 24 mm Hg. In moist air it is less; at 50% relative humidity, for example, it is half as much. In any event, the magnitude of the vapor pressure that drives the outward diffusion of water is some one hundred times as high as the inward driving pressure for carbon dioxide diffusion. As a consequence of this unfavorable situation, plants have a very high requirement for water.

The situation for plants is compared with that for animals in Figure 1.5. In animals the inward driving force for oxygen is the 21% O_2 in the air, or 159 mm Hg (21.2 kPa). At 25 °C the outward driving force for loss of water to dry air is 24 mm Hg (3.2 kPa), or only a small fraction of the inward driving pressure for oxygen. Even at high temperatures, say 37 °C, the water vapor pressure is small compared with the pressure for inward movement of oxygen. There is thus a great contrast between the unfavorable water balance plants must cope with and the favorably high oxygen concentration air breathing animals enjoy (at least, hopefully so).

One way for plants to reduce the water loss associated with photosynthesis and uptake of CO_2 is used by many drought-tolerant plants, one of special interest being the pineapple. During the night when the air humidity is high, these plants open their stomata and CO_2 can diffuse in with a lower loss of water than would occur in the daytime. Of course, the CO_2 cannot be photosynthesized in the dark, but it is stored in the plant, bound in the form of malic acid. In the daytime the stomata are kept closed, thus reducing water loss, and the now available sunlight is used for photosynthesis of the stored CO_2.

This process is known as CAM respiration. The name is derived from the term crassulacean acid metabolism, but the phenomenon is not restricted to the plant family Crassulaceae. Many other plants show CO_2 uptake at night with accumulation of malic acid, followed by depletion of the malic acid and photosynthesis during the day (Kluge and Ting 1978).

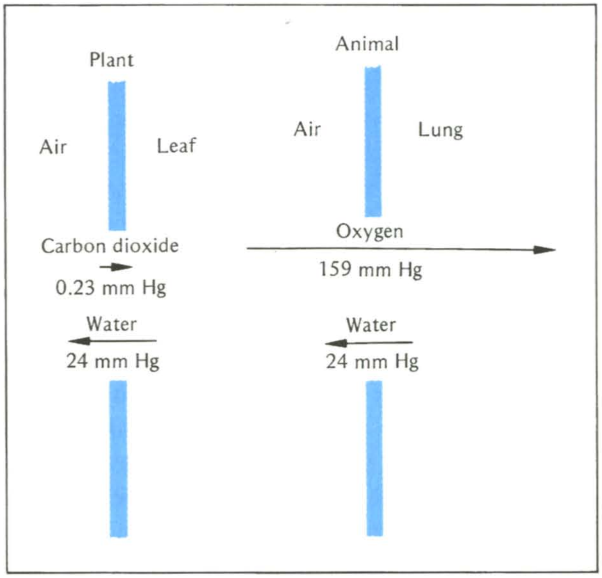


Figure 1.5 For plants it is difficult to obtain by diffusion the necessary carbon dioxide from the atmosphere without incurring a relatively tremendous water loss. For animals to obtain oxygen, the water loss presents less of a problem because of the high partial pressure of oxygen in air (ca. 700 times as high as the carbon dioxide pressure).

With the knowledge we now have of the physical properties of gases in both air and water, we can move on to the question of how animals manage to live and function within these bounds.

RESPIRATION IN WATER

Some of the simplest arrangements for respiratory gas exchange are found in aquatic animals. Many small organisms obtain oxygen by diffusion through their body surfaces, without having any special respiratory organs and without circulating blood. Larger and more complex animals often have specialized surfaces for gas exchange and also a blood system to transport oxygen more rapidly than diffusion alone can provide.

Animals without specialized respiratory organs

The simplest geometrical shape of an organism is a sphere. For our considerations it is important that a sphere has the smallest possible surface corresponding to a given volume; any deviation from the spherical shape gives a relative enlargement of the surface area. If we assume that a spherical organism is to be supplied with oxygen by diffusion through the surface and into every part of the body, the longest diffusion distance is from that surface to the center.

For oxygen to reach the center, the oxygen concentration at the surface must be of a certain magnitude, for as oxygen diffuses inward it is consumed by the metabolism of the organism. The necessary oxygen tension at the surface, sufficient to supply the entire organism with oxygen by diffusion, can be calculated from an equation developed by E. Newton Harvey (1928), who was well known for his studies of luminescent organisms in the sea:

$$F_{O_2} = \frac{\dot{V}_{O_2} r^2}{6\,K}$$

In this equation F_{O_2} is the concentration of oxygen at the surface expressed in fractions of an atmosphere, $\dot{V}_{O_2}$ is the rate of oxygen consumption as cm^3 of oxygen per cm^3 tissue per minute, r is the radius of the sphere in centimeters, and K is the diffusion constant in square centimeters per atmosphere per minute. K signifies the cubic centimeters of oxygen that will diffuse per minute through an area of 1 cm^2 when the gradient is 1 atm cm^{-1}. For a further discussion of diffusion, see Appendix B.

Taking as a hypothetical example a spherical organism with a radius of 1 cm, an oxygen consumption rate of 0.001 ml O_2 g^{-1} min^{-1}, and a diffusion constant of 11×10^{-6} cm^2 atm^{-1} min^{-1} (the same as for connective tissue and many other animal tissues), we find that the required oxygen concentration at the surface, necessary to supply the entire organism to the center by diffusion, is 15 atm. This shows clearly that the organism cannot be supplied by diffusion alone if it has the postulated metabolic rate, which, incidentally, is rather low even for an invertebrate.

The conclusion is that the organism, to be supplied with oxygen, must either be much smaller or have a much lower metabolic rate. Let us consider a smaller organism, choosing a radius of 1 mm. We then find that the required oxygen concentration at the surface is 0.15 atm. Because well-aerated water is in equilibrium with the atmosphere, which contains 0.21 atm oxygen, such an organism could obtain enough oxygen by diffusion only, and would be quite feasible.

If we consider real animals we find that these calculations have given quite reasonable orders of magnitude. Organisms that are supplied with oxygen by diffusion only (e.g., protozoans, flatworms) are mostly quite small, less than 1 mm or so, or have very low metabolic rates, as jellyfish do. Although a jellyfish can be very large, it may contain less than 1% organic matter; the rest is water and salts. It has a very low average rate of oxygen consumption, and the actively metabolizing cells are located along the surfaces, where the diffusion distances are relatively short.

An organism that deviates from the spherical shape has a larger relative surface and shorter diffusion distance than a sphere. This holds for a variety of relatively simple organisms. They are flattened or threadlike, have pseudopodia, or have very large and complex surfaces (such as corals and sponges) and can thus obtain enough oxygen by diffusion, although some may be much larger than the sizes used in the preceding calculations.

Animals with respiratory organs

Although a small organism can get enough oxygen by diffusion through the surface, this is usually not true for larger organisms. Of course, any shape deviating from the sphere has a larger surface, and the diffusion distances are also reduced. However, in most cases this does not suffice, and we find specialized respiratory organs with greatly enlarged surfaces. Often these organs also have a thinner cuticle than other parts of the body, thus facilitating gas exchange.

If the respiratory surface is turned out, forming an evagination, the resulting organ is usually called a *gill*. Secondarily, the gill may be enclosed in a cavity, such as in a fish, but this does not change the fact that gills fundamentally are evaginations.

If the general body surface is turned in, or invaginated, the resulting hollow is called a *lung*. Our own lungs are a good example, although secondarily they are finely subdivided and have a quite complex structure. Simpler lungs exist; a pulmonate land snail, for example, has a lung that is little more than a simple saclike invagination in which gas exchange takes place. The term *lung* is used whether the respiratory medium is water or air.

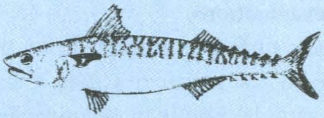
Insects have a special form of respiratory system. Small openings on an insect's body surface connect to a system of tubes (*tracheae*) that branch and lead to all parts of the body. In this case the respiratory organ combines a distribution system (the tubes) with the gas-exchange system, for most of the gas passes through the walls of the finest branches of this system and diffuses directly to the cells.

In general, gills mostly serve for aquatic breathing and lungs for breathing in air. There are exceptions: Sea cucumbers have water lungs in which most of the gas exchange seems to take place. Gills may also be modified for use in air, but on the whole they are rather unsuited for atmospheric respiration. For example, most fish when taken out of water rapidly become asphyxiated, although there is far more oxygen in air than in water. The reason is that in water the weight of the gills is well supported, but in air the gills cannot support their own weight.

This is because an effective respiratory organ requires (1) a large surface and (2) a thin cuticle. Both these demands make it difficult to provide the mechanical rigidity for support of a gill in air. Furthermore, in air the surfaces of the fish gill tend to stick together because of surface adhesion. Therefore, the surface area exposed to air is reduced to a minute fraction of what is exposed to water, severely impeding oxygen uptake.

Ventilation of gills

If a gill removes oxygen from completely still water, the immediately adjacent boundary layer of water will soon be depleted of oxygen. Renewal of this water is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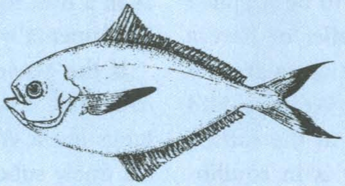
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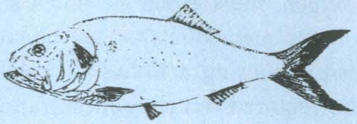
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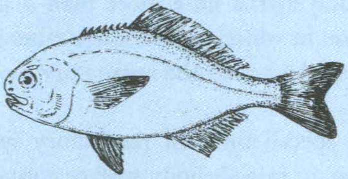
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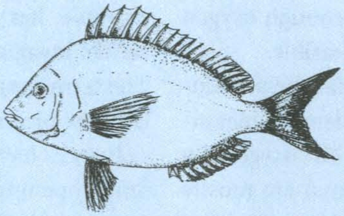
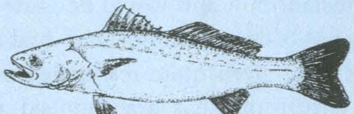

Scup – 1323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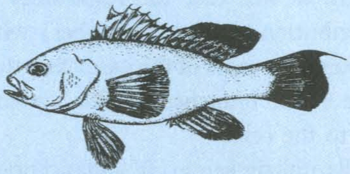
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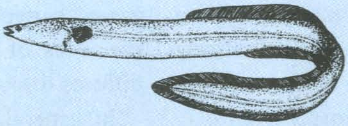
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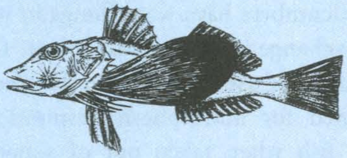
Remora – 892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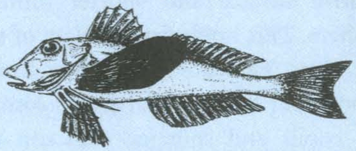
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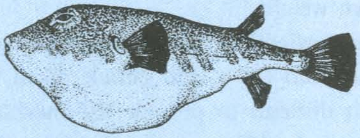
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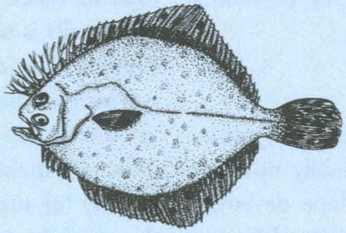
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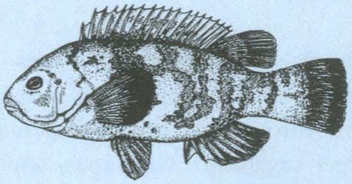
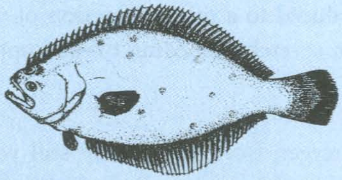
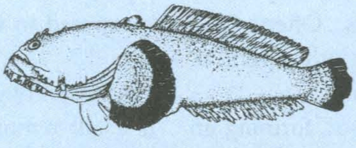
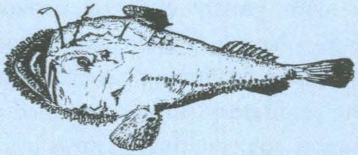

Tautog – 442


Summer flounder – 268


Toadfish – 137


Goosefish – 51

therefore important in supplying oxygen, and various mechanical devices serve to increase the flow of water over the gill surface. Increased flow can be achieved in two ways: by moving the gill through the water or by moving water over the gill.

Moving the gill through the water is practical only for small organisms. Some aquatic insect larvae – mayfly larvae (Ephemeridae), for example – ventilate their gills in this way. The difficulty is that, if a gill is moved through the water with its base serving as a pivot point, the force needed to overcome the resistance to the movement is too great. This resistance increases with the square of the linear velocity of the organ, and therefore the energy needed to move the gill increases in the same proportion. The mechanical strength of the gill would also need to be increased, again with the square of the linear velocity, as would the force applied to the base of the gill to make it move through the water. The large aquatic salamander known as the mudpuppy (*Necturus*) does move its gills, but the movements are very slow.

Moving water over the respiratory surface is a much more feasible solution. The movement may be achieved by ciliary action, as in the gills of mussels and clams. Sponges move water through their ostia by the action of flagella.

Moving the water with a mechanical pumplike device is more common. Fish and crabs, for example, move water over their gills in this way. As a matter of principle, it is less expensive to move water slowly over a large surface than to move water fast over a smaller surface.

For some animals their own locomotion contributes to the movement of water. This is true of many pelagic fish; the large, fast-swimming tunas have practically immobile gill covers and obtain the required high water flow over the gills by swimming rapidly through the water. They probably cannot survive if kept from swimming forward, and when these fish are maintained in captivity it is common to keep them in large circular tanks so that they can keep moving without meeting obstacles.

Figure 1.6 Highly active, fast-swimming fish have larger gill areas than sluggish, bottom-living fish. The number after each name indicates the total surface area of the gills expressed in arbitrary units per gram body weight of the fish. [I. E. Gray, based on Gray 1954]

Also in squid and octopus there is a close correlation between locomotion and water flow over the gills. A squid or octopus ventilates its gills by taking water into the mantle cavity, and by ejecting the water through the siphon, it propels itself through the water by *jet propulsion*. In this case the ventilatory system has been modified for locomotion, but as is true of fish, as increased swimming increases the call for oxygen, oxygen is automatically provided in greater amounts.

Other functions of gills

Gills may have functions other than respiratory gas exchange, and sometimes it is difficult to decide what is the primary or only function of a gill. Some so-called anal gills of mosquito larvae function in osmotic regulation: They absorb ions from the surrounding water, and it is doubtful that they play any major role in respiration. The gills of both fish and crabs serve in osmotic regulation, but in these it is quite clear that the gills also serve a primary function in respiration.

To evaluate the role in gas exchange of a gill or other suspected respiratory organ, we must have information about the amount of oxygen taken up, and preferably also about the carbon dioxide given off, through this organ. By comparing this with the oxygen consumption of the entire organism, we can see whether the organ is responsible for virtually all oxygen uptake, a large part, a small part, or just a trivial amount.

If an organism has definite and well-developed respiratory organs, there is usually a need for a circulatory system as well to carry oxygen to the various parts of the body. (This does not hold for the tracheal system of insects, which in principle is independent of a circulatory system.)

The gills of mussels and clams were mentioned above as establishing water currents by ciliary action. In the filter-feeding bivalves the gills are arranged so that they act as a sieve, retaining particles suspended in the water,

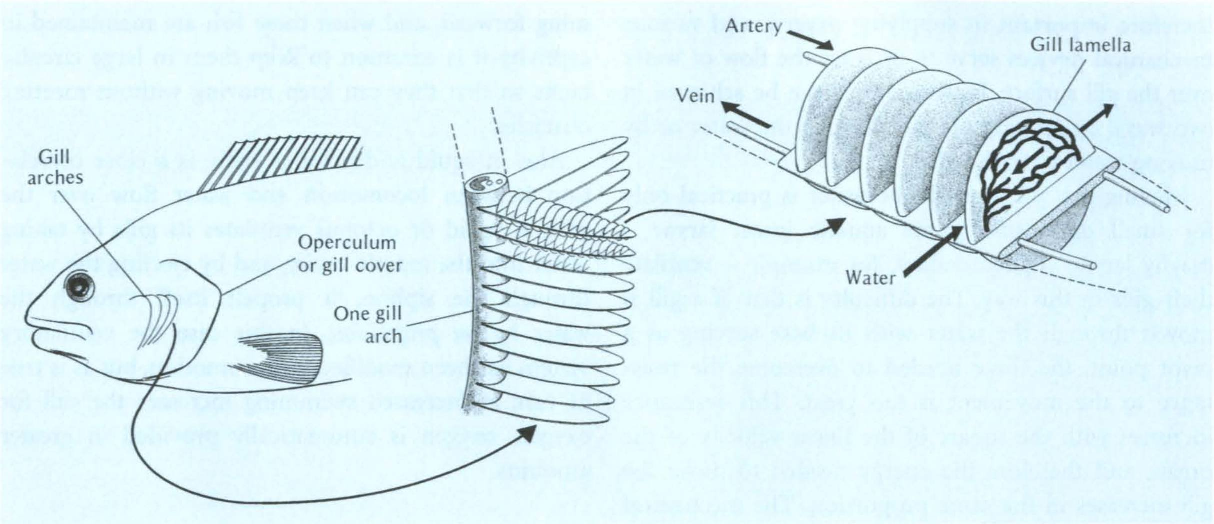


Figure 1.7 The gills of a fish consist of several gill arches on each side. Each arch carries two rows of gill filaments. Each filament carries thin parallel, platelike lamellae. In these lamellae the blood flows, in a direction opposite to that of the water which flows between the lamellae. [Randall 1968]

which afterward are carried to the mouth and ingested. The gills therefore have a primary function in food uptake; whether they also are of importance in gas exchange is less certain. Bivalves on the whole have quite low metabolic rates, and it is possible that the surface of the mantle is sufficient to provide the required gas exchange.

Gas exchange and water flow

The fact that gill surface area must be large enough to provide adequate gas exchange is well expressed in fish. Highly active fish have the largest relative gill areas (Figure 1.6). The fast-swimming mackerel's gill surface area, expressed per unit body weight, is some 50 times as high as the sluggish, bottom-living goosefish's.

