All organisms use diffusion to exchange substances such as food, waste, gases and heat with their surroundings.

**Reminder:** the rate at which a substance can diffuse is given by **Fick's Law:**

\[
\text{Rate of diffusion} \propto \text{surface area} \times \text{concentration difference} \div \text{Distance}
\]

So the rate of exchange of substances depends on the surface area of the organism that's in contact with the surroundings and on its metabolic rate. It is the organism’s cells that require the materials so the total demand is proportional to its volume. Therefore the ability to meet the requirements depends on the surface area to volume ratio (SA/Vol ratio). As organisms get bigger their volume increases by the cube of their size, whilst their surface area increases by the square of their length, so volume increases much faster than surface area.

This can be seen with some simple calculations for different-sized organisms. For ease of calculation, we’ll assume the organisms are cube shaped! The surface area of a cube with length of side \( L \) is \( L \times L \times 6 \), while its volume is \( L \times L \times L \) (i.e \( L^3 \)).

<table>
<thead>
<tr>
<th>Organism</th>
<th>Length</th>
<th>SA (( \text{m}^2 ))</th>
<th>Vol. (( \text{m}^3 ))</th>
<th>SA / Vol</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacterium</td>
<td>1( \mu \text{m} )</td>
<td>( 6 \times 10^{-12} )</td>
<td>( 10^{-18} )</td>
<td>6,000,000:1</td>
</tr>
<tr>
<td>Amoeba</td>
<td>100 ( \mu \text{m} )</td>
<td>( 6 \times 10^{-8} )</td>
<td>( 10^{-12} )</td>
<td>60,000:1</td>
</tr>
<tr>
<td>Housefly</td>
<td>10 mm</td>
<td>( 6 \times 10^{-4} )</td>
<td>( 10^{-6} )</td>
<td>600:1</td>
</tr>
<tr>
<td>Dog</td>
<td>1 m</td>
<td>( 6 \times 10^{0} )</td>
<td>( 10^{0} )</td>
<td>6:1</td>
</tr>
<tr>
<td>Whale</td>
<td>100 m</td>
<td>( 6 \times 10^{4} )</td>
<td>( 10^{6} )</td>
<td>0.06:1</td>
</tr>
</tbody>
</table>

So as organisms get bigger their **surface area/volume ratio gets smaller**.

- **Bacteria are all surface** with not much inside, while **whales are all insides** without much surface, so:
  - **Bigger organisms have more difficulty** in exchanging materials with their surroundings.

Organisms also need to exchange heat with their surroundings, so large animals have an advantage in having a small surface area/volume ratio: they lose less heat than small animals. Large mammals keep warm quite easily and don't need much insulation or heat generation. That is why the biggest bears (Polar) and penguins (Emperor) are those found at the poles.

**Small mammals and birds lose their heat very readily, so need a high metabolic rate** in order to keep generating heat, as well as thick insulation. Thus large mammals can feed once every few days while small mammals must feed continuously – this also explains why African elephants have bigger ears than Indian elephants – they need to lose more heat. Human babies also lose heat more quickly than adults, which is why they need woolly hats.
**Systems that increase the rate of exchange**

Fick's law shows that for a fast rate of diffusion you must have a **large surface area**, a **small distance** between the source & the destination, and maintain a **high concentration gradient**. All large organisms have developed systems that are well-adapted to achieving these goals, as this table shows:

<table>
<thead>
<tr>
<th>SYSTEM</th>
<th>LARGE SURFACE AREA</th>
<th>SMALL DISTANCE</th>
<th>CONCENTRATION GRADIENT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human lungs</td>
<td>600 million alveoli with a total area of 100m²</td>
<td>each alveolus = 1 cell thick</td>
<td>constant ventilation replaces the air</td>
</tr>
<tr>
<td>Fish gills</td>
<td>feathery filaments with secondary lamellae</td>
<td>lamellae = 2 cells thick</td>
<td>water pumped over gills in counter-current to blood</td>
</tr>
<tr>
<td>Leaves (tree)</td>
<td>- SA of leaves =200m²;</td>
<td>gases diffuse straight into leaf cells</td>
<td>wind replaces air round leaves</td>
</tr>
<tr>
<td></td>
<td>- SA of spongy cells inside leaves = 6000m²</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*For comparison, a tennis court has an area of 250 m² and a football pitch has an area of about 5000 m².*

Gas exchange takes place at a **respiratory surface** - a boundary between the external environment and the interior of the body. For simple **unicellular organisms the respiratory surface is the cell membrane**, but for large organisms it is part of specialised organs like lungs, gills or leaves.

This name can cause problems - in biology the word "respiration" means cellular respiration (ATP generation inside cells), however sometimes (such as here) it can also refer to breathing, which is what most non-biologists mean by it anyway.

