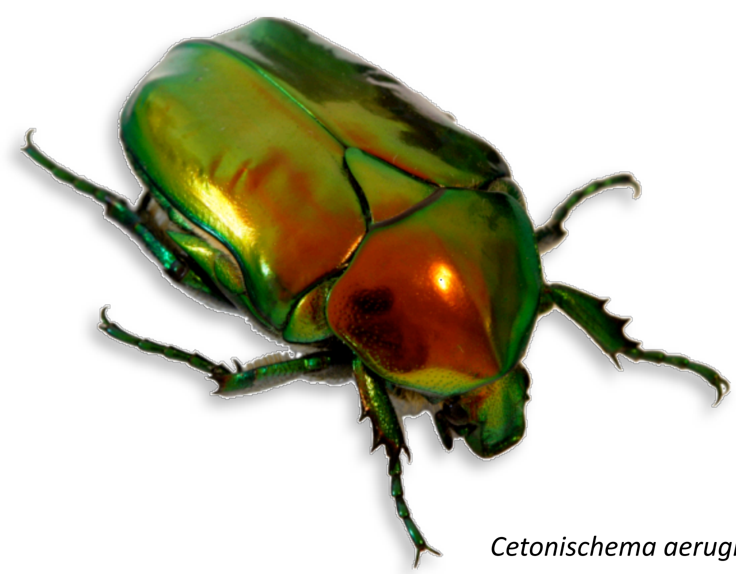
Insect Respiration

Philip G. D. Matthews



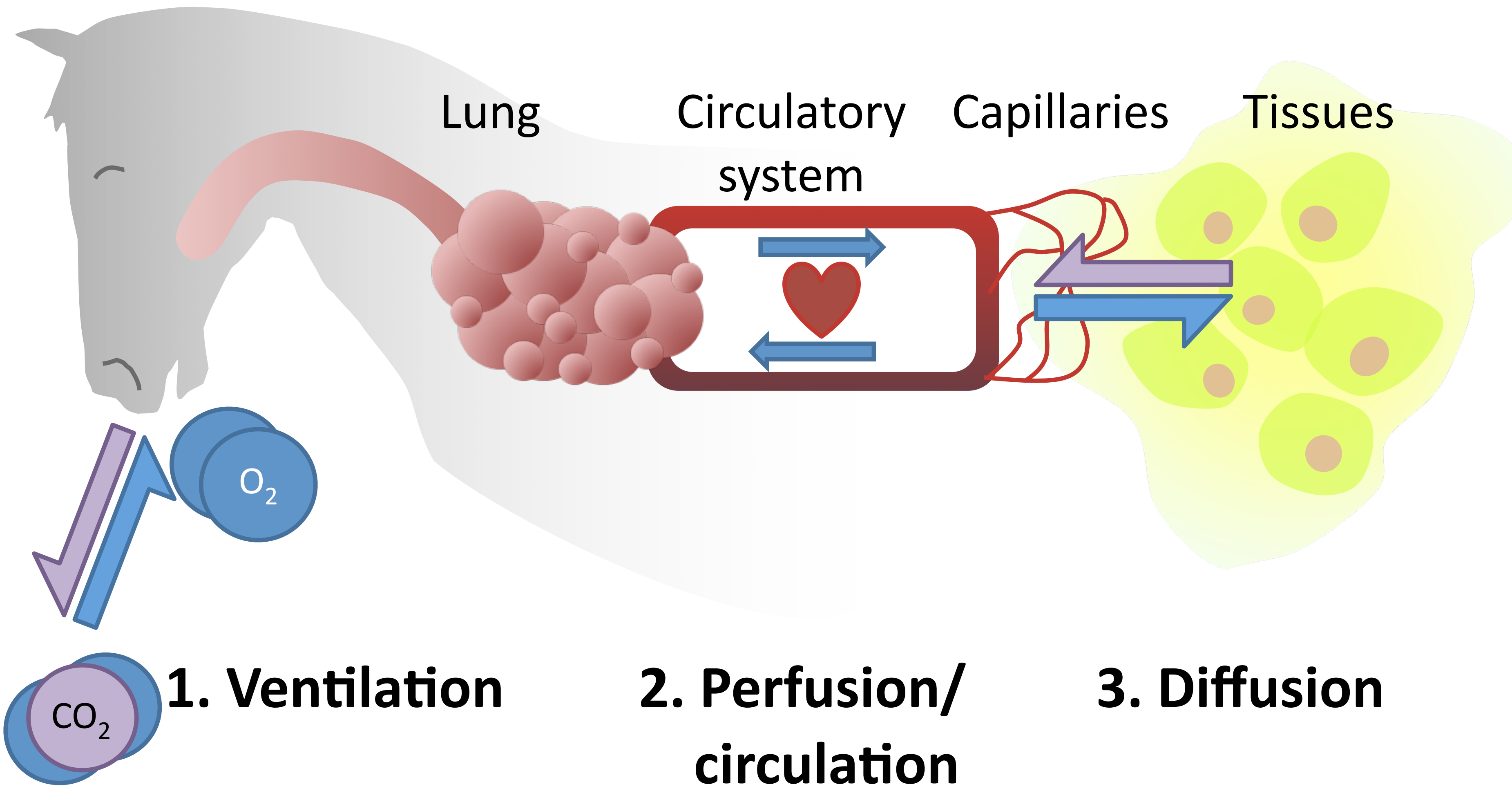
Cetonischema aeruginosa

Insect Respiration

- Outcomes:
  - Be able to identify the different parts of the tracheal system
  - Understand how insects exchange oxygen and carbon dioxide between their tissues and their environment