For the gas exchange to be adequate, a high rate of water flow and a close contact between the water and the gill are necessary. This is achieved by the anatomical structure of the gill apparatus. The gills are enclosed in a gill cavity, which provides protection for these rather fragile organs and, equally important, permits water to be perfused over the gills in a most effective way. A special advantage is gained by an arrangement that makes the stream of water flowing over the gill and the stream of blood running within the gill flow in opposite directions to each other. This we call a *countercurrent* flow. To understand the importance of this arrangement, it is necessary to know the structure of the gill (Figure 1.7).

Countercurrent flow

Fish gills consist of several major *gill arches* on each side. From each gill arch extend two rows of *gill filaments.* The tips of these filaments from adjoining arches meet, forcing water to flow between the filaments. Each filament carries densely packed, flat *lamellae* in rows. Gas exchange takes place in these lamellae as water flows between them in one direction and blood within them in the opposite direction.

This countercurrent type of flow has an important consequence. Just as the blood is about to leave the gill lamella, it encounters water whose oxygen has not yet been removed. Thus, this blood takes up oxygen from water which still has the full oxygen content of inhaled water, and this permits the oxygen content of the blood to reach the highest possible level. As the water runs further between the lamellae, it meets blood with a lower and lower oxygen content, and it therefore continues to give up more oxygen. Thus, the lamella, along its entire length, serves in taking up oxygen from the water, and the water may leave the gill having lost as much as 80 or 90% of its initial oxygen content (Hazelhoff and Evenhuis 1952). This is considered a very high oxygen extraction. In contrast, mammals remove only about one-quarter of the oxygen present in the lung air before it is exhaled.

We can express the effect of the countercurrent type of gas exchange in a diagram (Figure 1.8). This figure shows how blood, as it flows through the gill lamellae, takes up more and more oxygen and approaches the oxygen tension of the incoming water. The outflowing water has had most of its oxygen removed and has a tension far lower than that of the blood leaving the gill. If the flows of water and blood were in the same direction, this would be impossible, for the blood could at best reach the oxygen tension of the outflowing water. Because the pumping of water over the gills requires energy, the countercurrent flow through the increased oxygen extraction also reduces the energetic cost of pumping.

It was previously believed that sharks have no countercurrent flow in their gills, although they are excellent swimmers and might be expected to have superbly functioning respiratory organs. However, sharks do indeed have countercurrent flow in their gills (Grigg 1970).

Countercurrent flow is found also in the gills of some crabs, but in these the efficiency of oxygen removal from the water often is far less than in fish. In part this may be because the water flow is less effective, but probably it is mainly because the gill–blood diffusion barrier is greater. The latter explanation seems to be the case in the European shore crab (*Carcinus*), in which the oxygen extraction, in spite of countercurrent flow, may range between no more than 7 and 23% (Hughes et al. 1969). In other crabs, for example the Dungeness crab (*Cancer magister*), the oxygen extraction from the respired water often exceeds 50% (McDonald et al. 1980).

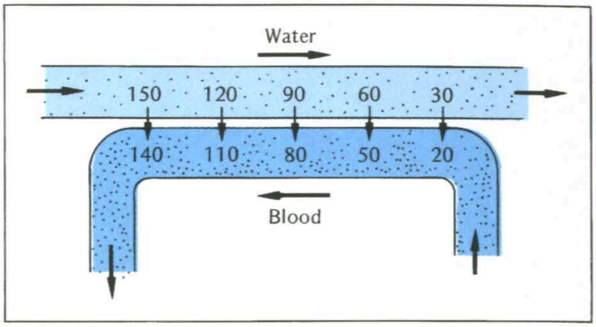
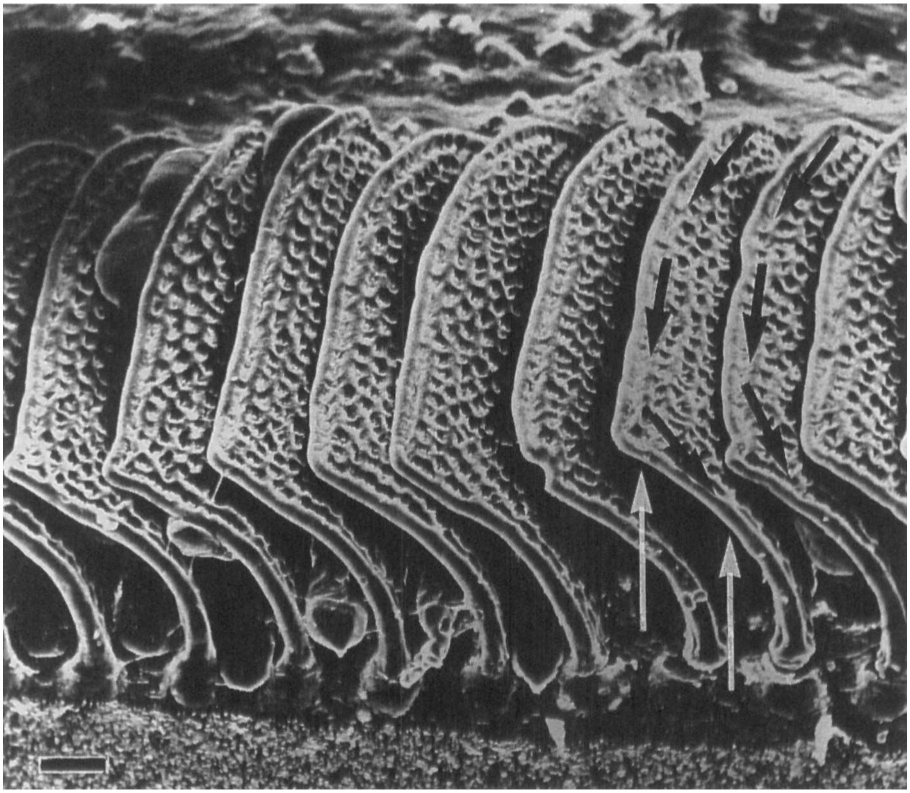


Figure 1.8 Diagram of the countercurrent flow in fish gills. The numbers indicate partial pressures of oxygen (P_{O_2}) in water and blood. The blood enters the gill at a low P_{O_2} (in this example 20 mm Hg), and oxygen diffuses from the water into the blood. As the blood runs along the lamella, it takes up more and more oxygen from the water, and as it leaves the lamella, it has nearly reached the P_{O_2} of the incoming oxygen-rich water. The water, flowing in the opposite direction, gradually loses more and more of its oxygen and leaves the gill after having lost most of its oxygen content.

Gill resistance. Because the lamellae in the fish gill are very close, it has been suggested that there is a high resistance and virtually no flow of water between them. There can be as many as 30 or 40 lamellae per millimeter with a space between them of less than 0.02 mm. The pressure that drives the water through the gills is often less than 10 mm H_2O, and such a low pressure appears insufficient to drive water through the narrow space.

A careful analysis of this problem was carried out by Hughes (1966), based on the width of the passageway between the lamellae, its height, and its length. Using a modified form of Poiseuille's equation (see Chapter 3), Hughes calculated that the flow through the gills of a 150-g tench (*Tinca*), for a pressure of 5 mm H_2O, would be 10.1 ml s^{-1}. The normal volume of water pumped through the gills of this fish is about 1 to 2 ml s^{-1}; the obvious conclusion is that the gill lamellae do not offer much resistance to flow, as they would allow a greater flow than actually occurs in the living fish. Similar calculations for more than a dozen other species of fish showed that in all cases the calculated ventilation volumes could easily be greater than those measured in the living fish.



FISH GILL Scanning electron micrograph of gill filaments of a sturgeon (*Acipenser transmontanus*). White arrows show the direction of water flow and black arrows the direction of blood flow. The bar in the lower left corner represents 0.05 mm. [Burggren et al. 1979; courtesy of Warren W. Burggren, University of Massachusetts]

It is interesting that the highest water flows are found in some Antarctic fish, the icefish, which are very unusual because they have no hemoglobin in their blood. We shall return later to these peculiar fish and how they can live without the normal oxygen-carrying mechanism of the blood.

Water pumping

To move water over the gills, teleost fish use a combined pumping action of the mouth and the opercular covers, aided by suitable valves to control the flow. A model of this pump is shown in Figure 1.9. The system actually consists of a double set of pumps. The volume of the first, the oral cavity, can be enlarged by lowering the jaw and especially the floor of the mouth. The volume of the second, the opercular cavity, can be increased by movements of the opercular covers while backflow of water around the edges is prevented by a skin flap acting as a passive valve. The diagram shows only one opercular pump; in reality there are two opercular chambers, one on each side.

The action of the two pumps is such that a flow of water through the gills is maintained throughout nearly the entire respiratory cycle. This flow continues although the pressure in the mouth during part of the cycle may be less than that in the surrounding water; the reason is simply that the pressure in the opercular cavities is maintained even lower than in the mouth.

This is evident from pressure recordings made in the mouth and the opercular cavities during the respiratory cycle (Figure 1.10). The graph shows that the pressure changes are synchronized with the movements of the mouth and the opercula. Furthermore, the difference between the pressures in the mouth and in the opercular cavities (as shown by the curve at the bottom of the graph) remains positive almost throughout the

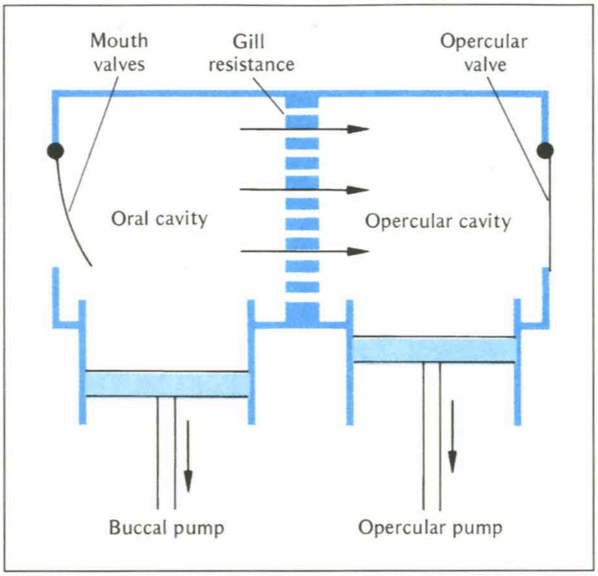


Figure 1.9 Water is pumped over the gills of a fish by a dual pumping system. With the aid of suitable valves, the pumps provide a unidirectional flow of water over the gill surface. [Hughes 1960]

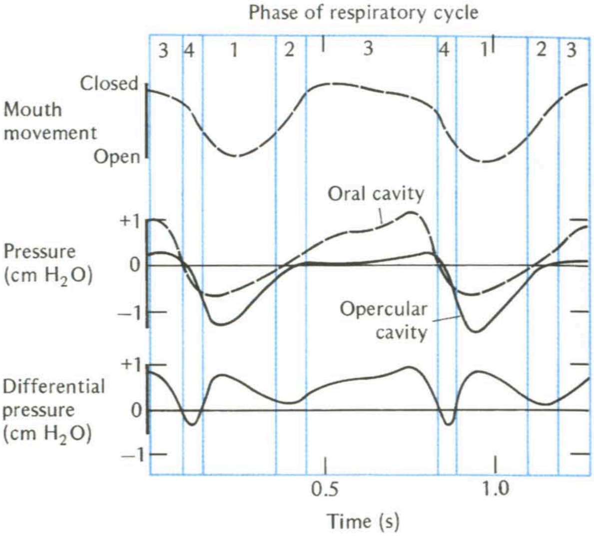


Figure 1.10 Record of pressure changes in the respiratory pump of a carplike fish, the roach (*Rutilus*). The lower curve shows the difference between the pressures in the oral and the opercular cavities. A pressure of 1 cm H_2O ≈ 0.1 kPa. [Hughes and Shelton 1958]

cycle and provides the pressure that drives water through the gills. Only during a brief moment is there a slight pressure reversal. The details of the pressure curves differ from fish to fish, but all those studied so far are, in principle, the same: During almost the entire respiratory cycle the pressure in the oral cavity remains higher than in the opercular cavities, providing for a nearly continuous flow of water over the gills.

Ram ventilation

Some fish are unable to breathe this way. Fish biologists have long known that the large tunas cannot be kept alive in captivity unless they can swim continuously; this can be arranged by keeping them in large ring-shaped tanks where they can cruise without stopping. The fish swims with its mouth partly open, there are no visible breathing movements, and water flows continuously over the gills; this is called *ram ventilation.*

Ram ventilation is not restricted to large, fast-swimming pelagic fish. Many fish breathe by pumping at low speed and change to ram ventilation at higher speeds. The transition takes place around speeds of 0.5 to 1 m s^{-1}, and above this speed active breathing movements cease (Figure 1.11).

The change to ram ventilation does not mean that the gills are ventilated for free; it means only that the work of breathing is transferred from the muscles of the opercular pumps to the swimming muscles of the body and tail. The open mouth causes increased drag, and this has to be paid for with increased muscular work. However, the continuous flow during ram ventilation is more economical in energy than opercular pumping at the high rates required for fast swimming.

The reduced cost in energy as a fish changes from opercular pumping to ram ventilation is shown in Figure 1.12. The rate of oxygen consumption, which expresses the energy cost of swimming, increases with increasing speed. This is expected because the drag on the fish increases with its speed, and the cost of respiratory pumping also increases as more water must

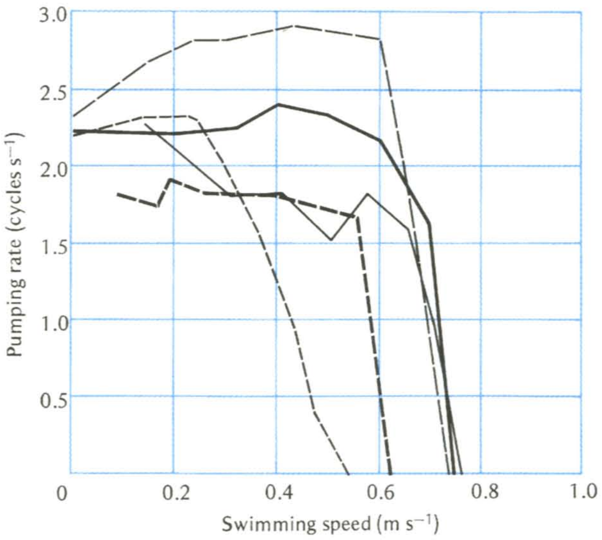


Figure 1.11 When the swimming speed of a mackerel increases to between 0.5 and 0.8 m s^{-1}, opercular pumping ceases and the fish breathes entirely by ram ventilation of the gills. The records in this graph were obtained from five individuals weighing about 70 g each. [Roberts 1975]

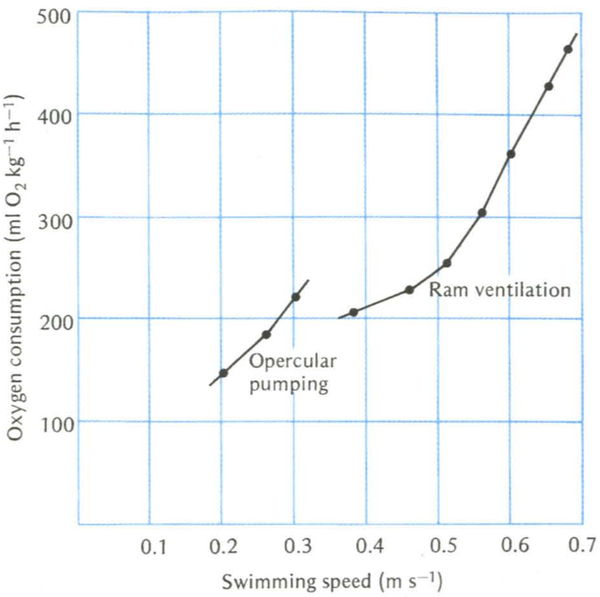


Figure 1.12 The rate of oxygen consumption of a swimming fish, indicating its total energy expenditure, increases with increasing swimming speed. However, when the fish changes from opercular pumping to ram ventilation, there is a drop in oxygen consumption in spite of the higher swimming speed. The record is from a striped bass (*Morone saxatilis*) of 25 cm length and 214 g body mass. [Data from Freadman 1981]

be pumped over the gills to supply the increased need for oxygen. The surprise comes when the fish changes to ram ventilation. In spite of the higher speed, the oxygen requirement now decreases. It then increases again as the speed of the fish increases further. We can surmise that, had opercular pumping been maintained at the higher swimming speeds, the cost of pumping would by far exceed what was measured when the fish used ram ventilation.

The degree of opening of the mouth during ram ventilation seems to be adjusted to give just the right flow of water over the gills, keeping the drag to the lowest possible level compatible with the ventilation requirement. This conclusion is based on experiments in which mackerel were kept swimming at constant speeds, but subjected to a progressive lowering of the oxygen content in the water. This resulted in a graded increase in mouth gape so that the lowered oxygen supply was compensated for by increased water flow (Steffensen 1985).

As water flows over the gills, solid particles suspended in the water tend to get caught in the gills. Such material can be dislodged by a sudden reversal of the flow, which is brought about by enlarging the oral cavity with closed lips, causing a sudden lowering of the pressure in the mouth. This maneuver is analogous to coughing, which removes material from the respiratory passageways of mammals.

Crabs keep their gills clean in a somewhat similar way. The flow of water over the gills is unidirectional practically all the time, but at intervals the pumping is stopped and there is a sudden reversal of the flow for a few seconds. The frequency of the abrupt reversal varies greatly. It may happen once a minute or once in 10 minutes, or even less frequently (Hughes et al. 1969). We assume that such abrupt reversals of water flow serve to remove particles that have become lodged in the gills.

The physiological basis for respiratory gas exchange as outlined here depends on some very simple physical principles. We have seen how these principles are used, and how animal function is adapted to the requirements of the physical environment. We shall now examine how equally simple physical principles apply to the physiology of respiratory gas exchange in animals that breathe air.

RESPIRATION IN AIR

Air-breathing animals have three major types of respiratory organs: gills, lungs, and tracheae.

Gills. On the whole, gills are rather poorly suited to respiration in air and are used by only a few animals – mostly some that relatively recently have invaded the terrestrial habitat, taking with them the remnants of their previous mode of aquatic respiration. Land crabs are good examples. The coconut crab (*Birgus latro*), which has adopted an almost completely terrestrial existence (including climbing coconut palms), has gills that are sufficiently rigid to remain useful for respiration in air.