**Gases cross the respiratory surface by diffusion**, so from Fick's law we can predict that respiratory surfaces must have:
- a **large surface area**
- a **thin permeable surface**
- a **moist exchange surface**

Many also have
- a way of **maximising the diffusion gradient** by replenishing the source and/or sink.

We shall examine how these requirements are met in the gas exchange systems of humans, fish, insects and plants.
Human Breathing System

In mammals the gas exchange surfaces are the **lungs**, which develop in the embryo from the gut wall - which relates us to some fossil fish! The **larynx** is formed from **cartilage** which formed the gills of our fossil ancestors. It is connected to the **trachea** - a flexible tube held open at all times by incomplete rings of cartilage. The trachea divides into the left and right **bronchi** which then enter the lungs and continue to divide forming the narrower **bronchioles**, which are surrounded by circular smooth muscle fibres. At the ends of the bronchioles are groups of **alveoli** or **air-sacs**. **It is in the alveoli that gas exchange actually occurs.**

The lungs have the typical features required by an efficient gas exchange system:

- a **large surface area** (about the area of a doubles tennis court);
- a **short diffusion pathway** (only two layers of cells from the alveolar air to the blood);
- **high concentration gradients** (maintained by ventilation and flow of blood in the capillaries);
- a **gas permeable surface** (the moist surface of the alveoli allow gases to dissolve and then diffuse through the cells).

The actual respiratory surface is the walls of the **alveoli** inside the lungs:

1. An average adult has about 600 million alveoli, giving a total surface area of about 100m², so the area is huge.
2. The walls of the alveoli are composed of a single layer of flattened **epithelial cells**, as are the walls of the capillaries, so **gases need to diffuse through just two thin cells**.
3. The alveoli walls are kept moist by water diffusing from the surrounding cells. **Oxygen dissolves in this water** before diffusing through the cells into the plasma, where it is taken up by haemoglobin in the red blood cells. The water also contains a soapy **surfactant** which reduces its surface tension and stops the alveoli collapsing. The alveoli also contain phagocytes to kill any bacteria that have not been trapped by the mucus.

4. The steep concentration gradient across the alveoli wall is maintained in two ways: by blood flow on one side and by air flow on the other side. This means that **oxygen can diffuse down its concentration gradient** from the air to the blood, while at the same time **carbon dioxide can diffuse down its concentration gradient** from the blood to the air.

The flow of air in and out of the alveoli is called **ventilation** and has two stages: **inspiration** (or inhalation) and **expiration** (or exhalation). Lungs are not muscular and cannot ventilate themselves, but instead the whole **thorax** moves and changes size, due to the action of two sets of muscles: the **intercostal muscles** and the **diaphragm**.
Inspiration
- The **diaphragm contracts** and flattens downwards
- The **external intercostal muscles contract**, pulling the ribs up and out
- Therefore the **volume of the thorax increases** (and so the lung and alveoli volume)
- this **decreases the air pressure** in the alveoli, so
- **air flows in** to equalise the pressure

Normal expiration
- The **diaphragm relaxes** and curves upwards
- The **external intercostal muscles relax**, allowing the ribs to fall
- Therefore the **volume of the thorax decreases** (and so the lung and alveoli volume)
- this **increases the air pressure** in the alveoli, so
- **air flows out** to equalise the pressure

Forced expiration
- The **abdominal muscles contract**, pushing the **diaphragm upwards**
- The **internal intercostal muscles contract**, pulling the ribs downward
- This gives a larger and faster expiration, used in exercise

These movements are transmitted to the lungs via the **pleural sac** surrounding each lung. The outer membrane is attached to the thorax and the inner membrane is attached to the lungs. Between the membranes is the **pleural fluid**, so if the thorax moves, the lungs move too. The alveoli are elastic and collapse if not held stretched by the thorax (as happens in stab wounds).
Fish

Gas exchange is more difficult for fish than for mammals because the concentration of dissolved oxygen in water is less than 1%, compared to 20% in air. Fish have developed specialised gas-exchange organs called gills, which are composed of thousands of filaments. The filaments in turn are covered in feathery lamellae which are only a few cells thick and contain blood capillaries. This structure gives a large surface area and a short distance for gas exchange. Water flows over the filaments and lamellae, and oxygen can diffuse down a concentration gradient the short distance between water and blood, whilst CO₂ diffuses in the opposite direction, also down its concentration gradient. Each gill is covered by a muscular flap (the operculum) on the side of a fish's head. The gills are so thin that they cannot support themselves without water, so if a fish is taken out of water after a while the gills will collapse, the SA/Vol ratio falls, and the fish suffocates.