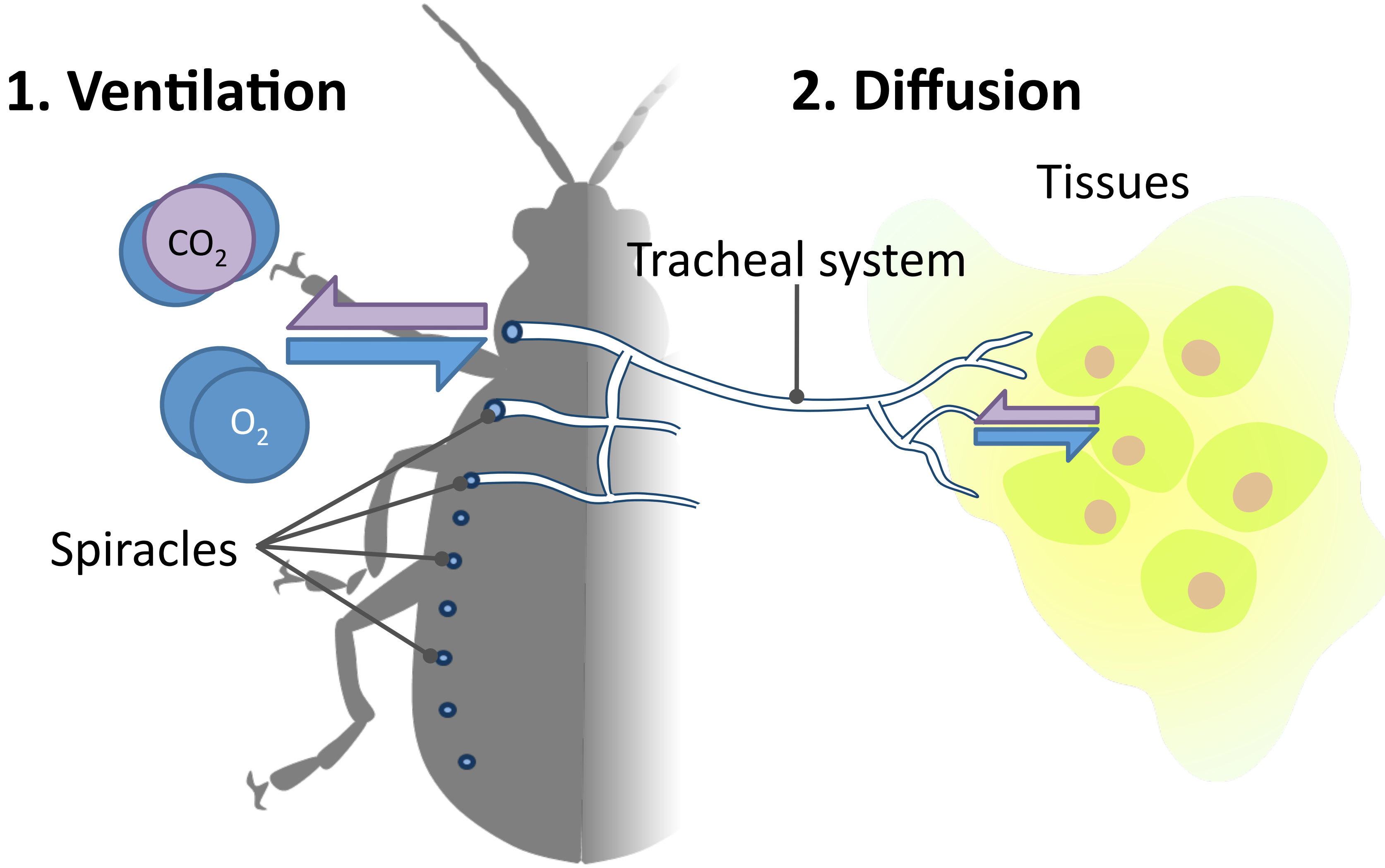
Hi. Welcome to this mini-lecture on insect respiration. This talk will cover the structure and function of the insect's respiratory system. It will cover both the anatomy of the insect's respiratory system and the processes insects use to obtain sufficient amounts of oxygen from the atmosphere while eliminating carbon dioxide

Respiratory system: Vertebrate



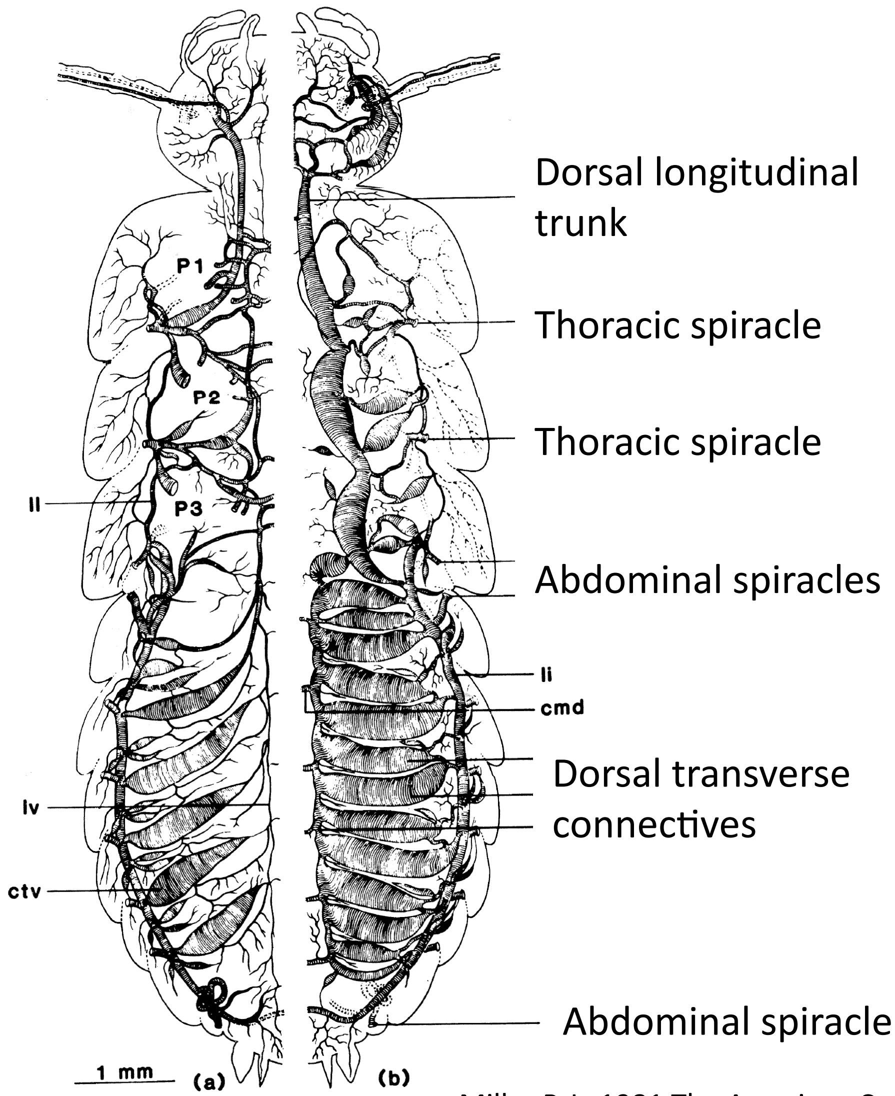
Before we get to insects, let's start by looking at how respiration works in something we are all familiar with – a vertebrate. Firstly, the task of any respiratory system is to supply oxygen to the various tissues in the body, while at the same time removing carbon dioxide. In a vertebrate, the exchange of oxygen and carbon dioxide with the environment can be divided into three parts. First, ventilation, where the animal's gas exchange organ, in this case the lungs, are ventilated with atmospheric air. Blood containing a respiratory pigment, in this case haemoglobin, is loaded with oxygen as it passes through the lung while releasing carbon dioxide it has carried form the tissues. From the lungs the blood is then actively circulated around the body by the heart through blood vessels. As blood moves through the capillaries, it unloads its oxygen which then diffuses across the walls of the capillaries to the tissues where it is consumed within the respiring cells. So there are three main steps to get oxygen in and CO2 out: Ventilation of a gas exchange organ, perfusion of a circulatory system and finally diffusion from the circulatory system to the respiring tissues

Respiratory system : Insect



Now let's look at an insect's respiratory system. Firstly, you can see that the insect doesn't have lungs, or a circulatory system which pumps blood containing haemoglobin. Instead what you find is a network of silvery air-filled tubes running throughout all parts of the insects body. These air-filled tubes comprise the tracheal system, and they open to the atmosphere through holes in the cuticle called spiracles. The air-filled tracheae are large near the spiracles, but they branch and ramifying into smaller and smaller tubes within the insect. The finest branches of the tracheal system are called the tracheoles, and they are the tips of the tracheal tree: they are blind ending and lie in among the tissues. So you can see that the insect respiratory system allows oxygen and carbon dioxide to be exchanged with the atmosphere through their spiracles, while the tracheal system provides an air-filled pathway for the movement of gases from the spiracles to the tips of the tracheoles in among the tissues. This arrangement is quite different to that of a vertebrate as it allows oxygen uptake and carbon dioxide exchange to occur without needing a circulatory system or respiratory pigments like haemoglobin. It is sort of like oxygen is being delivered "whole-sale" without the middle-man of a circulatory system.