Another land crab, *Cardiosoma*, is particularly interesting because it can survive indefinitely either in air *or* in water, whereas the coconut crab will drown if it is kept submerged (Cameron and Mecklenburg 1973). Another crustacean group with air-breathing gills is the terrestrial isopods (commonly known as sow bugs, pill bugs, or wood lice); these animals usually prefer to live in moist surroundings, and those that are most successful in the terrestrial habitat have their gills within cavities that can be regarded as functional lungs.

Among fish that can breathe air, functional gills have been maintained in some, but not in all. The common eel (*Anguilla vulgaris*) survives quite well in air if it is kept reasonably cool and moist. Much of the oxygen is then taken up through the skin and less through the gills, for the filaments tend to stick together and expose only a small surface to the air in the gill chamber. As a consequence, the eel does not obtain its normal oxygen requirement, and the oxygen uptake in air is reduced to only about one-half of that in water (Berg and Steen 1965).

Lungs. We can distinguish two types of lungs: *diffusion lungs* and *ventilation lungs.* In diffusion lungs the air exchange with the surrounding atmosphere takes place by diffusion only. Such lungs are found in relatively small animals such as pulmonate snails, scorpions, and some isopods.

Ventilation lungs are typical of vertebrates. Substantial and regular renewal of the air in the lung is necessary for a large body size combined with a high metabolic rate. Vertebrate respiratory systems are ventilated by an in-and-out, or tidal, flow of air. The respiratory system of birds, however, which is far more complex than that of mammals, is arranged so that the air can flow unidirectionally through the lung during both inspiration and expiration (see Bird Respiration, later in this chapter).

Tracheae. This type of respiratory organ is characteristic of insects. It consists of a system of tubes that supply oxygen directly to the tissues, thus obviating the need for circulation of blood for the purpose of gas transport. Exchange of gas in the tracheal system may take place by diffusion only, but in many, especially in highly active insects, there is active unidirectional pumping of air through parts of the tracheal system. The advantage of unidirectional flow is that it permits a far better gas exchange than is obtained by pumping air in and out.

Respiratory movements

Vertebrate lungs are ventilated by active pumping of air. (Tracheal ventilation will be discussed later, for insects differ from other animals in so many respects that it is convenient to treat them separately.) Ventilation of the vertebrate lung can be achieved in two different ways. Filling of the lung can take place with the use of a pressure pump, as in amphibians, or a suction pump, as in most reptiles, birds, and mammals.

A frog fills its lungs by taking air into its mouth cavity, closing its mouth and nostrils, and pressing air into its lungs by elevating the floor of its mouth. As a result of this filling mechanism, a frog can continue to take in repeated volumes of air several times in sequence without letting air out, and thus can blow itself up to a considerable size.

Nevertheless, Bentley and Shield (1973) have shown that, contrary to commonly accepted opinion, at least some amphibians can also breathe with the aid of suction-type pumping. Whether this is universal for amphibians is not known.

Positive pumping, similar to the amphibian mechanism, is found in some reptiles. The chuckawalla (*Sauromalus*), a desert lizard from southwestern North America, often hides in a rock crevice where, by inflating its lungs, it lodges itself so firmly that it cannot be pulled out. One way to dislodge the animal, used by Indians who want it for food, is to puncture it with a pointed stick.

The normal mechanism for filling the lungs in reptiles is the same as in birds and mammals: The lungs are filled by suction. Exhalation can be passive, following inhalation by elastic recoil, or it can be actively aided by muscular contraction. A suction-type pump requires a closed thoracic cavity where the pressure during inhalation is less than the surrounding atmosphere. In mammals inhalation is aided by contraction of the muscular diaphragm. Birds have a membranous diaphragm attached to the body wall by muscles, but its function differs from the mammalian diaphragm's. The common statement that birds have no diaphragm is incorrect.

Role of the skin in respiration

Gas exchange through the skin is normal and important for amphibians, which have moist and well-vascularized skin. In fact, some small salamanders (plethodont salamanders) have no lungs, and all gas exchange takes place through the skin surface, except for a small contribution by the oral mucosa (Feder and Burggren 1985).

In frogs the relative roles of skin and lungs change through the year (Figure 1.13). In winter, when the oxygen uptake is quite low, the skin takes up more oxygen than the lungs. In summer, when oxygen consumption is high, the uptake through the lungs increases several-fold and far exceeds the cutaneous uptake. The fact that oxygen uptake through the skin remains nearly constant throughout the year is related to the constant oxygen concentration in the atmosphere, which provides a constant diffusion head. If the oxygen concentration in the blood remains uniformly low through the year, the diffusion through the skin should not change much, for diffusion rates change very little with temperature. Because the need for oxygen increases greatly in summer, the increase could not be handled by the skin and must be covered by additional uptake in the lung, as is indeed the case.

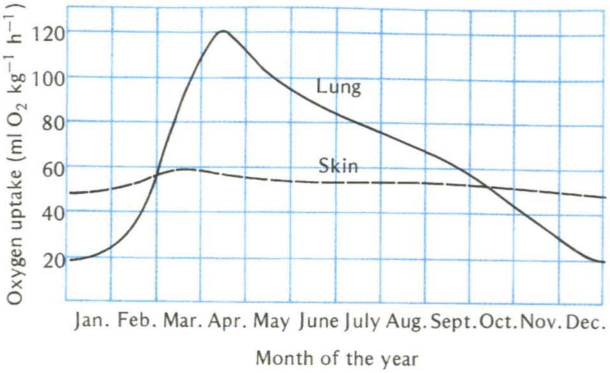


Figure 1.13 Oxygen uptake through the skin of frogs is nearly constant throughout the year. The increased oxygen consumption during summer is covered by a greatly increased oxygen uptake through the lung. [Dolk and Postma 1927]

Is the change with the seasons a result of the changing temperature? This question has been studied with toads (*Bufo americanus*), which were kept at three different temperatures: 5, 15, and 25 °C (Figure 1.14). At the two higher temperatures, the pulmonary oxygen uptake exceeds that through the skin, but at the lowest temperature the cutaneous oxygen uptake is greater. This is similar to the situation in the frog. For carbon dioxide exchange the skin is more important at all temperatures. At the lowest temperature the skin is

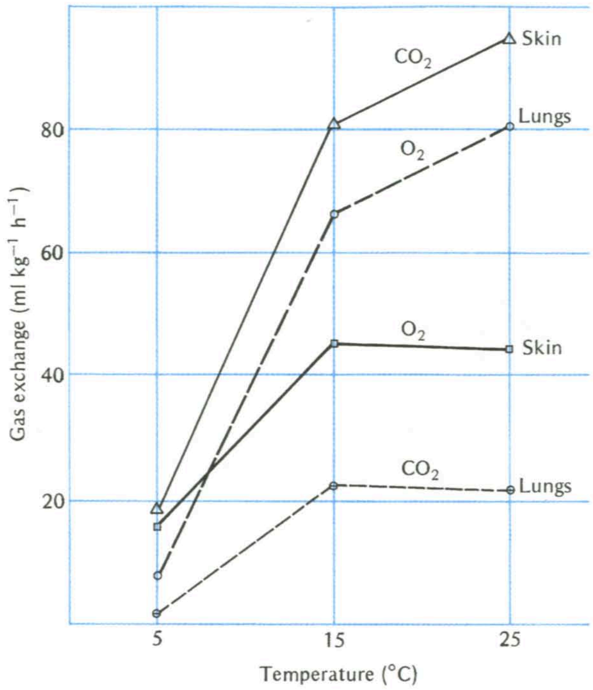


Figure 1.14 Pulmonary and cutaneous gas exchange in the toad *Bufo americanus* at different temperatures. [Hutchison et al. 1968]

therefore more important than the lungs, both for carbon dioxide and for oxygen.

Salamanders of the family Plethodontidae are unusual because they have neither lungs nor gills. These salamanders are by no means uncommon – they constitute about 70% of existing salamander species. They are quite small and occur both in terrestrial and aquatic habitats. Gas exchange and the role of the blood in gas transport have been studied in *Desmognathus fuscus*, which as adult weighs about 5 to 7 g.

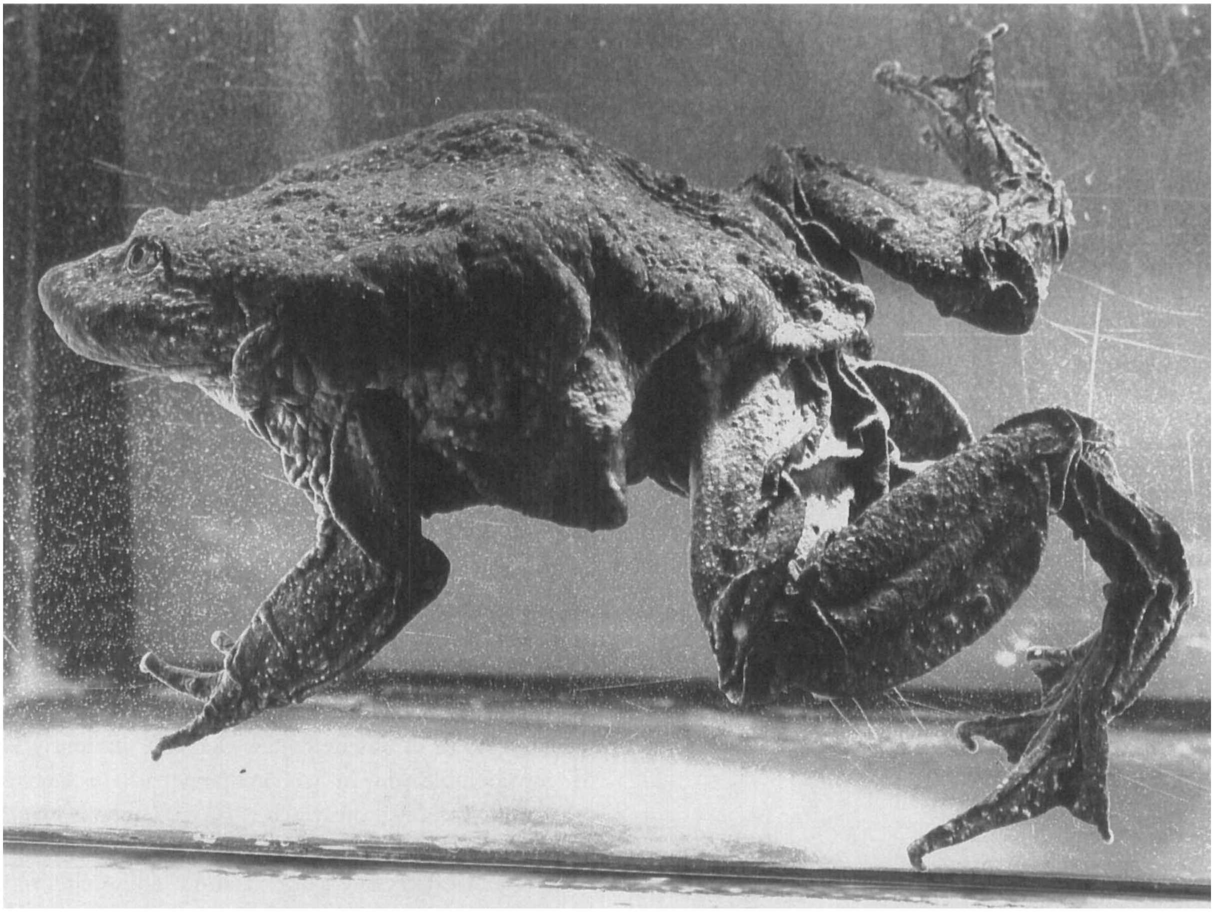
This animal is essentially a skin breather, although about 15% of the total gas exchange takes place across the mucosa of the mouth and pharynx. The blood has no exceptional characteristics: Both its hemoglobin content and its oxygen affinity are in the same range as in other salamanders, both aquatic and terrestrial. There is no special blood vessel carrying the oxygenated blood from the skin to the heart, and oxygen-rich blood leaving the skin is mixed with the general venous blood.

In other amphibians there is a partial separation of oxygenated and venous blood in the heart, but such separation appears to be absent in the plethodont salamanders, and as a result their arterial blood is never fully saturated with oxygen. Nevertheless, their common occurrence indicates that the plethodont salamanders are quite successful with what from our viewpoint appears a rather inadequate respiratory apparatus.

Reptiles, in contrast to amphibians, are often believed to have nearly impermeable skin. They breathe with lungs, and most of them are terrestrial. However, the true sea snakes are marine and some even bear living young at sea. They are excellent swimmers and are able to dive to a depth of at least 20 m. When the sea snake *Pelamis platurus* is submerged, it can take up oxygen through the skin at rates up to 33% of its total standard oxygen uptake and excrete carbon dioxide at rates up to 94% of the total. Although the lung is the primary organ of gas exchange, the skin obviously is of considerable aid in gas exchange as this snake pursues juvenile fish on which it preys (Graham 1974).

In mammals gas exchange through the skin is trivial. There is an oft-repeated legend about some children who for a religious procession in Italy were painted with gold paint; the story goes that they all died of asphyxiation because the skin could not "breathe". Death from asphyxiation is out of the question, for oxygen uptake through the skin is barely measurable and carbon dioxide loss from the skin is less than 1% of that from the lung (Alkalay et al. 1971). The gold-painted children must have died from other causes. A plausible explanation is that the gold paint was made by amalgamating gold and mercury and suspending the amalgam in oil, a common paint base. Mercury emulsifies readily in oil and is then rapidly absorbed through the skin, and the children may well have died from acute mercury poisoning.

Bats have a relatively much larger skin surface than other mammals; the large, thin, hairless wing membranes are highly vascularized and may contribute



A FROG THAT BREATHES THROUGH ITS SKIN The Titicaca frog (*Telmatobius culeus*) lives in the depths of Lake Titicaca at 3812 m altitude. This animal does not surface to breathe and obtains oxygen entirely by diffusion through the skin surface, which is highly vascularized and enlarged by loose folds. [Courtesy of Victor H. Hutchison, University of Oklahoma]

to gas exchange. There is, in fact, some carbon dioxide loss from the wing membrane. In the bat *Eptesicus fuscus* 0.4% of the total carbon dioxide production is lost from the wing skin at 18 °C. The amount increases with temperature, and at an air temperature of 27.5 °C as much as 11.5% of the total carbon dioxide is lost this way (Herreid et al. 1968). The uptake of oxygen through the wing membranes, however, is not sufficiently great to be of any significance; as discussed earlier, the diffusion between water and air is some 25-fold slower for oxygen than for carbon dioxide.

MAMMALIAN LUNGS

As we move up through the vertebrate classes, the lungs become increasingly complex. In amphibians the lung is a single sac, subdivided by a few ridges that give an increased surface. The mammalian lung is much more finely divided into small sacs, the *alveoli*, which vastly increase the surface area available for gas exchange. Measurements of the surface of the frog lung indicate that 1 cm^3 lung tissue has a total gas-exchange surface of 20 cm^2; the corresponding figure for normal mice is over 800 cm^2 surface per 1 cm^3 lung tissue (Weibel 1984). The large surface area is essential for the high rate of oxygen uptake required for the high metabolic rate of warm-blooded animals.

The membrane that separates the air in the lungs from the blood must be thin so that oxygen can diffuse readily into the blood while carbon dioxide moves in the opposite direction. In the human lung much of the alveolar membrane where gas exchange takes place is no more than 0.2 μm thick. What this means is difficult to imagine. The thickness of a single page in this book is about 50 µm; if one page could be sliced into 250 parallel layers, each layer would be the thickness of the alveolar membrane. Consider now that the total surface area of the human lung is about 100 m^2, or nearly the size of a tennis court, and strong enough to tolerate being stretched more than 20 000 times per day (Weibel 1984). This large area in combination with the minute thickness of the membrane provides a physical barrier between air and blood that permits very high rates of gas exchange.

Lung volume

The lung volume of a mammal constitutes about 5% of the body volume, irrespective of the body size (Figure 1.15). If the lung volume were to remain the exact same proportion of body size, the slope of the regression line in Figure 1.15 would be exactly 1.0. The best fitting regression line has a slope of 1.06, i.e., there is a slight deviation from strict proportionality: Larger animals tend to have proportionately larger lung volumes.

As expected, the individual points do not fall exactly on the line, but there are no large characteristic deviations. This means that small mammals, which have high specific metabolic rates, obtain sufficient oxygen with lungs of the same relative size as in large animals.

It is worth noting that diving animals, such as porpoise, manatee, and whale, follow the common mammalian pattern in regard to lung size. One might expect that these animals, in order to stay under water longer, would have very large lungs that they could fill with air before a dive. This is not the case; as we shall see later, diving animals do not depend for diving on the oxygen reserves in their lungs.