Fish ventilate their gills to maintain the gas concentration gradient. Unlike mammals and birds with their ‘push-pull’ system of breathing, fish continuously pump water over their gills by moving their mouth and opercula, sucking in water from in front of the fish, passing it over the gills and then expelling the ‘stale’ water behind. The opercular valve ensures the one-way flow that the high density of water requires.

The gill lamellae are arranged as a series of flat plates sprouting from the gill arch. On their upper and lower surfaces there are many thin vertical flaps which contain blood capillaries. The blood flows through these capillaries in the opposite direction to the flow of water over the gills. This is called a counter-current flow system and gives a highly efficient diffusion pathway since as the blood flows along and picks up oxygen it meets water which always has a greater oxygen content than itself and the diffusion of oxygen into the blood will be maintained.

Counter-current flow

As the blood flows in the opposite direction to the water, it always flows next to water that has given up less of its oxygen. In this way, the blood is absorbing more and more oxygen as it moves along. Even as the blood reaches the end of the lamella and is 80% or so saturated with oxygen, it is flowing past water which is at the beginning of the lamella and is 90 or 100% saturated. This ensures that the maximum possible gas exchange occurs – it is a very ‘efishent’ system (ho ho ho!)

Consider the diagram (left). The left system shows parallel flow and the right shows counter-current flow. The numbers refer to the concentration of a material dissolved in the flowing solutions and the small arrows indicate diffusion. Notice that with parallel flow the diffusion process stops once the concentration gradient is equalised whereas with counter-current flow this does not occur and more material is absorbed from the water.
The detailed structure of the fish gill is shown (right), where the **continuous** flow of water from front to back runs counter to the direction of blood flow in each lamella, thus maximising gas exchange.

Gills in marine fish are also responsible for the secretion of salt, whilst **all** fish gain or lose very large volumes of water by osmosis through their gills; marine fish thus produce very little urine, whilst freshwater fish produce copious quantities – despite having bodies covered with mucilage to reduce water uptake.

Counter-current flow systems are found in many biological structures, for example the kidney, liver and the blood vessels in the legs of penguins and polar bears (see left).
**Insects**

In insects the *waterproof and gas-proof exoskeleton* (which made life on land possible) means that insects had to evolve a separate gas exchange system called the *tracheal system*. Unlike vertebrate systems, this gives every insect cell a *continuous* airline to the atmosphere. Each segment of the insect (apart from the head) has a pair of lip-like openings called *spiracles*, which lead to a tree-like series of tubes called *tracheoles* which repeatedly divide until, finally, their numerous microscopic ends penetrate into individual body cells.

The *spiracles can be closed to prevent loss of water* through the tracheae and opened when greater respiration is needed, and by contracting muscles between each body segment the insect can compress the tracheae and so pump gases in and out of its body.

Some insects have further adaptations, making this system even more efficient - by opening and closing the spiral valves in a particular order it is possible for the insect to suck air into the tracheal system at one end of the body and to circulate the air through the system and pass it out at the other end of the body. It must be remembered that insects generally have a small volume and therefore are in great danger of desiccation, so control of gas intake and release from the tracheal system is most important.

A further refinement is that, in response to changes in water potential, water can leave the body cells and fill the trachea, thus reducing its effective surface area when asleep or dormant. This water leaves the trachea, again by osmosis, when the insect is most active, producing the maximum respiratory surface when required.
Plants

All living (NB xylem is dead) plant cells respire all the time, and plant cells containing chloroplasts also photosynthesise when illuminated, so plants also need to exchange gases. The main gas exchange surfaces in plants are the spongy mesophyll cells in the leaves. Leaves, of course, have a huge surface area, and the irregular-shaped, loosely-packed spongy cells increase the area for gas exchange still further. You are expected to know leaf structure in the detail shown in the diagram:

Gases enter the leaf through stomata - usually in the lower surface of the leaf. Stomata are enclosed by guard cells that can swell up and close the stomata to reduce water loss. The gases then diffuse through the air spaces inside the leaf, which are in direct contact with the spongy and palisade mesophyll cells. Plants do not need a ventilation mechanism because their leaves are exposed to the air, so the gas immediately surrounding them is constantly being replaced in all but the calmest of days (or in a greenhouse). In addition, during the hours of daylight photosynthesis increases the oxygen concentration inside the leaf, and decreases the carbon dioxide concentration. This increases the concentration gradients for these gases, increasing diffusion rate.

The palisade mesophyll cells are adapted for photosynthesis. They have a thin cytoplasm densely packed with chloroplasts, which can move around the cell - by cyclosis - to ensure that every chloroplast receives the same exposure to light. The palisade cells are also closely packed together in rows to maximise light collection, and in 'shade plants' there may be two rows of palisade cells.

The spongy mesophyll cells are adapted for gas exchange. They are loosely-packed with large intercellular air spaces where gases can readily diffuse. They have fewer chloroplasts than palisade cells, so carry out less photosynthesis.