The tracheal system



Miller P. L. 1981 The American Cockroach

Components of the tracheal system:

- Spiracles
- Tracheae
- Tracheoles
- Air sacks (expanded, soft-walled tracheae)

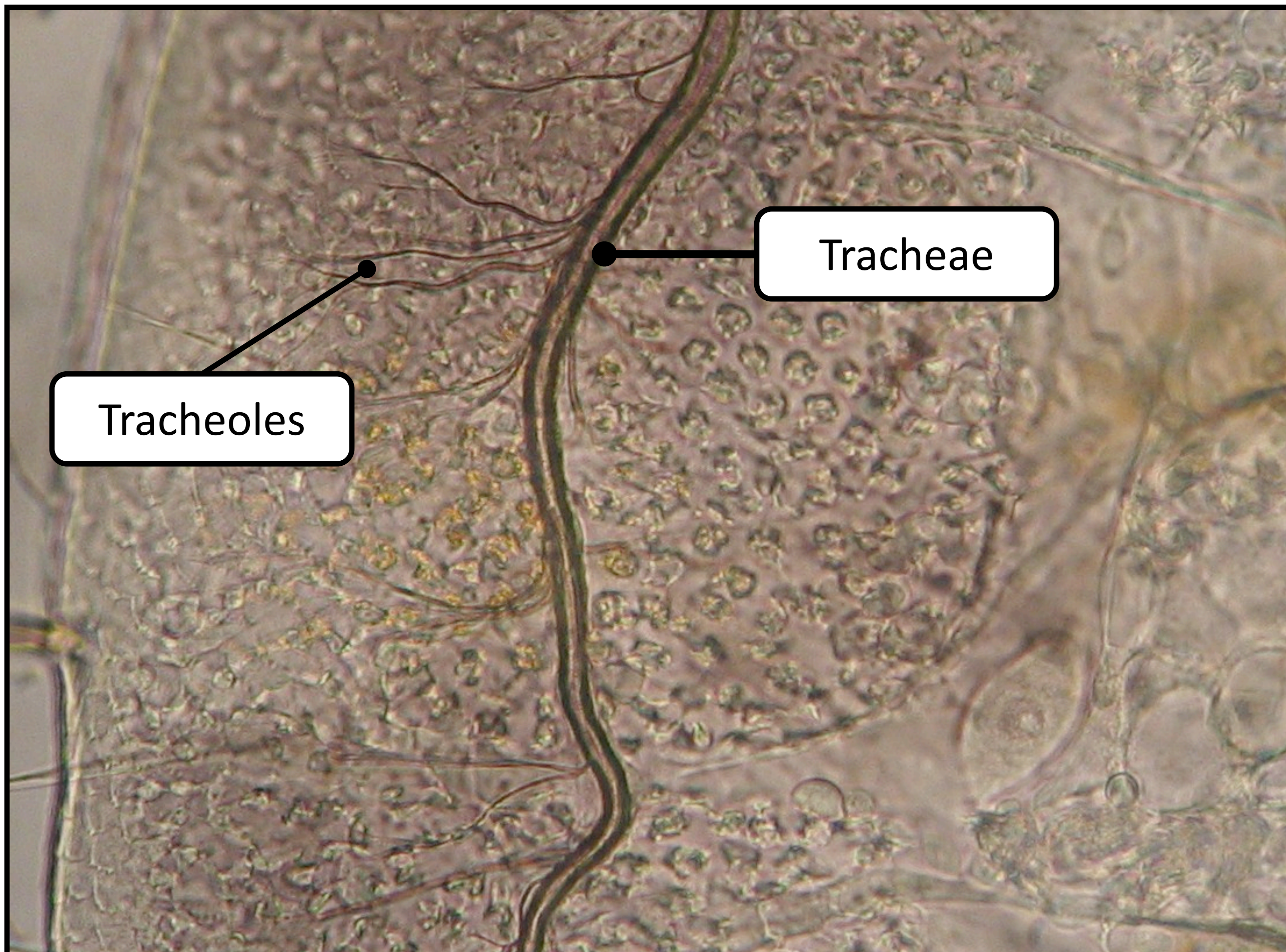
Now lets look at the tracheal system in a bit more detail. This is the tracheal system of a cockroach. It gives a good overview of all the basic components of the insect's tracheal system. The left side is the ventral view and the right side is the dorsal view of the dissected cockroach. So the main components of the tracheal system are the spiracles, which you can see associated with each segment, and these then lead to longitudional tracheal trunks which are these tracheal tubes which run the length of the insect. Branching from these longitudinal trunks are tracheoles – the finer branches of the tracheal system, and air sacks, these large expanded tracheal branches. The longitudinal trunks which link up all the insect's spiracles, and the air-sacks play a vital role in ventilating the tracheal system – which is something I'll talk about later.

The tracheal system

Water boatman 1st instar: *Agraptocorixa eurynome*

This is just to show you an actual tracheal system within the insect. This is a dorsal view of the head and thorax of an aquatic hemipteran, a bug called a water boatman. This is a newly hatched first instar. Its cucticle is transparent, and you can clearly see the longitudinal trunks branching into the finer tracheoles.

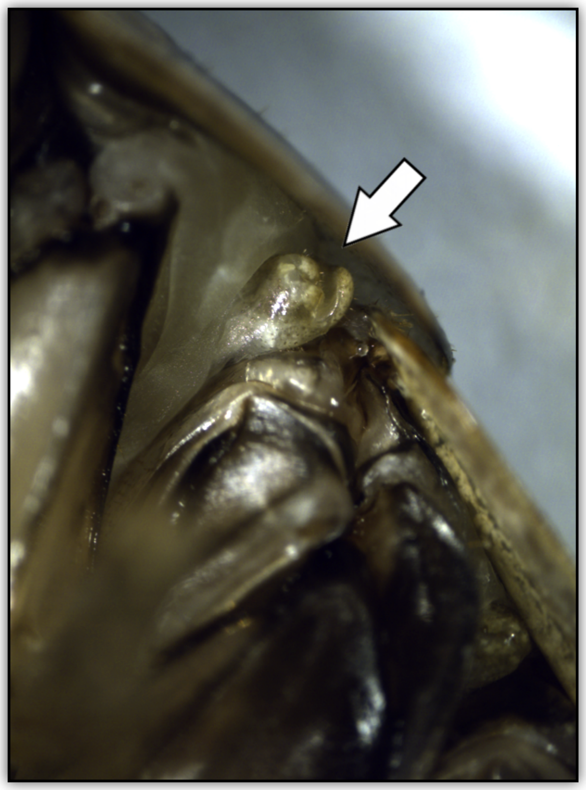
The tracheal system



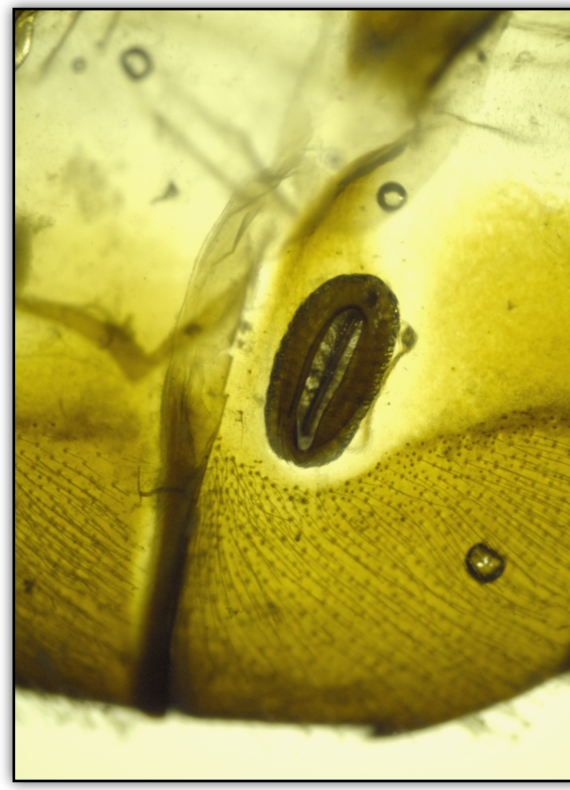
Water boatman 1st instar: *Agraptocorixa eurynome*

Zooming in here, you can see these blind-ending tracheoles branching off from the main tracheal trunk and lying in amongst the insect's cells.