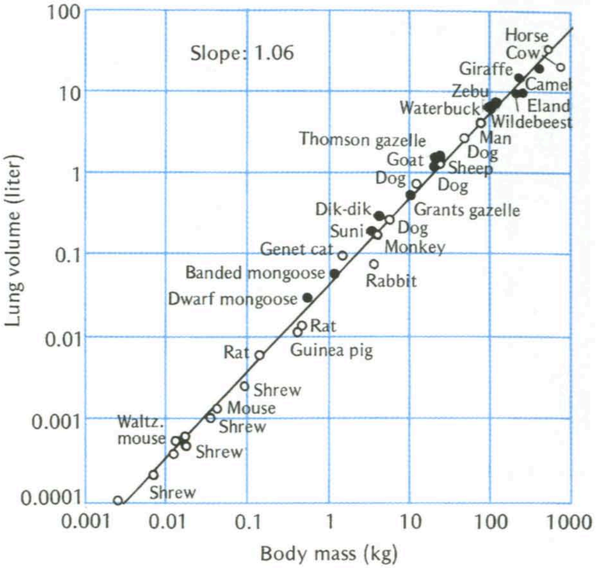


Figure 1.15 The lung volumes of mammals, when plotted against body size, fall close to a straight line with a slope of 1.06. Closed circles, African mammals, open circles, other species. [Gehr et al. 1981]

The regression line in Figure 1.15 can be described by the equation:

$$V_{\mathrm{L}} = 0.046 \cdot M_{\mathrm{b}}^{1.06}$$

where V_L is the lung volume in liters and M_b the body mass in kilograms.* For a mammal of 1 kg body mass the expected lung volume would be 0.046 liter, or 46 ml. Assuming that the body volume in liters equals the body mass in kilograms (this is for practical purposes

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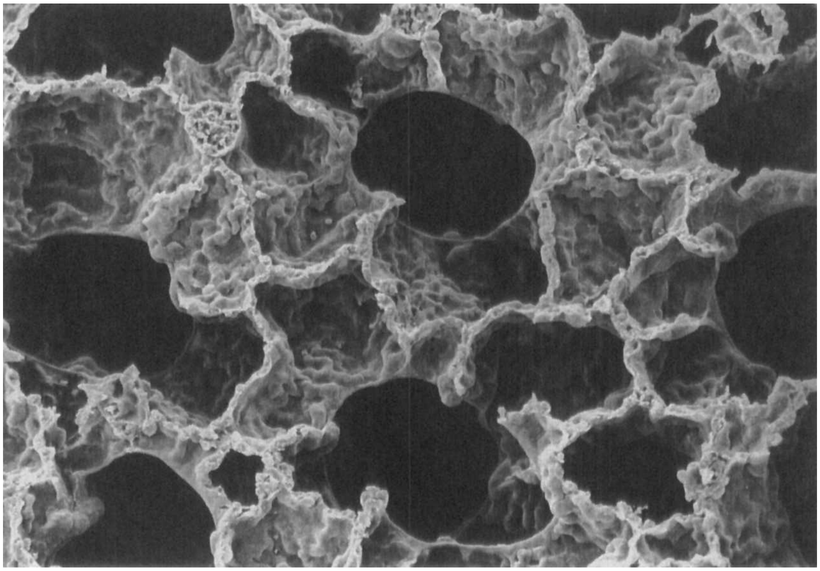
* Mass is a fundamental property of matter, and weight refers to the force exerted on a given mass by a specified gravitational field. In the gravitational field of the earth mass and weight, if both are expressed in kilograms, numerically have the same value. In a different gravitational field the mass is unchanged but the weight is different. For example, on the moon a 70 kg person still has a mass of 70 kg, but his weight is only one-sixth of that on the earth, or about 12 kg (more correctly, kilogram force or kgf). Because of the similarity between mass and weight on earth, it is very common not to distinguish between them. However, the correct statement is that the mass of our person is 70 kg, whether he is on the earth, on the moon, or in space; but his weight will be 686 N on earth, about 110 N on the moon, and zero in space.



MAMMALIAN LUNG Scanning electron micrograph of the lung structure of a wildebeest (*Connochaetes taurinus*). The capillaries, filled with red blood cells, are visible as a bulging network in the alveolar walls. The distance across the photograph corresponds to about 0.5 mm in the lung. [Courtesy of Ewald Weibel, University of Berne, Switzerland]

correct, for we know that a person is close to neutral buoyancy in water and therefore has a density near 1.0), the lung volume is 4.6% of the body volume. (For those unfamiliar with the arithmetic manipulation of exponential equations, a brief discussion is included in Appendix C.)

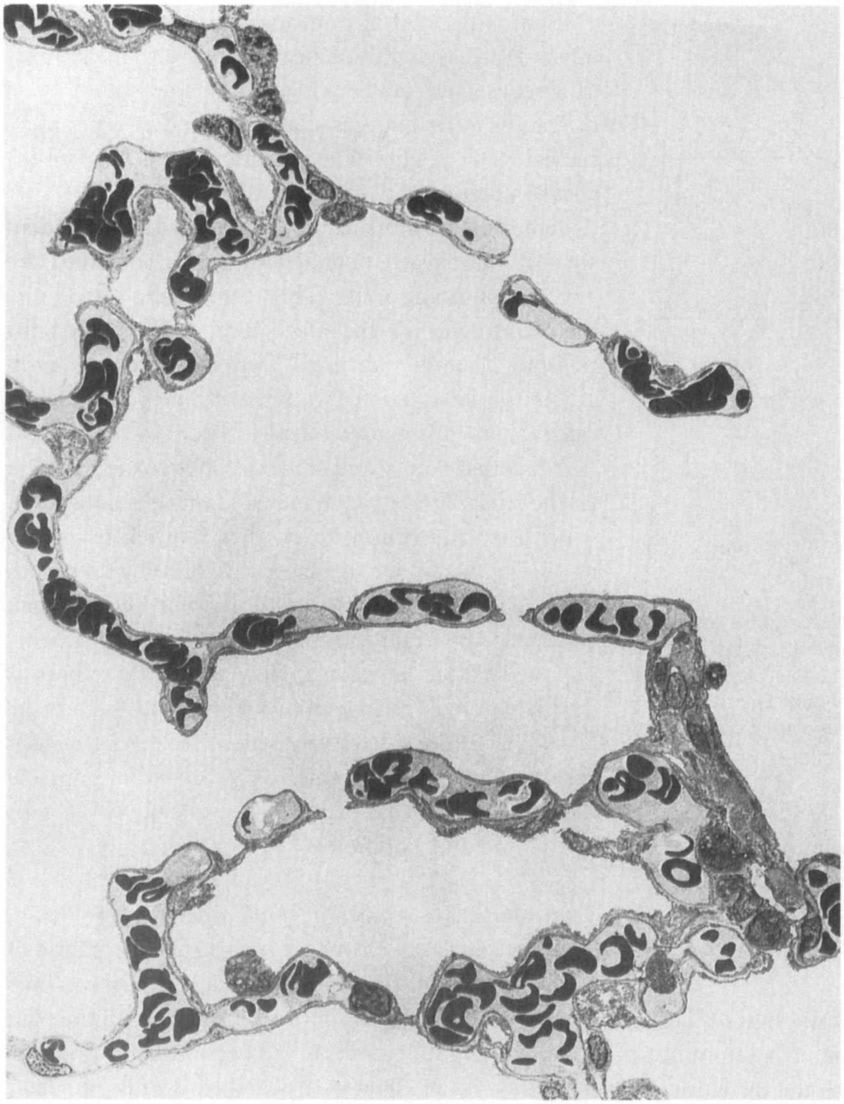
Inhalation and exhalation

Gas exchange in the lung takes place in the alveoli; the trachea, the bronchi, and their branches are only connecting tubes. At the end of an exhalation these tubes are filled with "used" air from the lung, and when inhalation follows, this air is pulled back into the lungs before fresh outside air enters.

The volume of air in the passageways reduces the amount of fresh air that enters the lung and is called the *dead space*. The volume of air inhaled in a single breath is the *tidal volume*. A normal person at rest has a tidal volume of about 500 cm^3. Because the dead space is about 150 cm^3, only 350 cm^3 of fresh air will reach the lungs. The dead space thus constitutes about one-third of the tidal volume at rest. In exercise, the relative role of the dead space is less. For example, if a person who breathes heavily inhales 3000 cm^3 air in a single breath, a dead space of 150 cm^3 is now only about one-twentieth of the tidal volume. Therefore, the dead space is a substantial fraction of the tidal volume at rest, but in exercise it is relatively insignificant.

An important aspect of respiration is that the lungs are never completely emptied of air. Even if a person exhales as much as possible, there is still about 1000 cm^3 of air left in his lungs. It is therefore impossible for a person to fill his lungs completely with "fresh" air, for the inhaled air is always mixed with air that remained in the lungs and the dead space.

In respiration at rest a person may have about 1650 cm^3 of air in the lungs when inhalation begins. During inhalation, 350 cm^3 fresh air reach the lungs and are mixed with the 1650 cm^3 already there. The renewal of air is therefore only about one part in five. The result is that the composition of the alveolar gas remains quite constant at about 15% oxygen and 5% carbon dioxide. This composition of alveolar air remains the same during exercise; in other words, the increased ventilation during exercise is adjusted to match accurately the increased use of oxygen.



ALVEOLAR STRUCTURE Cross section of the alveolar structure of a dog's lung. The irregular dark spots are red blood cells, which become distorted as they flow through the capillaries. The thickness of the alveolar membrane, separating blood from air, is only a fraction of 1 μm. The distance across the photograph corresponds to about 0.15 mm in the lung. [Courtesy of Ewald Weibel, University of Berne, Switzerland]

Surface tension

Every person who has blown soap bubbles knows that, when the connection to the atmosphere is open, the bubble tends to contract and expel air until it collapses. The vertebrate lung is somewhat similar; the bubble-like shape and high curvature of the alveoli mean that the surface tension of the moist inner surface tends to make the "bubbles" contract and disappear. The surface tension should make the lung collapse, but this tendency is minimized by the presence on the inner surface of the alveoli of substances that greatly reduce the surface tension (Goerke and Clements 1986).

These substances are phospholipids, and their effect on surface tension has given them the name *surfactants.* Surfactants are found in the lungs of all vertebrates – mammals, birds, reptiles, and amphibians. Even the lung surface of lungfish is covered with surfactants. The amount of surfactant present in the vertebrate lung

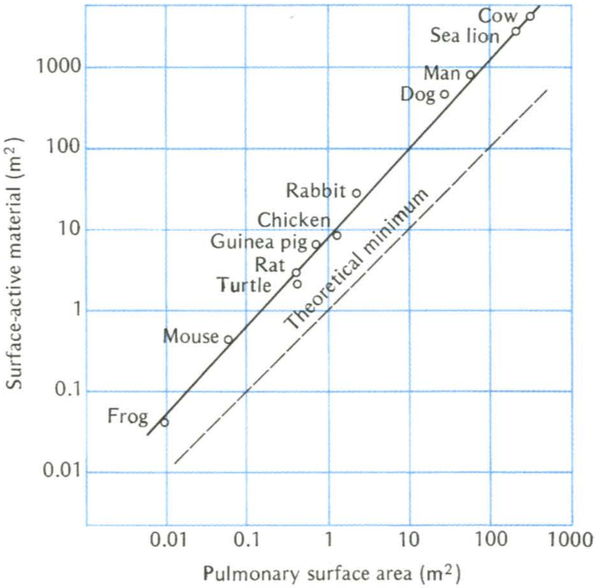


Figure 1.16 The amount of surfactant that can be extracted from the lungs of various vertebrates plotted against the surface area of the lung. The extracted amount is uniformly greater than the theoretical minimum amount needed to cover the lung surface with a monomolecular layer. [Clements et al. 1970]

seems always to be above the minimum required to cover the pulmonary surface with a monomolecular layer (Figure 1.16).

Mechanical work of breathing

The movement of air in and out of the lungs requires work, and it is of interest to compare the amount of oxygen it takes to run the pump with the total amount of oxygen the organism obtains in the same period of time.

An accurate determination of the amount of oxygen used for breathing is difficult and has a substantial margin of error because the amount is small compared with the overall oxygen consumption. Most determinations indicate that the cost of breathing in a person at rest is 1.2% of the total resting oxygen consumption. With increasing ventilation, the cost of breathing increases, and in heavy exercise it may be as much as 3% of the total oxygen consumed (Margaria et al. 1960).

What is the cost of pumping water over the gills of a fish? Water is 800 times heavier than air and 50 times as viscous (see Table 1.5), and the low solubility of oxygen in water requires a large volume of water to be moved over the gills. What effect does this have on the cost of breathing?

Some investigators have suggested that more than 50% of the oxygen obtained by a fish goes into the work of pumping water. This seems quite unrealistic, for an estimate of the mechanical work needed for pumping, can be obtained from the pressure drop across the gills and the volume of water flow. These calculations give figures closer to 1%.

A fish that seems well suited to answer the question is the sharksucker or remora (*Echeneis naucrates*), which may attach itself to another, larger fish and get its gills ventilated for free by merely keeping its mouth open as the larger fish swims along. The gills are then ventilated by ram ventilation, the energy being provided by the larger fish. However, if the remora is detached, it must change from this free ride and breathe like other fish by active ventilation. Its rate of oxygen consumption then increases by 3 to 5%, presumably representing the cost of pumping water over the gills (Steffensen and Lomholt 1983).

Synchronization of breathing and locomotion

When a kangaroo moves rapidly across the plains of Australia in long hops, its breathing rate is synchronized with the hopping in a 1:1 ratio. The mechanism is fairly straightforward. At the beginning of a hop, as the body is accelerated up and forwards, the soft organs in the abdominal cavity are forced by inertia in the posterior direction. This in turn pulls on the diaphragm and the lungs fill with air. When, at the end of the hop, the hind legs hit the ground, the viscera are forced against the diaphragm and air is forced out of the lungs. It is as if the viscera act as a piston, moving air in and out of the lungs (Baudinette et al. 1987).

Synchronization between breathing and locomotion has been observed in many mammals and birds, but the mechanism is not always as easy to analyze. Birds lack a muscular diaphragm and depend on movements of the sternum for ventilation. Since the flight muscles are attached to the sternum, it seems reasonable that wing movements should influence ventilation, and in many birds there is indeed a link between wing beat and breathing. In some species the link is in a 1:1 ratio, but in others the ratio may be 2:1 or 3:1, and in some not necessarily an even ratio. The reasons for such differences are not easily explained.

Not only kangaroos, but many other mammals show synchrony between breathing and locomotion. Bats, from 100 to 870 grams in size, have an exact 1:1 coupling between wing beats and breathing (Carpenter 1986). Galloping mammals, ranging in size from gerbils to rhinoceros, breathe in synchrony with their locomotion in a 1:1 ratio, taking exactly one breath per stride (a stride is defined as one complete cycle of leg movements). In trotting dogs, observed with the aid of x-ray films, the diaphragm showed a forward and back movement twice during each stride (the trunk undergoes two accelerations and decelerations during one stride, once for each of the two front feet). However, the alternation of the forces exerted by the forelimbs on the chest wall suggests a more complicated movement of air between the two lungs (Bramble and Jenkins 1993).

Regulation of respiration

If the need for oxygen increases, the ventilation of the respiratory organs must be increased accordingly. Likewise, if the oxygen concentration in the medium falls, there must be compensation by increasing the ventilation, or by increasing the amount of oxygen removed from the respired air, or by both means.

In warm-blooded vertebrates – mammals and birds – the ventilation of the lungs is very precisely adjusted to the need for oxygen, but interestingly, the primary agent responsible for the regulation is the carbon dioxide concentration in the lung air. This is readily demonstrated by adding carbon dioxide to the inhaled air. This causes a rapid increase in pulmonary ventilation (Figure 1.17). Normal atmospheric air contains virtually no carbon dioxide (0.03%), and if 2.5% CO_2 is added to the inhaled air, the ventilation volume is approximately doubled. The effect is similar in mammals and birds.

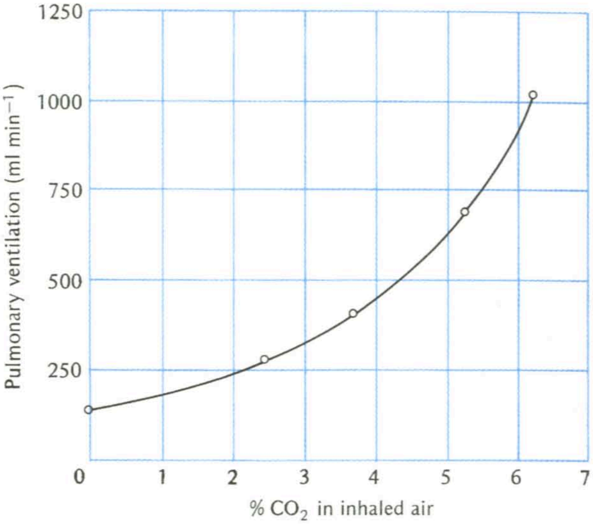


Figure 1.17 The effect on pulmonary ventilation volume of increased carbon dioxide content of the inhaled air in chickens. [Johnston and Jukes 1966]

This 2.5% CO_2 is really not much, for the lung air of mammals already contains about 5% CO_2. If the carbon dioxide concentration in inhaled air is increased to what is normally found in the lung, the increase in respiratory ventilation volume is several-fold. In much higher concentrations carbon dioxide becomes narcotic and therefore induces abnormal responses.

Oxygen has a much smaller effect on ventilation. If we reduce the oxygen concentration in inhaled air by 2.5%, from 21% to 18.5% O_2 there is virtually no change in respiration.

The respiratory center

Breathing in mammals is brought about by the muscles of the diaphragm and the intercostal muscles. The rhythmic movements of these muscles are controlled by a respiratory center, which is located in the area of the medulla oblongata and the pons of the brain.

The respiratory center contains a number of separate neurons for inspiration and expiration that alternate in their activity. When the inspiratory neurons send stimulatory impulses to the respiratory muscles, inhibitory impulses to the expiratory neurons keep these from activity. When the activity of the inspiratory neurons ceases, the expiratory neurons become active, and in this way the alternating action of the two sets continues indefinitely.

The respiratory center is sensitive to the increased carbon dioxide or increased acidity in the cerebrospinal fluid, and an increased P_{CO_2} in the blood acts because carbon dioxide rapidly diffuses from the blood to the cerebrospinal fluid. Acidity in the blood, without an increase in carbon dioxide, is less effective because the hydrogen ion does not readily diffuse into the cerebrospinal fluid.

As an adequate supply of oxygen is essential, it may seem peculiar that the respiratory center is very insensitive to a decrease in the oxygen in the blood. However, there are peripheral chemoreceptors that are sensitive to a decrease in oxygen. These are located partly in a carotid body and partly in the aortic arch near the heart. A decrease in the P_{O_2} in the arterial blood activates these chemoreceptors, which cause an increase in both the depth and the frequency of respiration. However, the effect will not be very profound because an increased ventilation volume leads to a loss of carbon dioxide from the blood, which in turn reduces the ventilation volume. As a result, a moderate decrease in oxygen has very minor effects on the respiration, which under normal circumstances is regulated primarily to maintain a normal P_{CO_2} and acid–base balance in the blood.

During exercise respiration increases, and this increase occurs before the increased oxygen consumption and carbon dioxide production of the muscles have altered the oxygen and carbon dioxide content of the blood. What happens is that impulses from the motor cortex of the brain, as well as from proprioceptors in the muscles, affect the respiration so that in the end the P_{CO_2} of the blood during exercise is maintained at very nearly the normal resting level and oxygen is supplied at the rate with which it is consumed by the muscles.

The sensitivity of respiration to the carbon dioxide concentration is often used by swimmers who wish to stay under water for long periods. By breathing deeply for some time, a person can increase the loss of carbon dioxide from the lungs and from the blood. This removes the usual stimulus to respiration, and as a consequence, a person who has hyperventilated can remain under water longer before he is forced to the surface by the urge to breathe.

This practice is extremely dangerous. As a person swims under water, the oxygen in his blood is gradually depleted, but in the absence of the usual concentration of carbon dioxide the urge to breathe is not very strong. He therefore remains submerged, and as the blood oxygen falls, he may lose consciousness without even being aware of the danger. If in this state he is not immediately discovered and rescued, he will drown. This sequence of events has in fact been the cause of many drowning accidents, particularly in swimming pools, when good swimmers competitively attempt long underwater swimming feats (Craig 1961).

Diving animals

It has been stated that seals and whales are less sensitive to carbon dioxide than other animals and therefore are able to stay under water longer. However, the duration of a dive is probably limited by the amount of oxygen available, and it is unlikely that a dive could be prolonged merely by a decreased sensitivity to carbon dioxide.

If we want to examine the response to inhaled carbon dioxide in various animals, it is not enough to measure the respiration frequency. In some animals the respiration frequency increases considerably in response to carbon dioxide, but in others there may be little or no change in frequency and yet a considerable increase in tidal volume. This has, for example, been found in the spiny anteater (the echidna, *Tachyglossus*) (Bentley et al. 1967). The information we need is the *ventilation volume* (i.e., the product of respiration frequency and tidal volume).

If we determine the increase in ventilation volume in response to carbon dioxide, it turns out that the seal, at carbon dioxide concentrations up to 6%, is even

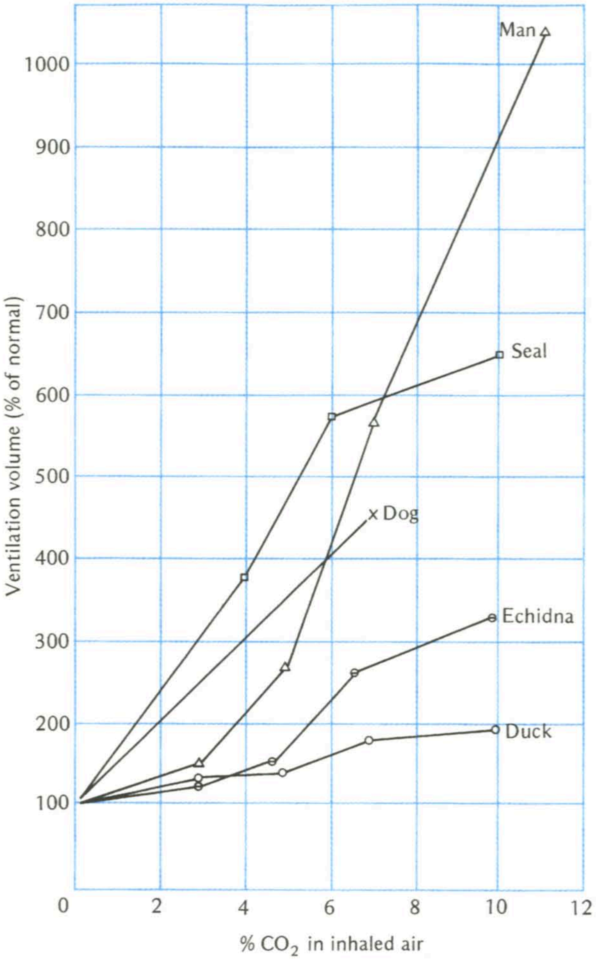


Figure 1.18 An increase in the carbon dioxide content of inhaled air causes a several-fold increase in respiration volume. Note that the seal is more sensitive to carbon dioxide than the dog. [Bentley et al. 1967]

more sensitive to carbon dioxide than nondiving animals such as human and dog (Figure 1.18). This contradicts the statements about diving seals being insensitive to carbon dioxide.

Comparison of air and aquatic respiration

In many aquatic invertebrates the regulation of respiration is poor or even absent. This is true especially in marine species that normally live in well-aerated water with a relatively constant oxygen supply. Some lower animals are quite tolerant of lack of oxygen; bivalve molluscs can keep the shells closed for long periods and, in the absence of ventilation, utilize anaerobic metabolic processes (see Chapter 5).

For most aquatic animals the primary stimulus to respiration is lack of oxygen. This is usual in crustaceans, octopus, fish, and so on. The effect of carbon dioxide on aquatic invertebrates is never very pronounced and may be absent. The carbon dioxide tension in natural water is almost always low, and, as we shall see in Chapter 2, because of the high solubility of carbon dioxide in water, aquatic animals cannot build up a high tension of this gas. If they were to depend on an increase in carbon dioxide tension for stimulation of respiration, an adequate supply of oxygen could not be assured.

If we compare two closely related forms, the marine lobster (*Homarus*) and the fresh-water crayfish (*Astacus*), we notice a characteristic difference. The lobster, a marine animal, does not show much change in ventilation with a decrease in oxygen in the water. The fresh-water crayfish, in contrast, responds to a decrease in oxygen with an increase in ventilation. The difference is readily understood. The lobster lives in cold waters where the oxygen is always high, and an elaborate mechanism for regulation of ventilation would be superfluous. The crayfish, on the other hand, may readily encounter fresh-water environments where oxygen is depleted, and a ventilatory response is needed.

Fish in general respond to a decrease in oxygen, and their response to changes in carbon dioxide is minimal. In this regard they resemble other aquatic animals rather than the air-breathing vertebrates. Insects are for the most part highly sensitive to carbon dioxide.

Can we generalize these differences? We have already mentioned that aquatic animals cannot readily base their respiratory regulation on carbon dioxide, not only because the carbon dioxide tension in natural waters usually is low, but also because it is an unreliable measure of the oxygen content. Sea water is highly buffered, so that the carbon dioxide tension never builds up to any appreciable extent. Stagnant fresh water, on the other hand, may have high carbon dioxide concentrations, usually associated with low oxygen. Aquatic animals could not possibly depend on something as unreliable as the carbon dioxide concentration; when their respiration is regulated, it is in response to oxygen concentration.

The question now becomes: Why have terrestrial air-breathing animals abandoned regulation on oxygen and gone over to carbon dioxide as the primary stimulus? The answer is probably that, as oxygen becomes easily available in the atmosphere, the carbon dioxide concentration tends to build up in the respiratory organs. For example, if a mammal reduces the oxygen in the respired air from 21% to 16%, this entails a simultaneous buildup of carbon dioxide to about 5%, an amount that greatly affects the acid–base balance of the organism. A decrease in oxygen to 16% does not have any profound physiological effect, but a change in 1% of the carbon dioxide concentration, say from 4% to 5%, constitutes a 25% increase in carbonic acid.

Also, it may be easier, physiologically speaking, to design a precise control system based on carbon dioxide and the detection of small changes in hydrogen ion concentration than to devise a system sensitive to small changes in oxygen concentration. Be this as it may, we universally find that air-breathing animals are far more sensitive to changes in carbon dioxide than to changes in oxygen.

AIR-BREATHING FISH

Many fish will respond to a decrease in the oxygen content in the water by swimming to the surface to take a bubble of air into the mouth, a response that greatly improves the oxygen supply. Goldfish that were kept in water with an oxygen tension of only 20 mm Hg would gulp air at the surface as often as 180 times per hour. This nearly doubled the oxygen content of the arterial blood of the oxygen-starved fish (Burggren 1982).

A number of other fish are specifically adapted to air breathing to a much greater extent than the goldfish. Everybody has heard about lungfish, but these are not the only fish that depend on air. Many fish will resort to breathing air only when the oxygen content in the water is low; relatively few depend on air to such an extent that they drown if kept submerged.

There are two main ecological reasons for using accessory or exclusive air breathing: (1) depletion of oxygen in the water and (2) the occurrence of periodic droughts. A lungfish, for example, during dry periods burrows deep into the mud, encases itself in a cocoon, and remains inactive until the next flood.

Most of the air-breathing fish are tropical fresh-water or estuarine species; few are truly marine. Oxygen-deficient fresh water is much more common in the tropics than in temperate climates. This is because there is much decaying organic matter in the water, the temperature is high and speeds up bacterial action, small bodies of water are often heavily shaded by overhanging jungle (which reduces photosynthesis and oxygen production in the water), and there is little temperature change between day and night and therefore minimal thermal convection to bring oxygen-rich surface water to deeper layers. Not all air-breathing fish belong in the tropics, however. The well-known bowfin (*Amia calva*) is found in the northern United States even where the lakes are frozen over in winter. During such periods they manage well without air breathing because the low temperature reduces their oxygen consumption.

It was explained that fish gills are not well suited for respiration in air. They lack the necessary rigidity and tend to stick together, but even so, some oxygen can be taken up through gills in air. Any other moist surface will supplement the gas exchange, provided it is a surface that has access to air and is supplied with blood. Some gas exchange can always take place through the skin and the surface of the mouth cavity, but in addition there may be other anatomically more specialized organs that aid in gas exchange. Organs commonly utilized in air breathing are gills, skin, mouth, opercular cavities, stomach, intestine, swimbladder, and lung.

Organ used for respiration in air	Fish	Habitat	Comment
Gills	*Synbranchus*	South America, fresh water	An eel-shaped fish without any common English name
Skin	*Anguilla*	North America, Europe	The common eel; breeds in the sea; larva migrates to fresh water
Skin	*Periophthalmus*	Tropical estuarine beaches	A common fish, often called mud skipper
Mouth and opercular cavities	*Electrophorus*	South America, fresh water	The electric eel
Mouth and opercular cavities	*Anabas*	Southeast Asia, fresh water	Called climbing perch, but not really a perch; related to betta, the Siamese fighting fish
Mouth and opercular cavities	*Clarias*	Southeast Asia, (Florida, introduced), fresh water	A catfish, known also as the walking catfish
Mouth and opercular cavities	*Gillichthys*	Pacific Coast of North America	Also called the mudsucker
Stomach	*Plecostomus*	South America, fresh water	A small catfish common in home aquaria
Stomach	*Anicistrus*	South America, fresh water	An armored catfish, protected by heavy spines and bony plates
Intestine	*Hoplosternum*	South America, fresh water	An armored catfish
Swimbladder	*Arapaima*	South America, rivers	The world's largest freshwater fish
Swimbladder	*Amia*	North America, fresh water	The bowfin; range extends north to areas where lakes remain ice-covered through winter; belongs to primitive group Holostei
Swimbladder	*Lepisosteus*	North America, fresh water	The garpike; belongs to the primitive group Holostei
Lung	*Polypterus*	Africa, fresh water	The bichir; has a lung, but is not a true lungfish (see text)
Lung	*Lepidosiren*	South America, fresh water	A true lungfish
Lung	*Protopterus*	Africa, fresh water	A true lungfish
Lung	*Neoceratodus*	Australia, fresh water, rivers	A true lungfish

Table 1.6 Fish that can use accessory air breathing or depend completely on air. Most are modern teleosts; only the last three are true lungfish.

Some air-breathing fish are listed in Table 1.6, with a few comments to place them in a familiar frame of reference. It is worth noting that all except the last five are ordinary higher bony fishes (Actinopterygii). The bowfin (*Amia*) is a representative of the primitive group Holostei, and the bichir (*Polypterus*) is peculiar because it has a lung, but both are considered primitive representatives of the Actinopterygii. Only the last three fish listed are the true lungfish (Dipnoi), which presumably are closely related to the Crossopterygii (the sub-class that contains the famous coelacanth, *Latimeria*). There is one genus of true lungfish in

Fish	Respiration organ	Habitat
Protopterus	Lung	Africa
Lepidosiren	Lung	South America
Arapaima	Swimbladder	South America
Hoplosternum	Intestine	South America
Ophiocephalus	Pharyngeal cavities	South Asia and Africa
Electrophorus	Mouth	South America

Table 1.7 Some fish that are obligatory air breathers.

each of three continents: Australia, Africa, and South America.

The need for air breathing depends on the amount of oxygen in the water and the temperature, for the rate of oxygen consumption increases with temperature. For this reason it is not always possible to say whether a given fish does or does not depend on air breathing. However, some fish are so dependent on air breathing that they cannot survive even in well-aerated water. They are obligatory air breathers and will "drown" if deprived of access to air. The fish listed in Table 1.7 are such obligatory air breathers; interestingly, the Australian lungfish, *Neoceratodus*, is not included.

We shall now discuss how some of the various mechanisms function and how effective they are by describing some fish that have been studied by physiologists.

Common eel

The common European and North American eel (*Anguilla vulgaris*) supposedly is able to crawl considerable distances over land and cross from one watercourse to another, especially at night and through moist grass. Fishermen often keep live eels in a box for days, merely covered by a wet sack to keep them from drying out.

When an eel is out of water, it keeps its gill cavities inflated with air. About once a minute it renews the air in the gill cavity. In contrast, when in water at 20 °C an eel respires at a frequency of about 20 per minute.

The oxygen consumption of an eel in air is about half of what it is in water at the same temperature. When an eel is moved to air, oxygen taken from the air is initially supplemented with oxygen removed from the swimbladder; this amount may, during the first hour, nearly equal that taken from the air. However, when an eel is kept in air longer, it gradually accumulates a substantial oxygen debt, and the lactic acid concentration in the blood increases. When returned to water, recovery is rapid, and in 2 hours the blood lactic acid has returned to the normal level.

At a lower temperature, 7 °C, the rate of oxygen consumption is much lower and there is no rise in lactic acid in the blood and apparently no oxygen debt. The permeability of the skin to oxygen should be nearly independent of temperature, and at the low temperature the combined oxygen uptake through skin and gills seems sufficient to cover the metabolic rate (Figure 1.19).

The relative importance to the eel of gills and skin differs in water and in air. In water (at 20 °C) about 90% of the total oxygen uptake is via the gills; the remainder through the skin. In air, only about one-third of the total oxygen uptake is via the gills; the remaining two-thirds via the skin. Although the gills are still of some use in air, they are far from adequate, and even with the aid of the skin the total available oxygen is insufficient to avoid an oxygen debt and formation of lactic acid, except at the lowest temperatures.

Electric eel

The South American electric eel (*Electrophorus electricus*) is known for its powerful electric discharges, which have been measured at 550 V, enough to stun or kill other fish and perhaps even a human. The electric eel is a mouth breather and drowns if denied access to air. The oral cavity, which is immensely vascularized, has multiple foldings and papillations that greatly enlarge its surface area.

The electric eel takes air into the mouth at intervals from a few seconds to several minutes. The oxygen in this air gradually decreases while the carbon dioxide increases, although not in the same proportion (Figure

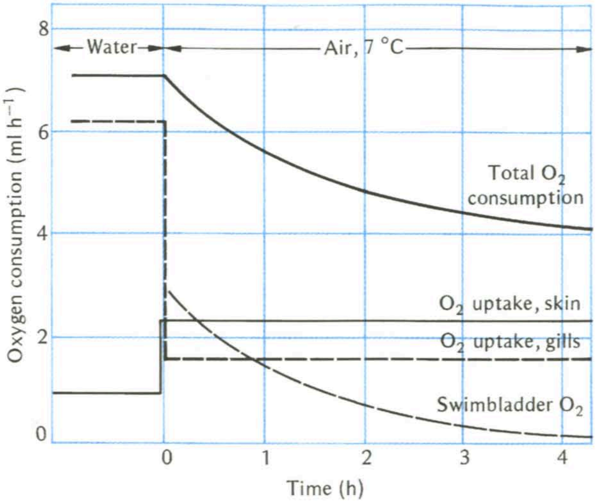


Figure 1.19 When an eel is transferred from water to air (at 7 °C), its rate of oxygen consumption gradually decreases and stabilizes at a lower level (top curve). Initially, oxygen is taken from the swimbladder, but when this is used up, the combined oxygen uptake from skin and gills suffices to sustain the lowered rate of oxygen consumption. [Berg and Steen 1965]

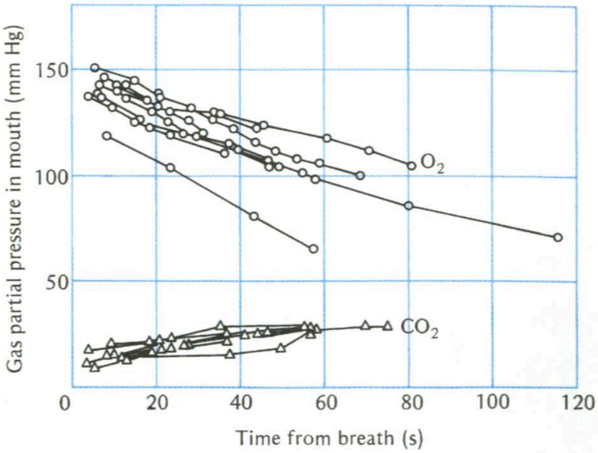


Figure 1.20 Air kept in the oral cavity of the electric eel gradually loses oxygen as it is used by the fish. The carbon dioxide in the mouth air gradually increases, but not to the same degree. When about one-third of the oxygen has been removed, the fish seeks to surface for renewal of the air. [Johansen et al. 1968]

1.20). When the oxygen has fallen by about one-third, the fish slowly moves to the surface for renewal of the air.

In an air breather in which the entire gas exchange takes place between the blood and a body of air, the buildup of carbon dioxide should correspond roughly to the oxygen depletion. As this is not the case for the electric eel, carbon dioxide must be lost elsewhere, perhaps through the rather rudimentary gills or, more likely, through the skin.

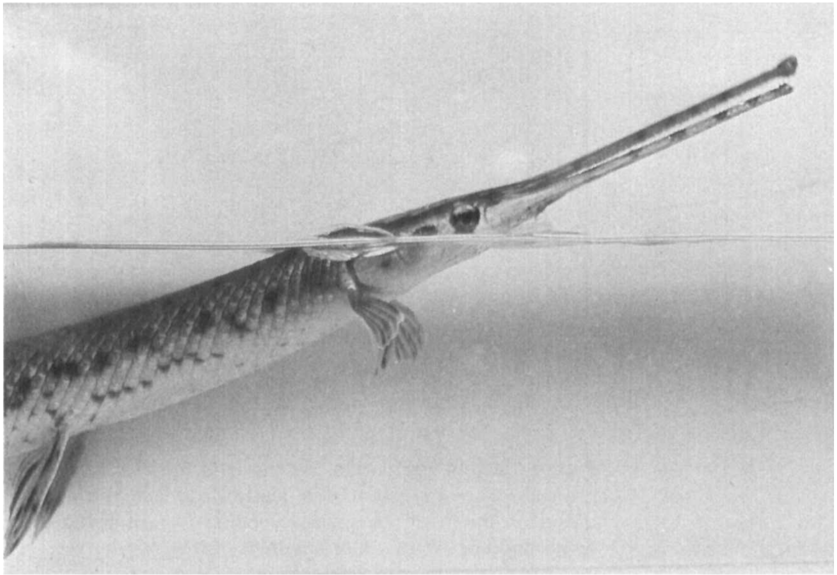
The regulation of respiration in the electric eel can be examined by changing the carbon dioxide and oxygen concentrations in the atmosphere it is allowed to breathe. The result is that a substantial increase in the carbon dioxide content in the air gives only a moderate increase in the rate of breathing, but a drop in the oxygen content causes a several-fold increase. Likewise, increasing the oxygen pressure above that in normal atmospheric air has a somewhat depressing action on the respiration (Johansen 1968).