Spiracles



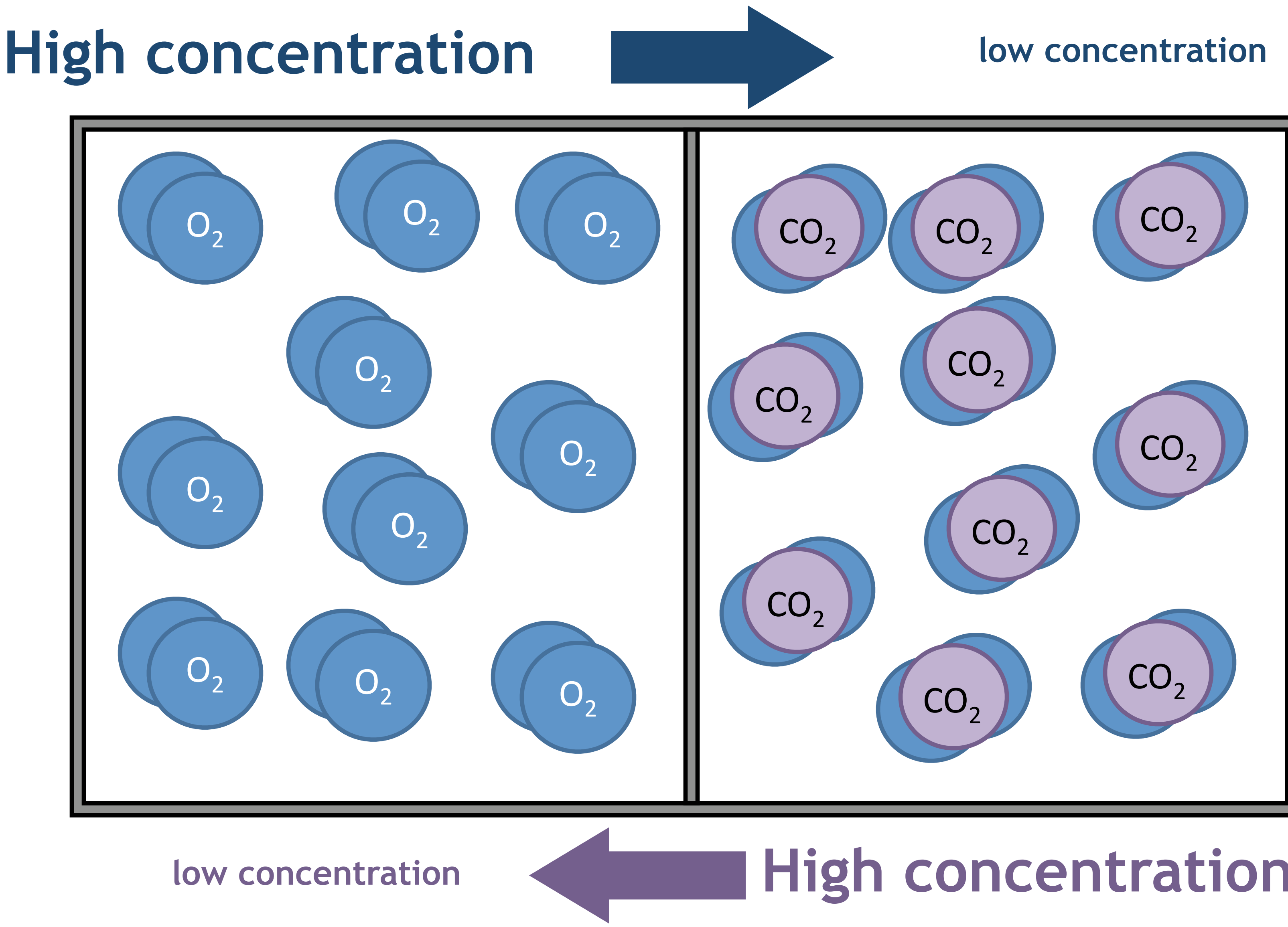
Thoracic spiracle
(speckled cockroach *Nauphoeta cinerea*)



Abdominal spiracle
(Rhinoceros beetle *Xylotrupes ulysses*)

Here are a couple of other pictures showing some different types of spiracular structures. On the left there is a picture of a thoracic spiracle of a cockroach – you can see it protrudes from the side of the insect like a mouth. And on the right you can see an abdominal spiracle from a rhinoceros beetle. You can see quite clearly that the spiracle consists of two segments with an opening between them. Muscles are attached to one of these segments, and by contracting it can pull the segments apart, opening the spiracle and allowing gas exchange between the tracheal system and environment. This is how insects control their respiration: by opening and closing their spiracles. You can also see that there are lots of hairs effectively covering the spiracle. This is part of a filtration mechanism to prevent dirt, dust and potentially parasites, from clogging up the spiracle. Most insects actually possess a spiracular atrium – a hair lined pit, with the spiracle located at the bottom. These are particularly well developed in insects from arid areas where dust is likely to be more of a problem, and insects which parasitise animals, as they are more likely to encounter oils and lots of fine particulate material like dander (effectively just animal dandruff) as they crawl around an animal's skin. Some aquatic insects have even more effective spiracle protection, since they risk their spiracles flooding while underwater. So many aquatic insects have a hydrophobic sieve plate – effectively a porous plate which sits above the spiracle, thereby protecting the spiracle valve beneath.