It is interesting that this fish is an obligatory air breather, but has retained the aquatic mode of regulating respiration on oxygen. Evidently, this is associated with the fact that carbon dioxide escapes through the relatively permeable skin, thus not building up to sufficient concentrations to be physiologically important.

Garpike

The garpike (*Lepisosteus osseus*) is a relic of the ancient group Holostei, which presently is confined to North America. It is a long-nosed fish with hard scales and not popular as a game fish. Often it can be seen to break through the water surface as it comes up to breathe air. It is a large fish that may exceed 10 kg in weight and is widely distributed and occurs in the northern United States even where the lakes are frozen over for several months in winter.

The garpike has gills and also uses its modified swimbladder for respiration. The frequency with which it comes to the surface to take fresh air into the swimbladder is a function of water temperature. At 22 °C the interval between breaths averages 8 minutes in an undisturbed fish, but in winter, when the water is



AIR-BREATHING FISH A garpike (*Lepisosteus osseus*) breathing air at the water surface. A bubble of air is visible at the posterior end of the head; it has just been expelled from the gill slit, and the fish is ready to take in air by lowering the floor of the mouth. The whole sequence of breathing requires only slightly more than 0.5 second before the fish returns below the surface. [Courtesy of Katharine Rahn, Buffalo, New York]

covered by ice, the fish obviously cannot breathe air and depends entirely on its gills. At 20 to 25 °C, air breathing meets about 70 to 80% of the total oxygen requirement; the remainder is met by the gills. Carbon dioxide elimination from the swimbladder is, of course, zero in winter when the fish depends entirely on the gills. In summer, carbon dioxide eliminated from the swimbladder approaches 10%, and the bulk of the carbon dioxide is eliminated via the gills and skin (Rahn et al. 1971). This is characteristic of many air-breathing fish: Although air breathing is important for the uptake of oxygen, carbon dioxide, because of its high solubility, is eliminated mostly to the water.

Lungfish

The African and the South American lungfish (*Protopterus* and *Lepidosiren*) were listed in Table 1.7 as obligatory air breathers. They live in stagnant bodies of water and in lakes where long droughts may cause complete drying out of their habitat. They estivate until the next wet period, when they come out from their cocoons in the mud and resume normal life. The Australian lungfish (*Neoceratodus*) lives in rivers and slow streams. It also estivates in dry periods, but it depends much less on the lung and is primarily a gill breather.

When the three kinds of lungfish are kept in water with access to air, the relative roles of gills and lungs are as shown in Figure 1.21. In the Australian lungfish the gills are the primary organs of gas exchange. In the African lungfish most of the oxygen is taken up by the lung and only a small fraction through the gills. In the South American lungfish virtually all the oxygen uptake is via the lung and only a minute amount via the gills. With carbon dioxide the situation is different; both the African and the South American lungfish exchange about half through the lung, the remainder through the gills. Hence, gills are important in carbon dioxide exchange, and the lung plays the dominant role in oxygen uptake.

The changes that take place as the lungfish are removed from water to air show a similar relationship among the three species (Figure 1.22). The oxygen consumption of the African and South American lungfish remains nearly unchanged in air. In contrast, the Australian lungfish shows a precipitous drop in oxygen consumption, because normally it is an aquatic breather and in air it cannot obtain sufficient oxygen.

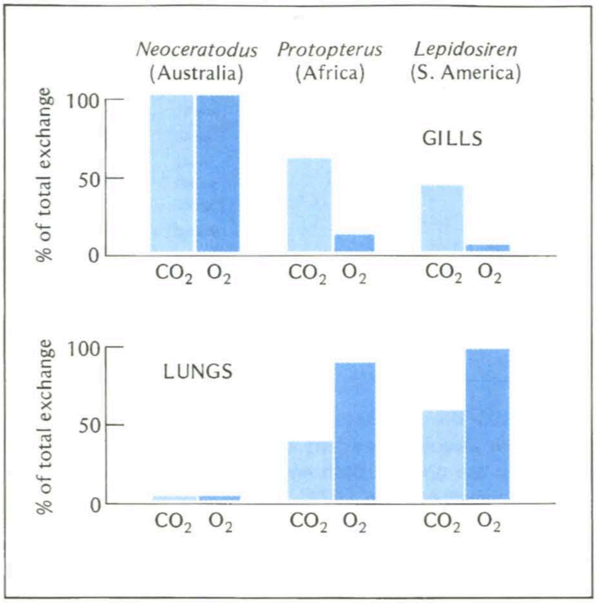


Figure 1.21 The relative roles of gills (upper panel) and lungs (lower panel) in respiratory gas exchange in three kinds of lungfish when kept in water and with access to air. [Lenfant et al. 1970]

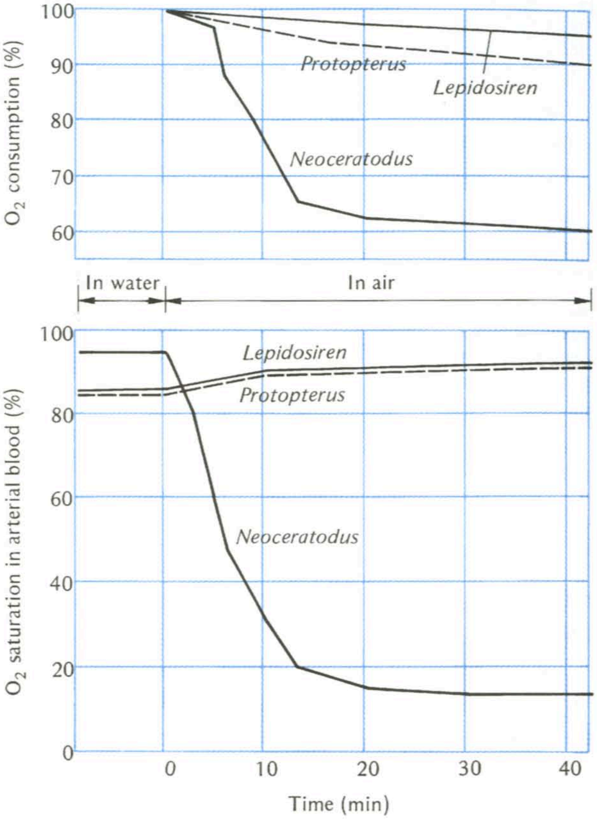


Figure 1.22 When African and South American lungfish are kept out of water, their rates of oxygen consumption remain nearly unchanged. The Australian lungfish shows a precipitous decrease in oxygen consumption when kept out of water. In this species the oxygen saturation in the arterial blood shows a corresponding drop. [Lenfant et al. 1970]

The oxygen saturation of the arterial blood (lower part of Figure 1.22) shows that the two obligatory air breathers maintain or slightly increase the oxygen saturation of the blood when they are removed to air; the Australian lungfish's arterial oxygen content drops to nearly zero, a clear indication that the fish is becoming asphyxiated.

The lungfish are among the best studied of the air-breathing fish. The information on many others is inadequate or virtually nil. The study of these could be very rewarding, although often technically difficult, for many are quite small.

BIRD RESPIRATION

Structure of the respiratory system

The respiratory organs of birds are very different from their counterparts in mammals. The small, compact bird lungs communicate with voluminous, thin-walled *air sacs* and air spaces that extend between the internal organs and even ramify into the bones of the extremities and the skull. This extensive and intricate respiratory system has been considered as an adaptation to flight. We can immediately say, however, that it is not *necessary* for flight, because bats (which have typical

	Bird	Mammal
Lung volume (ml)	29.6	53.5
Tracheal volume (ml)	3.7	0.9
Air sac volume (ml)	127.5	–
Total respiratory system volume (ml)	160.8	54.4
Tidal volume (ml)	13.2	7.7
Respiratory frequency (min^{-1})	17.2	53.5

Table 1.8 Volumes of the respiratory systems of typical birds and mammals of 1 kg body size. [Estimated from data collected by Lasiewski and Calder 1971]

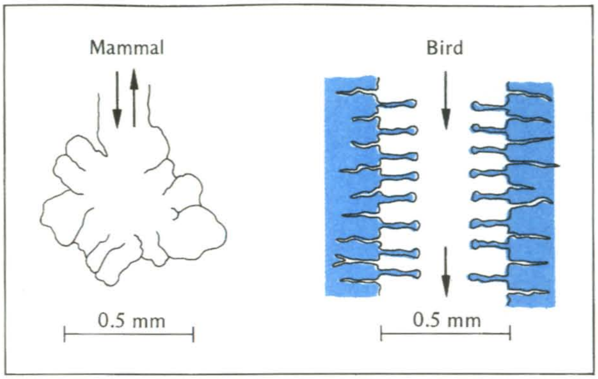


Figure 1.23 The smallest units of the mammalian lung are the saclike alveoli. In the bird lung the finest branches are tubes that are open at both ends and permit through flow of air. [Schmidt-Nielsen 1972]

mammalian lungs) are good fliers and at times even migrate over long distances.

We may imagine that flying birds should have a very high oxygen consumption and that the avian respiratory system should be seen in this light. However, the rates of oxygen consumption of resting birds and mammals of equal body sizes are very similar, and although normal flight requires an 8- or 10-fold increase in oxygen consumption, many mammals are capable of similar increases. Finally, during flight bats have an oxygen consumption very similar to that of birds of the same body mass. Nevertheless, although the avian-type respiratory system is not a prerequisite for flight, it may still have considerable advantages.

The presence of air spaces in the body of a bird can be said to make the bird lighter, but only in a very limited sense. The bird needs a digestive system, a liver, kidneys, and so on, and merely adding large sacs of air to the abdominal cavity does not make the bird any lighter. If we removed this air, or doubled its volume, the bird would still have exactly the same weight to carry during flight. On the other hand, if the marrow of a bone is replaced by an equal volume of air, the bone weighs less. The air-filled bones, therefore, do contribute to making the bird lighter, but the other large air spaces do not.

If we compare the volumes of the respiratory systems of birds and mammals, we find some conspicuous differences (Table 1.8). The lung volume of a typical bird is only a little more than half that of a mammal of the same body size. In contrast, the tracheal volume of a bird is much larger than that of a mammal. This can easily be understood in view of the bird's long neck, but we shall later see that it has other implications as well. The air sacs of a bird are large, several times as large as the lung, and mammals have no air sacs at all. Therefore, the total volume of the respiratory system of a bird is some three times as large as that of a mammal.

The difference between birds and mammals is not restricted to the air sacs; in structure the avian lungs differ radically from those of mammals. In mammals the finest branches of the bronchi terminate in saclike alveoli (Figure 1.23). In birds the finest branches of the bronchial system (known as *parabronchi*) permit through passage of air. Air can thus flow *through* the bird lung and continuously past the exchange surface; in mammals air must flow in and out. This is the most important difference between the respiratory systems of birds and mammals, and it has profound physiological consequences.

To understand how the avian respiratory system

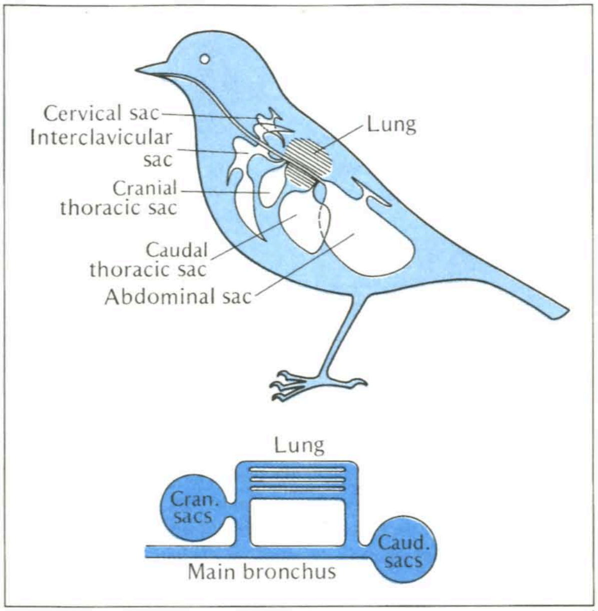
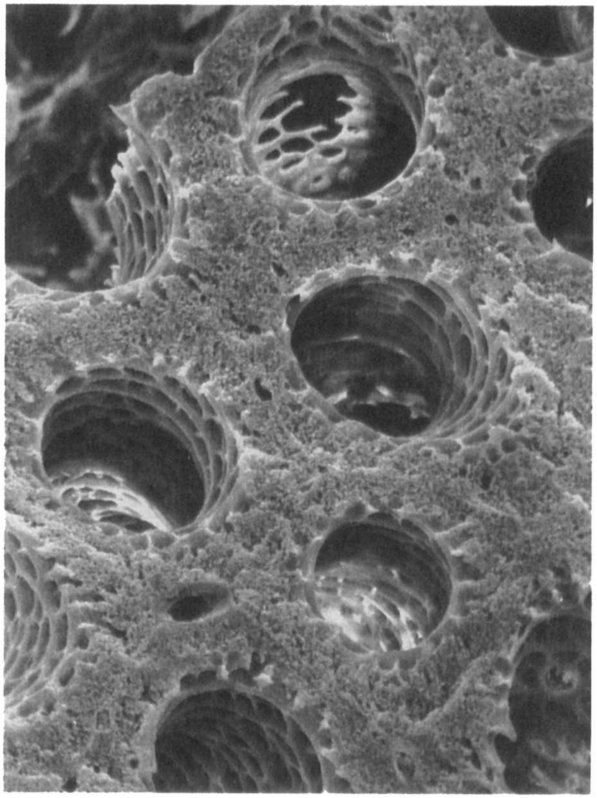


Figure 1.24 The body of a bird contains several large, thin-walled air sacs. The paired lungs are small and located along the vertebral column. The main bronchus, which runs through the lung, has connections to the air sacs as well as to the lung. Below the bird is a diagram of the system, simplified by combining all cranial sacs into one single space and all caudal sacs into another. [Schmidt-Nielsen 1972]



BIRD LUNG In cross section a bird lung shows cylindrical tubes (parabronchi) that allow the unidirectional through flow of air characteristic of bird lungs. The diameter of each tube in this picture, which is from a chick of domestic fowl, is slightly less than 0.5 mm. [Courtesy of Professor H.-R. Duncker, Giessen, Germany]

works, we must know a few additional facts about its complex anatomy; a diagram of the lungs and major air sacs will help (Figure 1.24). It is not necessary to learn the names of all the sacs, particularly as different investigators often use different names that merely confuse the nonspecialist. It is important, however, to know that the air sacs anatomically and functionally form two groups: *a posterior* or *caudal group* that includes the large abdominal sacs, and an *anterior* or *cranial group* that consists of several somewhat smaller sacs.

The trachea divides into two bronchi; each bronchus runs to and then actually through one of the lungs, and terminates in the abdominal sac. The cranial sacs connect to this main bronchus in the anterior part of the lung; the caudal sacs connect to the posterior part of the main bronchus. The main bronchus also connects to the lung, and furthermore, some of the air sacs connect directly to the lung tissue.

Function of the respiratory system

What is the function of the air sacs? Do they function in gas exchange, or do they serve as bellows to move air in and out?

The morphology of the air sacs does not indicate that they have any major role in gas exchange between air and blood. Their walls are thin, flimsy, poorly vascularized, and there are no foldings or ridges to increase the surface area.

A simple experiment that excluded a direct role in gas exchange was made in the last century by a French investigator. He plugged the openings from the large abdominal air sacs to the rest of the respiratory system and then introduced carbon monoxide into the sacs (Soum 1896). Birds are quite sensitive to carbon monoxide, but these birds showed no signs of carbon monoxide poisoning. Therefore, carbon monoxide had not been taken up by the blood from the air sacs. This conclusion can be generalized; it is valid for other gases that have similar diffusion properties – oxygen, for example.

A more plausible hypothesis for the function of the air sacs is that they serve as bellows to move air in and out. As an inspiration begins, there is a simultaneous pressure fall in both the cranial and caudal sacs as they expand (see diagram in Figure 1.24). This means that during inspiration air flows into all sacs but, as we shall see later, not all sacs fill with outside air. During exhalation the pressure in the sacs increases, and air flows out again.

To follow the flow of gas in greater detail, we could use a gas mixture of a composition different from the usual air and follow the movements of this gas through the respiratory system. A convenient gas is pure oxygen, for it is harmless and can easily be measured with an oxygen electrode. For such experiments the ostrich has the advantage that it breathes quite slowly (a single respiration lasts about 10 seconds), and changes in gas composition can therefore be followed readily.

When an ostrich is permitted to inhale a single breath of pure oxygen instead of air, the oxygen shows up in the caudal air sacs toward the end of this breath (Figure 1.25). This must mean that the inhaled oxygen reaches these sacs directly through the main bronchus. In the cranial sacs, on the other hand, the oxygen concentration never increases during the inhalation of oxygen; however, these sacs do expand during inhalation, and this means that they receive air from somewhere else. Toward the end of the second inspiration, when the bird again breathes ordinary air, the oxygen in the cranial sacs begins to increase. This can only mean that the oxygen that now appears has, in the intervening time, been located elsewhere in the respiratory system, presumably in the caudal sacs, and has passed through the lung to reach the cranial sacs.