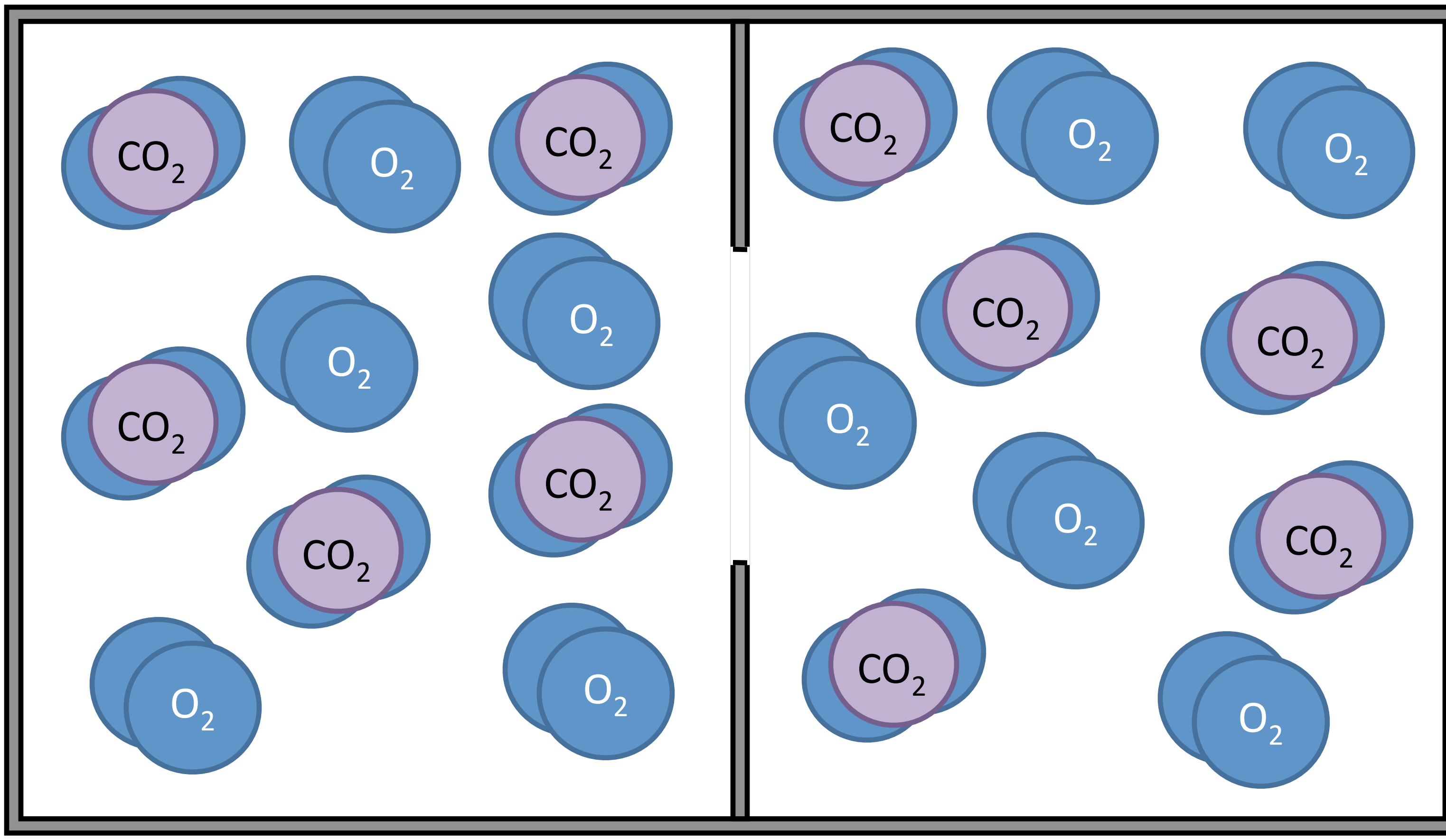
Diffusion



So now you know the structure of the insect's tracheal system, how does it supply oxygen to the insect's tissues while eliminating carbon dioxide? There are two transport phenomena which drive the all important movement of oxygen and carbon dioxide between the insect and its environment. The first we'll look at is diffusion. All molecules with a temperature above absolute 0 possess kinetic energy that causes them to move around and bump into each other. Diffusion is the random movement of these molecules which occurs due to this kinetic or thermal energy. Diffusion results in the net movement of molecules from a region of high concentration to low concentration – that is to say, there is net movement of molecules down a concentration gradient. In this diagram you can see a box which is divided by a partition. The on the left are oxygen molecules and on the right are carbon dioxide molecules. So there exists a high concentration of oxygen molecules in the left side of the box and a low concentration on the right, and a high CO2 concentration on the right, and low on the left. It is important to notice that there is no pressure difference between the two compartments as there is an equal number of molecules on both sides.

Diffusion

Equal concentration

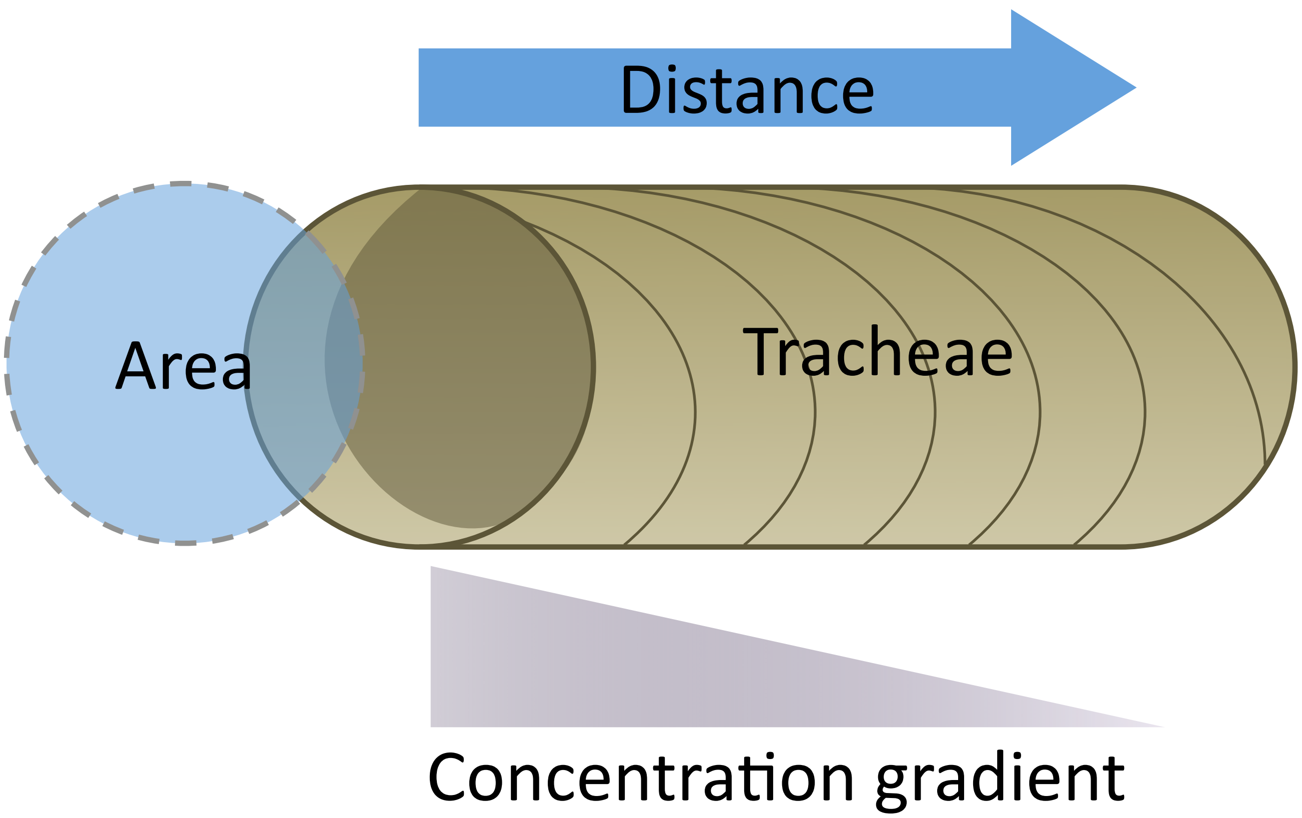


Equal concentration

If a hole is then cut in the partition, the randomly moving gas molecules would bounce around, colliding with each other and the walls of the box, diffusing down their respective concentration gradients resulting in a net increase in oxygen molecules on the right side of the box and a net decrease on the left, and vice versa for carbon dioxide. Given enough time, eventually the molecules would distribute themselves equally in each compartment as they randomly bounced around, until they were in equal concentration on both sides of the partition, at which point there would no longer be a concentration difference driving net diffusion. This means that while molecules would still be free to move across the partition, there would effectively be no increase or decrease in oxygen or carbon dioxide on either side of the partition. Because diffusion occurs due to individual molecules bouncing around and colliding with each other, it is fast over short distances, but as the diffusion distance increases, the time taken for a molecule to diffuse over that distance increases with the square of the distance: So diffusion time increases exponentially with distance travelled. This is because the molecular movement is random, it isn't in any particular direction. So while it might only take 10^{-4} (0.0001) seconds for an oxygen molecule to diffuse across a 1 micrometer distance, to diffuse ten times further (10 micrometers) would take 100 times longer (10 squared or .01 seconds), and over 1 mm, or 1000 times further, it would take one million times longer (100 seconds 1000 squared). So this shows you that while diffusion is very fast over short distances, it is really only fast enough to be biologically relevant over distances in the micro to millimetre range.