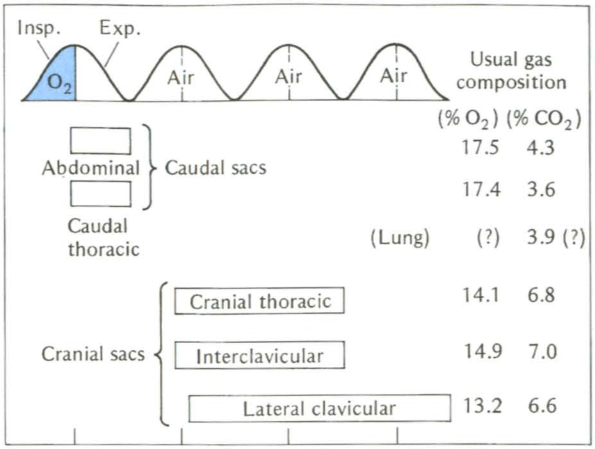


Figure 1.25 When an ostrich inhales a single breath of pure oxygen and then breathes ordinary air, the oxygen acts as a tracer gas. It is first found in the caudal air sacs. Only during the second or third respiratory cycle (indicated at top) does the gas show up in the cranial sacs. Respiratory rate about 6 cycles per minute. The usual gas composition in the air sacs is given at right. [Schmidt-Nielsen et al. 1969]

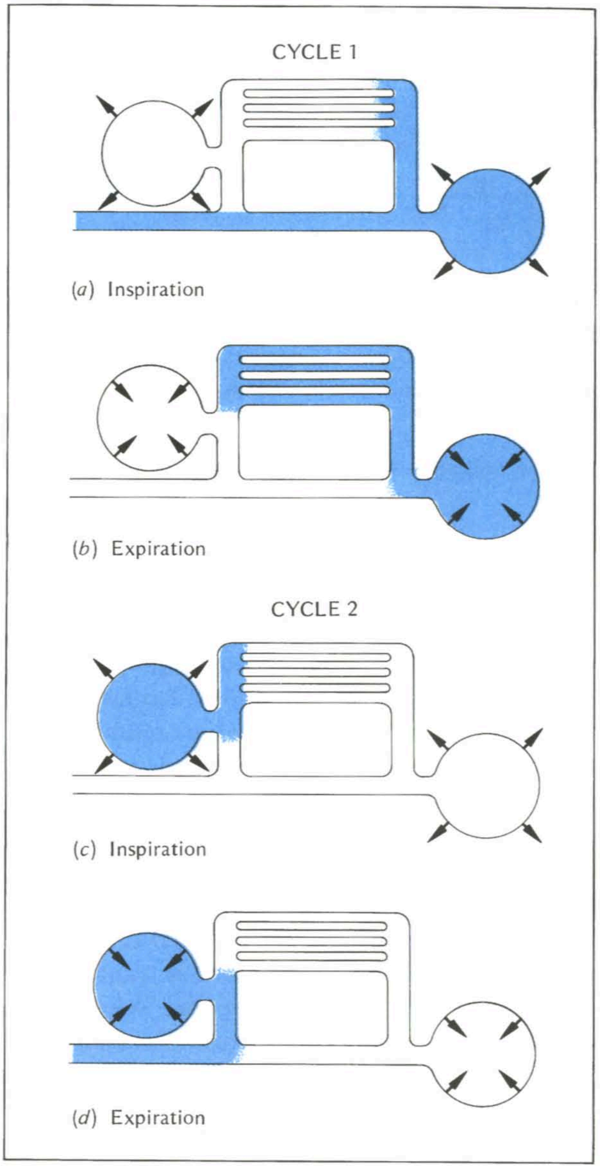
The gas concentrations found in the air sacs are interesting. The caudal sacs contain some 4% carbon dioxide (see Figure 1.25), and relative to atmospheric air the oxygen is depleted by a similar amount, from 21% to about 17%. In the cranial sacs, however, the carbon dioxide concentration is higher, between 6 and 7%, and the oxygen is correspondingly reduced to some 13 to 14%. These differences in gas composition might suggest that the caudal sacs are better ventilated and the cranial sacs contain more stagnant air, which therefore reaches a higher carbon dioxide concentration. This conclusion is not correct.

A marker gas can also serve to determine how rapidly air is renewed in a sac. After introduction directly into a sac, the concentration of the marker decreases stepwise in synchrony with each respiratory cycle, and the rate of washout indicates the extent of air renewal. The time required for the marker gas to be reduced to one-half the initial level can be designated as the *half time.* In the ostrich this half time was between two and five respiratory cycles for both cranial and caudal air sacs; this means that both sets of sacs are about equally well ventilated.

Similar determinations on ducks also gave about equal half times for cranial and caudal sacs (Bretz and Schmidt-Nielsen 1972). Because tracer gas experiments indicate that air flows into the cranial sacs from the lung (their carbon dioxide concentration is consistent with this conclusion), and because their air renewal is high, the evidence indicates that the air sacs serve as a holding chamber for air from the lung, to be exhaled on the next exhalation.

The flow of air can also be determined by placing small probes, sensitive to air flow, in the various passageways. Studies on ducks indicate the flow patterns illustrated in Figure 1.26, which shows how a single bolus of air would flow. During inhalation (*a*) most of the air flows directly to the caudal sacs. Although the cranial sacs expand on inhalation, they do not receive any of the inhaled outside air; instead, they receive air from the lung. On exhalation (*b*), air from the caudal sacs flows into the lung instead of out through the main bronchus. On the following inhalation (*c*), air from the lung flows to the cranial sacs. Finally, on the second exhalation (*d*), air from the cranial sacs flows directly to the outside. Two full respiratory cycles are required to move a single bolus of gas through the respiratory system. This does not mean that the two cycles differ in any way: They are completely alike, each bolus of gas being followed by another similar bolus, in tandem, on the next cycle.

The most notable characteristics of this pattern are that air always flows through the lung from the posterior in the anterior direction and that air moves through the lung during both inhalation and exhalation.



(*a*) Inspiration

(*b*) Expiration

(*c*) Inspiration

(*d*) Expiration

Figure 1.26 The movement of a single inhaled volume of gas through the avian respiratory system. It takes two full respiratory cycles to move the gas through its complete path. [Bretz and Schmidt-Nielsen 1972]

This flow pattern has an important consequence for gas exchange between air and blood that in principle is similar to the countercurrent flow in the fish gill (see Figure 1.7). It allows the oxygenated blood that leaves the lung to have a higher oxygen tension than the oxygen partial pressure in exhaled air. A highly simplified diagram explains this (Figure 1.27). Blood

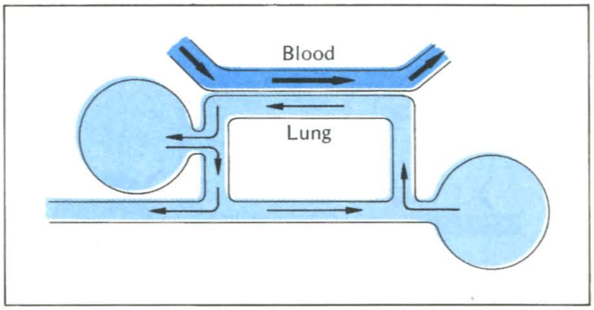


Figure 1.27. Gas exchange in the bird lung. This highly simplified diagram shows the flow of blood and air through the lung, each represented by a single stream with opposite flow directions. This flow pattern permits the oxygenated blood to leave the lung with the highest possible oxygen tension. [Schmidt-Nielsen 1972]

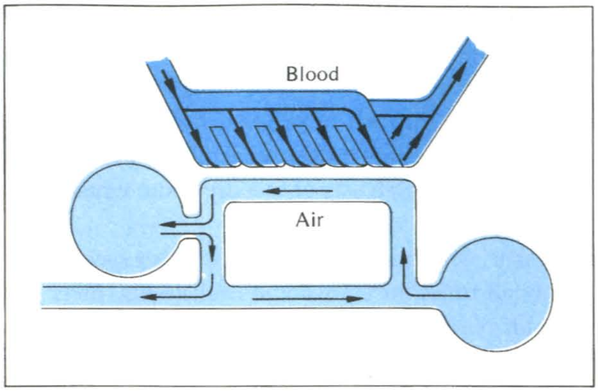


Figure 1.28 The blood in the avian lung does not flow in parallel capillaries, but rather in an irregular, complex network. The simplified diagram above shows that blood leaving the lung is a mixture of blood flowing through different parts of the lung and having different degrees of oxygenation. This pattern can be described as cross-current flow. [Scheid and Piiper 1972]

that is just about to leave the lung (right side of the diagram) is in exchange with air that has just entered the lung as it comes directly from the caudal sacs with a high oxygen partial pressure. As the air flows through the lung (toward the left in the diagram), it loses oxygen and takes up carbon dioxide. All along, this air encounters blood with a low oxygen tension and therefore gives up more and more oxygen to the blood. Due to this type of flow, the blood can become well saturated with oxygen, and yet be able to extract more oxygen from the pulmonary air and deliver more carbon dioxide to it, than is the case in mammals.

The flow of air in the bird lung is in fact not an ideal countercurrent exchange system, but rather a *cross-current* type of flow (Figure 1.28). The result, with regard to arterial gas tensions, is similar to that described above, although a cross-current system is not as effective as a true countercurrent system in achieving maximum advantage in gas exchange.

Altitude. The effectiveness of the unidirectional air flow in the avian lung is particularly important at high altitude. In experiments in which mice and sparrows were exposed to an atmospheric pressure of 350 mm Hg, corresponding to 6100 m or 20 000 ft altitude (slightly less than 0.5 atm), the mice were lying on their bellies and barely able to crawl, while the sparrows were still able to fly (Tucker 1968).

Mice and sparrows have the same body mass, their blood has the same affinity for oxygen, and their metabolic rates are similar, so the difference cannot be explained in terms of their rates of oxygen consumption or the chemistry of their blood. The flow pattern in the bird lung is the most plausible explanation, for it allows blood to take up oxygen from air that has a higher oxygen concentration than would be found in the mammalian system, and in addition, because of the unidirectional and continuous flow through the lung, to extract more oxygen from the air. It is consistent with these experiments that birds in nature have been seen in the high Himalayas, flying overhead at altitudes where mountain climbers can barely walk without breathing oxygen.

Canary song. Many who have listened to the song of a male canary have wondered how it is possible for such a small bird to sing continuously for as long as half a minute, apparently without pausing for breath. How can the bird produce such extended songs with the limited capacity of its respiratory system?

Could it be that the bird produces its song, not only during exhalation as we normally expect, but also during inhalation? This would explain the apparent continuity of the song. Or is the song actually discontinuous, interrupted by periods of inhalation, so short that we normally don't perceive them as pauses?

The answer is that the canary's song is always produced during expiratory air flow in the trachea. It consists of single notes or syllables that are repeated at high rates, each syllable lasting for 11 to 280 milliseconds. Between the syllables or notes are brief silent intervals, lasting from 20 to 35 ms, during which inspiration takes place. In other words, the song of the canary isn't continuous, it consists of extended series of syllables with pauses so brief that we don't notice them (Hartley and Suthers 1989).

RESPIRATION IN EGGS

The problem of supplying oxygen to the growing embryo and chick within the hard shell of a bird's egg forms an intriguing chapter in respiration physiology. Most of the work in this field has been concerned with hens' eggs, but the general principles apply to all birds' eggs, except for differences that result from the enormous differences in size. The smallest eggs, those of hummingbirds, may weigh less than 0.3 g; those of the ostrich weigh over 1 kg. The largest bird eggs known are those of the extinct *Aepyornis*, which average about 10 kg. Thus, there is more than a 30 000-fold difference in weight between the smallest and largest bird egg.

The newly laid egg is a microcosm that contains everything that is needed to produce a living chick, with one exception – oxygen. Therefore the shell must be permeable to oxygen, and as a result it is also permeable to other gases. Water vapor and carbon dioxide therefore are lost during incubation.

The overall changes in a hen's egg during incubation are shown in Figure 1.29. The egg initially weighs 60 g, and during the 21 days of incubation it takes up 6 liters of oxygen. At the same time it loses 4.5 liters of carbon dioxide. As the density of carbon dioxide is higher, the weight of the two gases is almost identical. However, because the shell is permeable, some water evaporates. The amount is 11 liters of water vapor, weighing 8.8 g or 14.7% of the initial egg weight. Just before hatching the 60 g egg has been reduced to 51 g, almost the entire loss being due to evaporation of water. The newly hatched chick that comes out of the egg weighs 39 g, the remaining 12 being shell and some membranes.

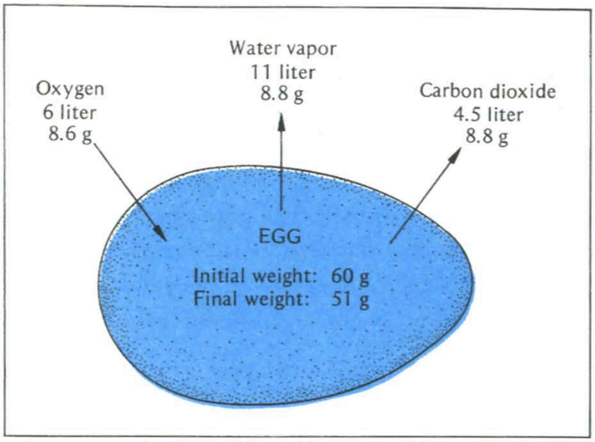


Figure 1.29 During the 21-day incubation period a 60 g hen's egg takes up oxygen while it loses both carbon dioxide and water. At the end of incubation, before the chick hatches, the egg weighs 51 g.

The shell of an egg consists of a hard outer layer of calcium carbonate, which on the inside has two soft membranes, called the outer and the inner shell membrane. The hard shell in much less permeable to gases than the shell membranes. When the egg is first laid, the permeability of the shell with its membranes is low, but it increases several-fold during the first few days after the egg is laid. This increase is correlated with a decline in the water content of the membranes, and most of the resistance to diffusion now resides in the hard shell (Kutchai and Steen 1971).

At the blunt end of the egg is an *air cell* that lies between the inner and outer shell membranes. This air space increases in size during incubation because water is lost from the egg by evaporation.

The hard shell of a typical hen's egg is perforated by about 10 000 pores. Because the surface area of the egg is about 70 cm^2, there is an average of 1.5 pores per square millimeter of shell. The pore diameter is about 0.017 mm, so that the total pore area of the egg is 2.3 mm^2. All gas exchange between the embryo and the surrounding atmosphere must take place through these pores.

The oxygen consumption and the carbon dioxide production increase throughout the incubation period, which lasts about 21 days. Because the diffusion characteristics of the eggshell during the later part of incubation remain constant, or nearly so, there must be a progressive increase in the gradients of gases between the ambient air and the embryo. The steeper gradients are produced by a progressive fall in the oxygen partial pressure within the egg and a concomitant increase in carbon dioxide during incubation (Figure 1.30).

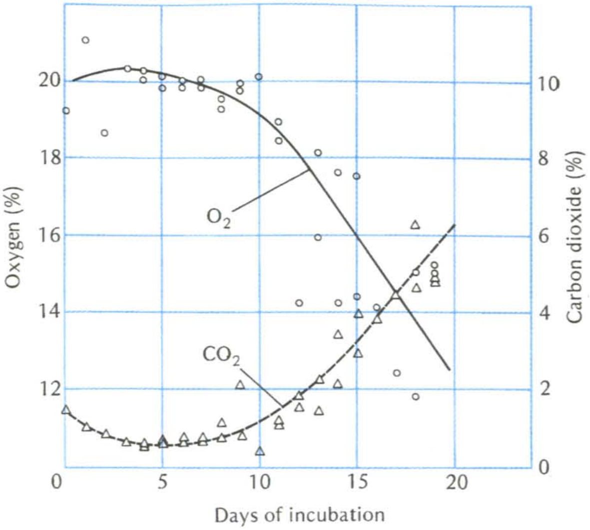


Figure 1.30 As the incubation of a hen's egg progresses, the oxygen concentration in the air cell gradually decreases as the carbon dioxide shows a corresponding increase. [Romijn and Roos 1938]

During the last day of incubation, things change rapidly. About 28 hours before hatching the chick perforates the air cell membrane, lung respiration begins, and the chick rebreathes the gas of the air space (which because of evaporation has increased to about 10 cm^3 in volume). About 12 hours later the chick begins to break through the eggshell, the stage known as *pipping*, and the main barrier to gas exchange is now broken. During the following hours, while the chick struggles to break out completely, pulmonary respiration has taken over the whole task of gas exchange.

At high altitude, where the oxygen pressure is reduced, the oxygen supply to the embryo is severely challenged. This problem was studied in a colony of white leghorns maintained for many years at the White Mountain Research Station in California at 3800 m altitude (barometric pressure = 480 mm Hg, or 64 kPa). When the colony was started, only 16% of the fertile eggs hatched, compared with the usual 90% at sea level. As the colony became established the hatching rate gradually increased and after eight generations reached 60%.

One consequence of a reduced air pressure is an increase in the diffusion coefficient for gases. At 3800 m the increase is slightly more than 1.5-fold, and this increase is beneficial to the delivery of oxygen to the embryo. However, the higher diffusion coefficient at low atmospheric pressure applies also to water vapor, and this heightens the danger of desiccation.

Eggs laid at high altitude are small, and the incubation period is longer than at sea level. The pore area per unit shell surface is decreased, though the thickness of the shell is unchanged. The reduction in pore area in combination with the increased gas diffusion coefficient results in an overall gas conductance that is similar at sea level and at high altitude. We can therefore see that the reduction in total pore area of an egg laid at high altitude is a necessary adaptation because the water loss otherwise would be excessive (Wangensteen et al. 1974).

Do the eggs of birds that are native to high altitude show similar diffusion characteristics? A study of six species that breed at altitudes above 2800 m (9300 feet) shows that the gas conductance of their eggs is significantly reduced as compared with similar species breeding at lower elevations. In this way the lower eggshell conductance compensates for the increased diffusion rates, and thus water loss (Carey 1980).

At very high altitude, however, there must be a compromise between reducing water loss on the one hand and the defense of the required oxygen supply to the embryo on the other (Monge C. et al. 1988).

One group of birds lay eggs that differ from the usual pattern. The mound-building birds of Australia, known as mallee fowl and brush turkeys, place their eggs in huge mounds of *decomposing* vegetation. The birds attend carefully to the mounds, open and rearrange them to maintain a nearly constant temperature of about 37 °C. The eggs hatch after nearly two months and the chicks dig themselves out.

The atmosphere within the mounds is saturated with water vapor and the eggs therefore do not lose water during incubation. However, because of the decomposition the oxygen is as low as 14% and the CO_2 may reach 9%. To admit sufficient oxygen the eggs are thin shelled and have a large pore area, but this is irrelevant to water loss because the air in the mounds is saturated (Seymour et al. 1986).