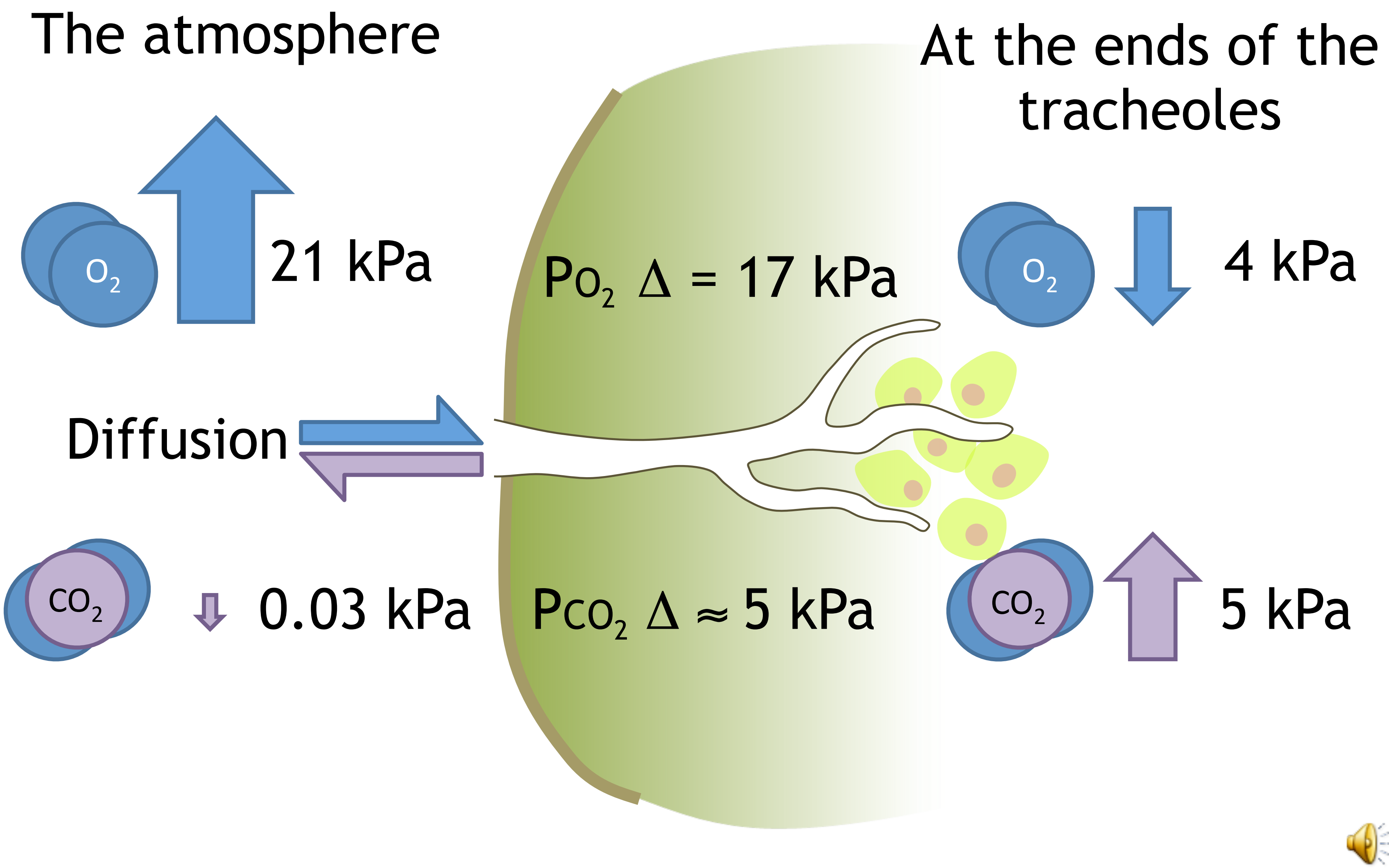
Fick's Law of diffusion

$$\text{Rate of diffusion} = K \frac{\text{Area}}{\text{Length}} (\text{Conc. gradient})$$



That being said, there are a number of factors that affect the speed with which diffusion occurs. And that brings me to this equation: Fick's law of diffusion. Basically what is says is that the rate of diffusion is proportional to the area of the diffusion pathway (so the cross-sectional area of a tracheole), inversely proportional to the distance of the diffusion pathway (the length of the tracheole), and proportional to the concentration gradient across the length of the tracheole. "K" is a diffusion coefficient relating distance diffused per unit time per difference in concentration. This constant is specific to the medium through which the molecule is diffusion (this medium is air in a tracheole, and the diffusion constant for oxygen in air is around 11 cm2 atm-1 min-1. If the tracheoles were filled with water the rate of diffusion would be around 320,000 times slower! This is another reason why being air-filled allows the tracheal system to rapidly spply oxygen to the insect's tissues) But the take home message of this diagram is: Increasing the area of the diffusion pathway or increasing the slope of the concentration gradient driving the diffusion will increase the rate of diffusion. Decreasing the length of the diffusion pathway will also increase the rate of diffusion.