This information about the mound-building birds has permitted some conclusions about the nesting habits of dinosaurs. Fragments of dinosaur eggs collected in southern France were thinner and had a higher porosity than bird eggs of the same size, and their gas conductance ranged from 8 to 24 times the value for bird eggs. This similarity to the mound-building birds suggests that the dinosaur eggs were incubated under similar conditions of high humidity, probably underground. This conclusion is supported by what we know about the eggs of living reptiles. Those that deposit hard-shelled eggs in locations of high humidity have eggs with conductances several times higher than bird eggs (Williams et al. 1984).

Reptile eggs

The eggs of reptiles are much more variable than bird eggs. Their structure can range from thin, extensible, and membrane-like shells to hard calcareous shells more like bird eggs. These differences are related to the habitat and especially to the humidity conditions where the eggs are laid.

The eggs of egg-laying reptiles can be assigned to three broad categories. The shells of most lizard and all snake eggs are relatively thin and highly extensible. Such eggs are usually placed in a relatively dry environment, and if the environment is moist, they would tend to take up water and increase in size. Such eggs are quite sensitive to the humidity of the environment, and hatchability depends on proper conditions.

In contrast, turtles have somewhat flexible eggshells with a well-defined calcareous layer. They are relatively independent of humidity conditions, which do not unduly affect hatchability.

The eggs of all crocodilians, some turtles, and a few lizards are hard and rigid. These eggs will therefore not swell unduly in a moist environment, such as the nests used by alligators and crocodiles (Packard et al. 1982).

Marine turtles spend almost their entire lives at sea. After they enter the water as hatchlings, only the females will ever again leave the sea, and then only for a brief time to deposit eggs in nests on sandy tropical beaches. A female turtle places a clutch of about 100 eggs in a carefully excavated chamber above the high-tide mark, about 0.5 m below the sand surface. The soft, leathery eggs are round and look like ping-pong balls. After a 60-day incubation period the eggs hatch simultaneously, and the hatchlings collectively dig their way to the beach surface and head for the water.

The soft shell of the turtle egg is much more permeable to gases than is the bird egg shell. This does not matter to the loss of water, for the atmosphere within the turtle's nest is water-saturated, and a high gas permeability is an advantage to the supply of oxygen and loss of carbon dioxide.

What is the supply of oxygen in the turtle's nest when 100 eggs simultaneously consume oxygen and release carbon dioxide? Based on determinations of the metabolic rates of eggs near hatching, the metabolic demand for oxygen of an average clutch of 100 eggs is about 300 to 600 cm^3 oxygen per hour. As a result the oxygen concentration within the nest decreases and establishes a gradient between the gases in the nest and the atmosphere above the beach surface. During the 60-day incubation period the P_{O_2} in the nest gradually decreases from about 150 to between 80 and 100 mm Hg (from about 20 to between 11 and 13 kPa), and the P_{CO_2} at the same time rises to 40 to 60 mm Hg (5 to 8 kPa).

The diffusion characteristics of gases through moist sand (but not wet sand) are sufficient to supply the nest with oxygen at the rate it is used by the clutch of eggs. The spaces between the eggs are not filled with sand, and because diffusion in the gas phase is rapid, the eggs in the center are also adequately supplied with oxygen. In fact, the 100-egg clutch exchanges respiratory gases in a manner quite similar to that of a bird egg, where the diffusion resistance resides in the hard shell. For the turtle nest the diffusion resistance is in the sand, and the respiratory environment for the eggs is always saturated with water vapor. Hence, a highly permeable eggshell is no liability, but rather a necessity.

The characteristics of the nesting beach are very important for the gas exchange and probably for the successful hatching of sea turtle eggs. The similarity between the entire clutch of sea turtle eggs and the single bird egg is striking. The physical characteristics of the beach and the nest chamber dictate the gas exchange and play an important role in explaining why all species of sea turtles lay clutches of about 100 eggs in similar, very carefully constructed nests (Prange and Ackerman 1974; Ackerman 1980).

INSECT RESPIRATION

Terrestrial life poses a continual conflict between the need for oxygen and the need for water. Conditions that favor the entry of oxygen also favor the loss of water. Insects, the most successful terrestrial animals, have a hard cuticle, which is highly impermeable to gases and whose covering wax layer makes it virtually impermeable to water as well. Gas exchange takes place through a system of internal air-filled tubes, the *tracheae*, which connect to the outside by openings called *spiracles* (Figure 1.31). The spiracles usually have a closing mechanism that permits accurate control of the exchange between the air in the tracheal system and the outside atmosphere.

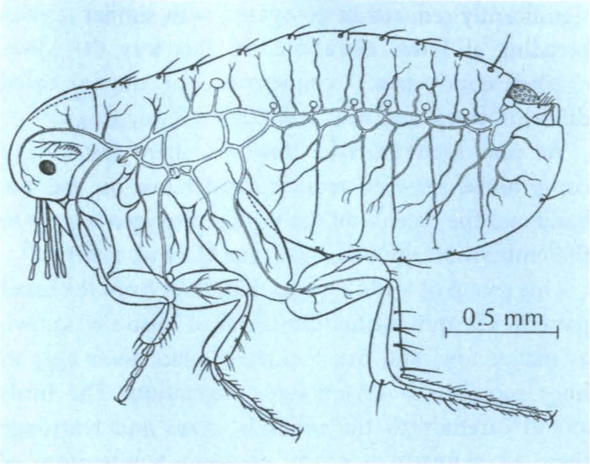


Figure 1.31 The tracheal system of insects consists of fine air-filled tubes, *tracheae*, that convey respiratory gases to and from all parts of the body. This drawing shows only the main branches of the tracheal system of a flea. The openings to the outside air, the *spiracles*, are indicated by the row of small circles along the side of the body. [Wigglesworth 1972]

The tracheae branch and ramify and extend to all parts of the body. The finest branches, the *tracheoles*, may be as little as 0.5 μm in diameter and can extend into individual cells, such as muscle fibers. The tracheoles cannot be much smaller, for diffusion is impeded when their size approaches the mean free path of molecules in air (the average distance a molecule travels before colliding with another molecule).

One question is why capillary action does not make these fine capillaries fill with liquid. The capillary force depends on the contact angle between liquid and wall, and because the inside of the tracheoles is covered with a nonwettable waxy substance, the contact angle will exceed 90°. Therefore, instead of liquid being pulled in, liquid will actually be forced out of the tubes (Denny 1993).

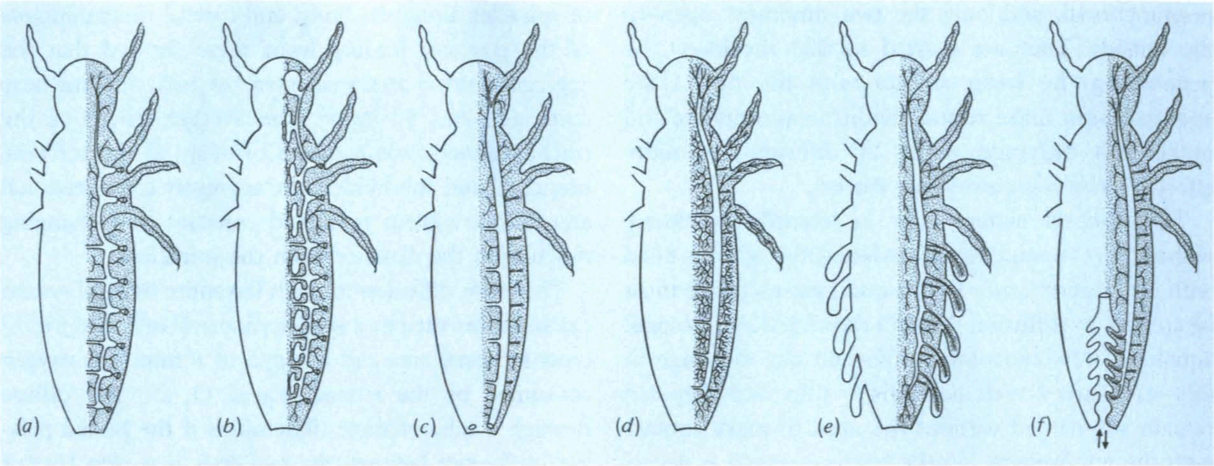


Figure 1.32 The basic pattern of the insect tracheal system (a) may be modified into a variety of other patterns (*b–f*). For details, see text. [Wigglesworth 1984]

The tracheal system conveys oxygen directly to the tissues and carbon dioxide in the opposite direction. This makes insect respiration independent of a circulatory system. Insect blood has no direct role in oxygen transport, in contrast to the role of blood in vertebrates. The comparison with vertebrates is by no means irrelevant, for the rates of oxygen consumption of a large moth and a hummingbird in flight are similar; the oxygen supply mechanisms, however, differ radically.

We cannot conclude that the circulatory system in insects is unimportant; it has many other functions. One role is obvious: During flight the muscles have a high power output, and while oxygen is provided through the tracheal system, fuel must be supplied by the blood.

The tracheal system

Tracheal systems are suitable primarily for respiration in air and must have evolved in air. Insects that secondarily have become aquatic have in principle maintained air respiration, but their tracheal systems have many interesting modifications that make them suitable for gas exchange in water.

Most tracheal systems show variations from a basic pattern in which there characteristically are 12 pairs of spiracles, 3 pairs on the thorax and 9 on the abdomen. Often there are fewer spiracles, and there may be none. Some of the possible variations are shown in Figure 1.32.

In a typical pattern the larger tracheae connect so that the system consists of tubes that all interconnect (Figure 1.32*a*). This pattern is commonly modified by the addition of enlarged parts of the tracheae, or air sacs, which are compressible (*b*). The volume of these sacs can be altered by movements of the body, thus pumping air in and out of the tracheal system. This is important, for in large and highly active insects diffusion alone does not provide sufficient gas exchange. The tracheae themselves have internal spiral ribs and are rather incompressible; the large air sacs are therefore necessary for ventilation. It is possible to achieve a unidirectional stream of air through the larger tracheal stems by having the spiracles open and close in synchrony with the respiratory movements, but out of phase with each other.

A modification characteristic of many aquatic insects is shown in Figure 1.32*c*. Most of the spiracles are nonfunctional, and only the two hindmost open to the outside. They are located so that the insect, by penetrating the water surface with the tip of the abdomen, can make contact with the atmosphere and obtain gas exchange, either by diffusion, or more effectively, by respiratory movements.

The tracheal system may be completely closed, without any opening to the surface, although it is filled with air (Figure 1.32*d*). In this event gas exchange must be entirely by diffusion through the cuticle. Many small aquatic insects can obtain sufficient gas exchange in this way; their cuticle is relatively thin, and they can remain submerged without the need to make contact with the atmosphere. Yet the tracheal system is necessary for gas transport inside the animal because diffusion through the tissues would be too slow. As we saw earlier, diffusion of oxygen in air is some 300 000 times faster than in water; this clearly points out the advantage of a tracheal system in conveying gases when the circulation of blood is unsuited for this purpose.

A further development on the same theme again represents an aquatic insect (Figure 1.32*e*). The closed tracheal system extends into abdominal appendages or "gills", which, with their relatively large surface and thin cuticle, permit effective gas exchange between the water and air within the tracheal system. Such tracheal gills are found, for example, in mayfly larvae (Ephemeroptera).

Another variation is shown in Figure 1.32*f*. The tracheal gills are located within the lumen of the rectum, and ventilation takes place by moving water in and out of the rectum. This system is found in some dragonfly larvae. These larvae may also use the water in the rectum for locomotion by expelling it rapidly, thus moving by jet propulsion like squid and octopus.

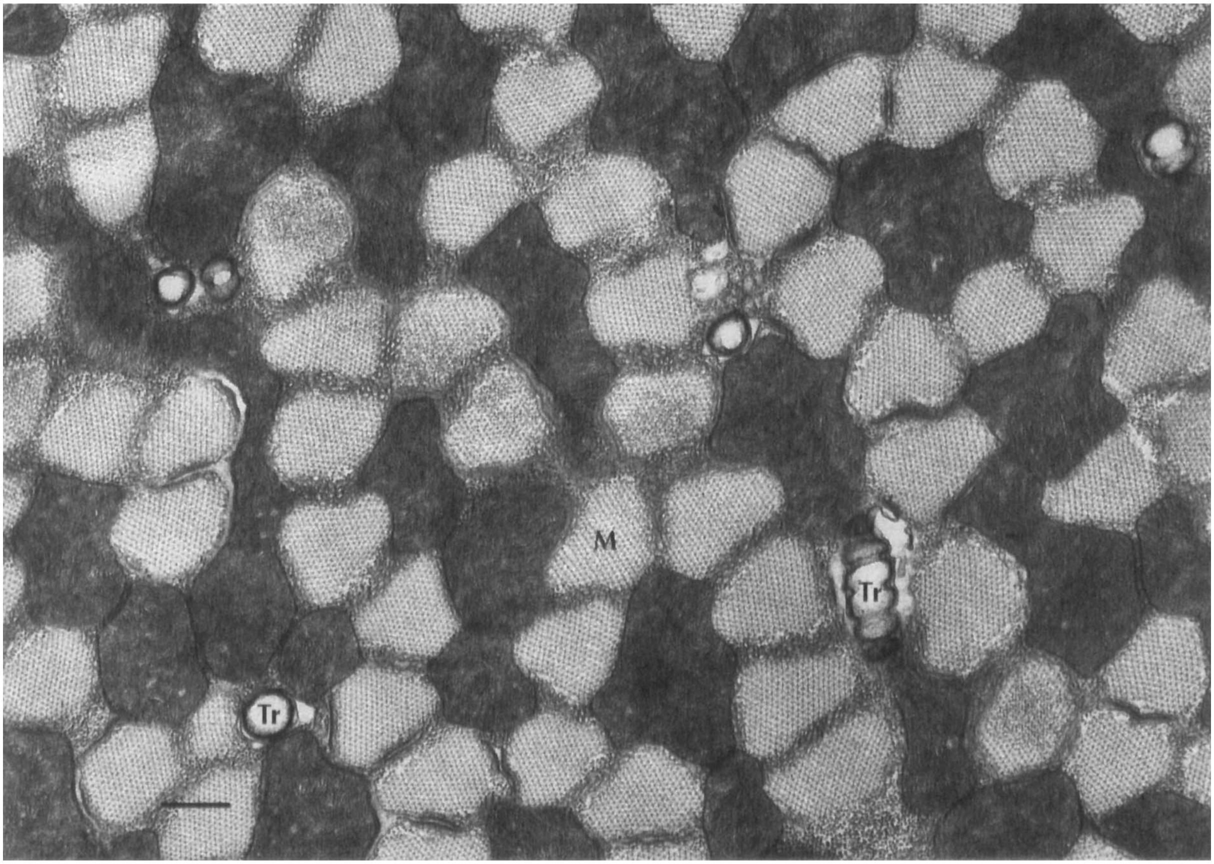
Diffusion and ventilation

Diffusion alone suffices for gas exchange within the tracheal system of many small insects and in relatively inactive large insects. As an example we will use a large wood-boring larva of the genus *Cossus* (goat moth), which was studied by Krogh (1920). This larva weighs about 3.4 g and is 60 mm long. There are nine pairs of spiracles along the body, and careful measurements of the tracheae leading from these showed that the aggregate cross-sectional area of all the tracheae combined was 6.7 mm^2. The average length of the tracheal system was 6 mm. Curiously, as the tracheae branched and subdivided, the aggregate cross sectional area of the system remained constant, not changing much with the distance from the spiracles.

Therefore, diffusion through the entire tracheal system can be represented by a single cylindrical tube of 6.7 mm^2 cross-sectional area and a length of 6 mm. The oxygen consumed by the animal, 0.3 μl O_2 s^{-1}, will diffuse through a tube of these dimensions if the partial pressure difference between the two ends is 11 mm Hg (1.5 kPa). This means that, with an oxygen pressure in the atmosphere of 155 mm Hg (20.7 kPa), the tissues could still have an oxygen tension of 144 mm Hg (19.2 kPa). Obviously, for the *Cossus* larva an adequate oxygen supply is secured by diffusion alone, even if the metabolic rate during activity should be increased several-fold.

Intuitively it may seem that the diffusion through 6 mm of air would be slow, but because the diffusion of oxygen in air is 300 000 times faster than in water, the diffusion through 6 mm of air is as fast as the diffusion through a water layer of 0.02 μm. The greatest barrier to oxygen reaching the tissues is therefore likely to be between the finest branches of the tracheoles and the cells. In very active tissues, such as insect flight muscles, electron micrographs reveal that the tracheoles are as close as 0.07 μm to a mitochondrion.

A quantitative consideration of the branched tracheal system gives information about another aspect of gas exchange. As the tracheae divide and subdivide, the aggregate wall area of the system increases. In the *Cossus* larva the largest tracheae are about 0.6 mm in diameter and the finest tracheoles 0.001 mm. The total cross-sectional area of the tubes remains constant, and the wall area of the tracheoles therefore increases to 600 times that of an equal length of the largest tracheae. Thus, the reduction in diameter alone increases the wall surface area 600-fold. This immediately tells us that virtually the entire area available for gas exchange is in the finest branches. Consider now



INSECT TRACHEOLES Tracheoles in the tymbal muscle of a cicada (*Tibicen* sp.). The tracheoles (Tr) are cut in cross section, except for one which is cut tangentially and shows the spirally ribbed wall. The diameter of these tracheoles is about 0.5 μm. The distance between the two labeled tracheoles is about 6.5 μm (i.e., about the diameter of a human red blood cell). The light areas (M) are muscle fibers in cross section; the dark areas are mitochondria. The bar in the lower left represents 1 μm. [Courtesy of David S. Smith, University of Miami]

that the wall thickness in the tracheoles is less than one-tenth of the wall thickness of the large tracheae, and it becomes evident that diffusion through the walls of the larger branches must be insignificant.

The spiracles

The openings of the tracheal system to the outside, the spiracles, are highly complex structures that can be opened or closed to allow a variable amount of gas exchange. Their accurate control helps impede the loss of water.

The spiracles open more frequently and more widely at high temperature and when there is increased activity, in accord with the increased need for oxygen. The spiracles do not necessarily all open simultaneously; they are under control of the central nervous system, and out-of-phase opening and closing permit the control of air flow through the tracheal system.

The ventilation of the tracheal system, and especially the function of the spiracles, is influenced by both carbon dioxide and lack of oxygen. Carbon dioxide seems to be a primary stimulus for opening of the