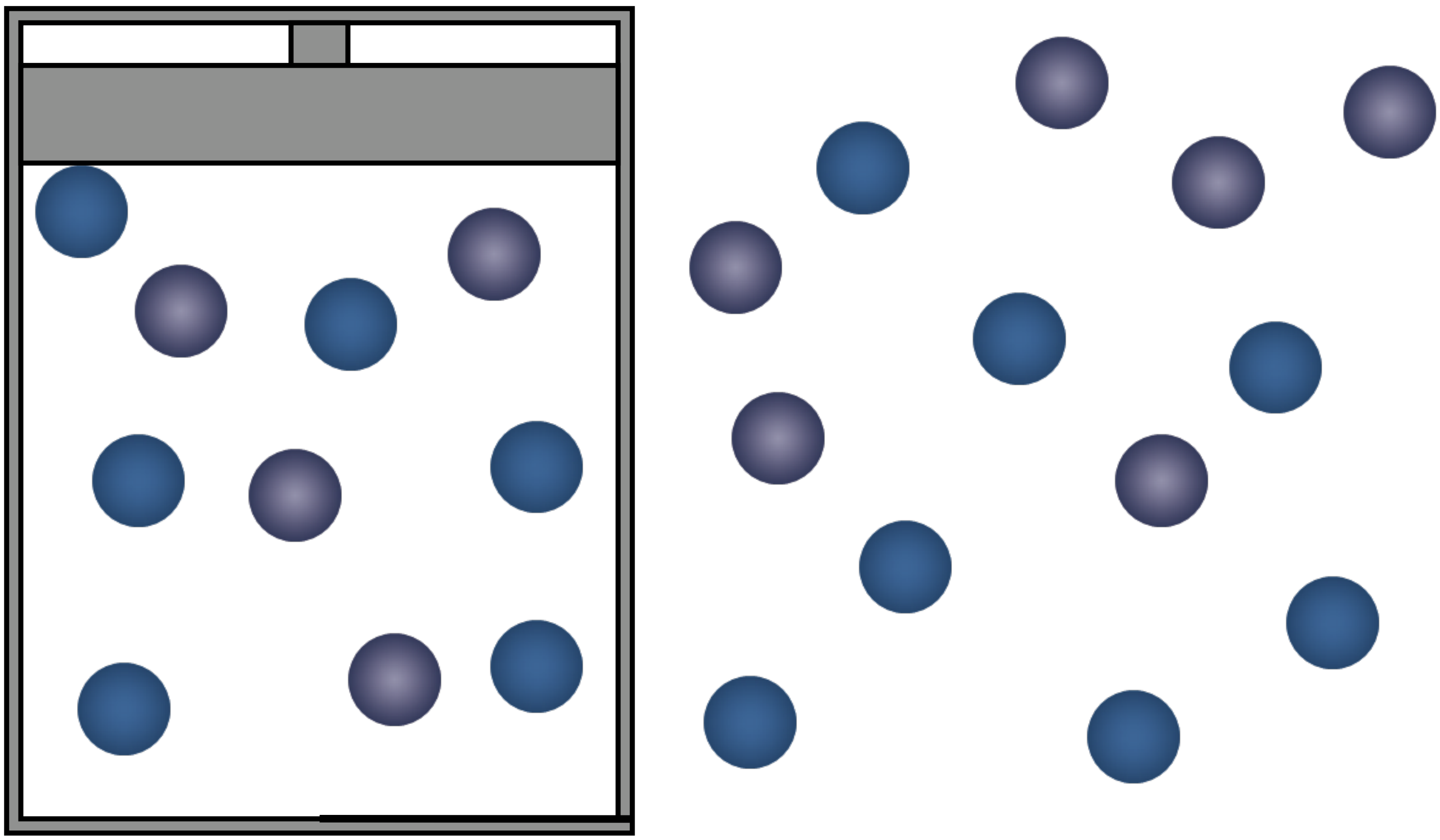
Diffusion



So how does all this physics apply to an insect? Well an insect is respiring aerobically, so its tissues are always consuming oxygen and producing carbon dioxide. This means that there is less oxygen and more carbon dioxide at the tips of an insect's tracheoles than there is out in the surrounding atmosphere. So there exists a concentration gradient driving the diffusion of oxygen into the insect down its concentration gradient, while carbon dioxide diffuses down its own concentration gradient from the tracheoles out to the atmosphere. And as oxygen is always being removed from the tips of the tracheoles while co2 is added, these concentration gradients which drive diffusion always exist – equilibrium is not reached. Instead the atmosphere is effectively an infinite source of oxygen while the insect is an oxygen sink, and diffusion occurs down this gradient.

Convection

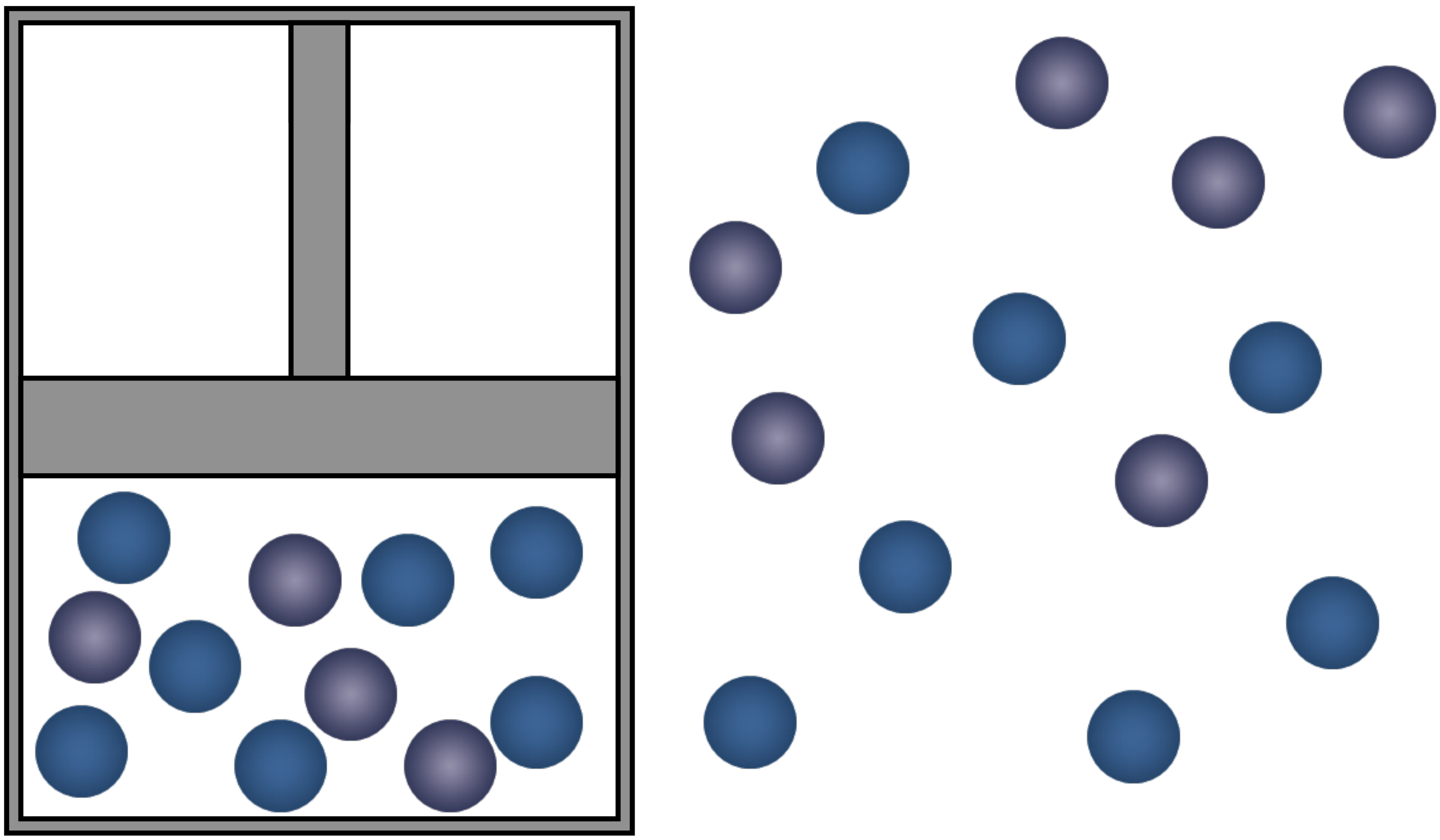
Equal Pressures



Convection is the bulk movement of molecules: it is the movement of a mass of molecules from a region of high pressure to a region of low pressure. This is what you do when you breathe in and out. Because diffusion could never move enough oxygen into your lungs fast enough to supply your respiratory requirements, you speed the process up by ventilating your lungs using convection: you breathe air in and out. This is achieved by generating a sub-atmospheric pressure in your chest when your diaphragm contracts and rib-cage rises which causes air to move by convection, from the higher pressure of the atmosphere to the lower pressure into your lungs. In this way you move a larger volume of gas more rapidly than would be possible relying solely on diffusion. And that is what this diagram is showing. There is a mixed gas in this box which has the same pressure as the surrounding atmosphere

Convection

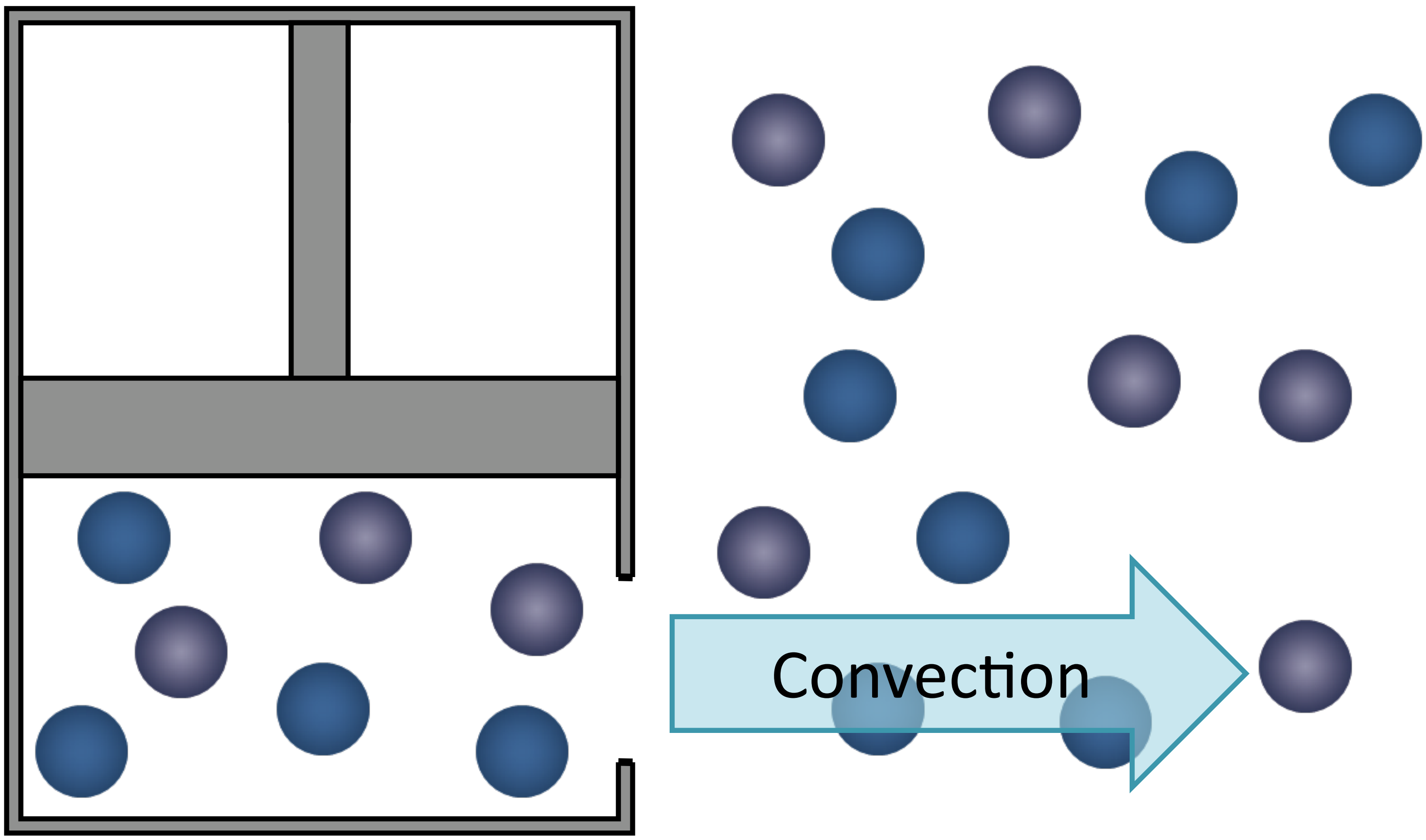
Positive Pressure



If a plunger then exerts a force on the gas in the box, the gas is compressed and now has a higher pressure than the gas in the surrounding atmosphere.

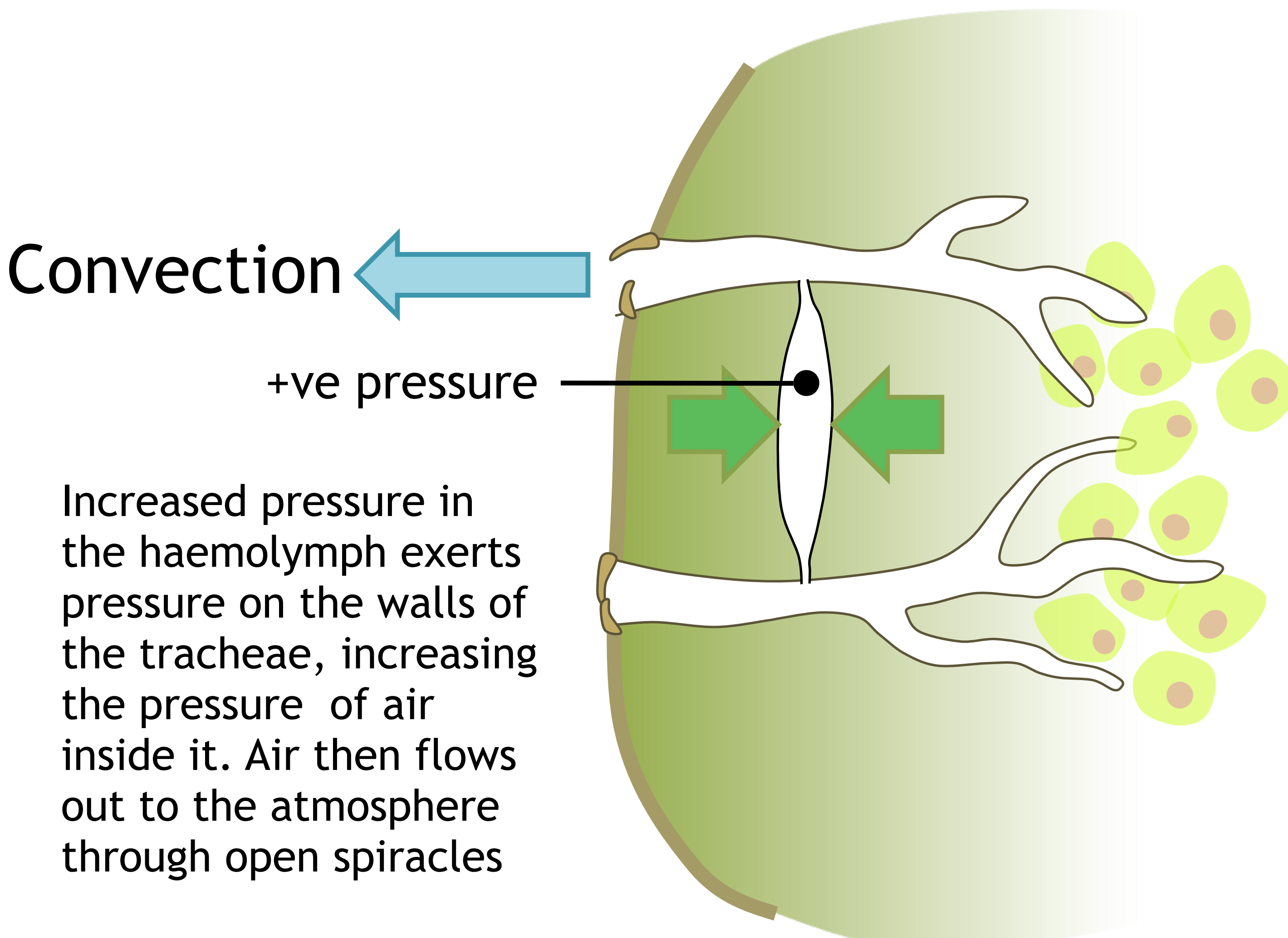
Convection

Equal Pressure



As molecules move from regions of high pressure to low pressure in order to restore pressure equilibrium, if the box is then opened, there would be a mass flow of molecules, a convective movement of gas out of the box as the gas moves from high to low pressure. Once the pressure within the box equals the atmospheric pressure, the convective flow stops. So this shows that in convection, all molecules move together at the same speed, unlike in diffusion where molecules move according to their individual concentration gradients.

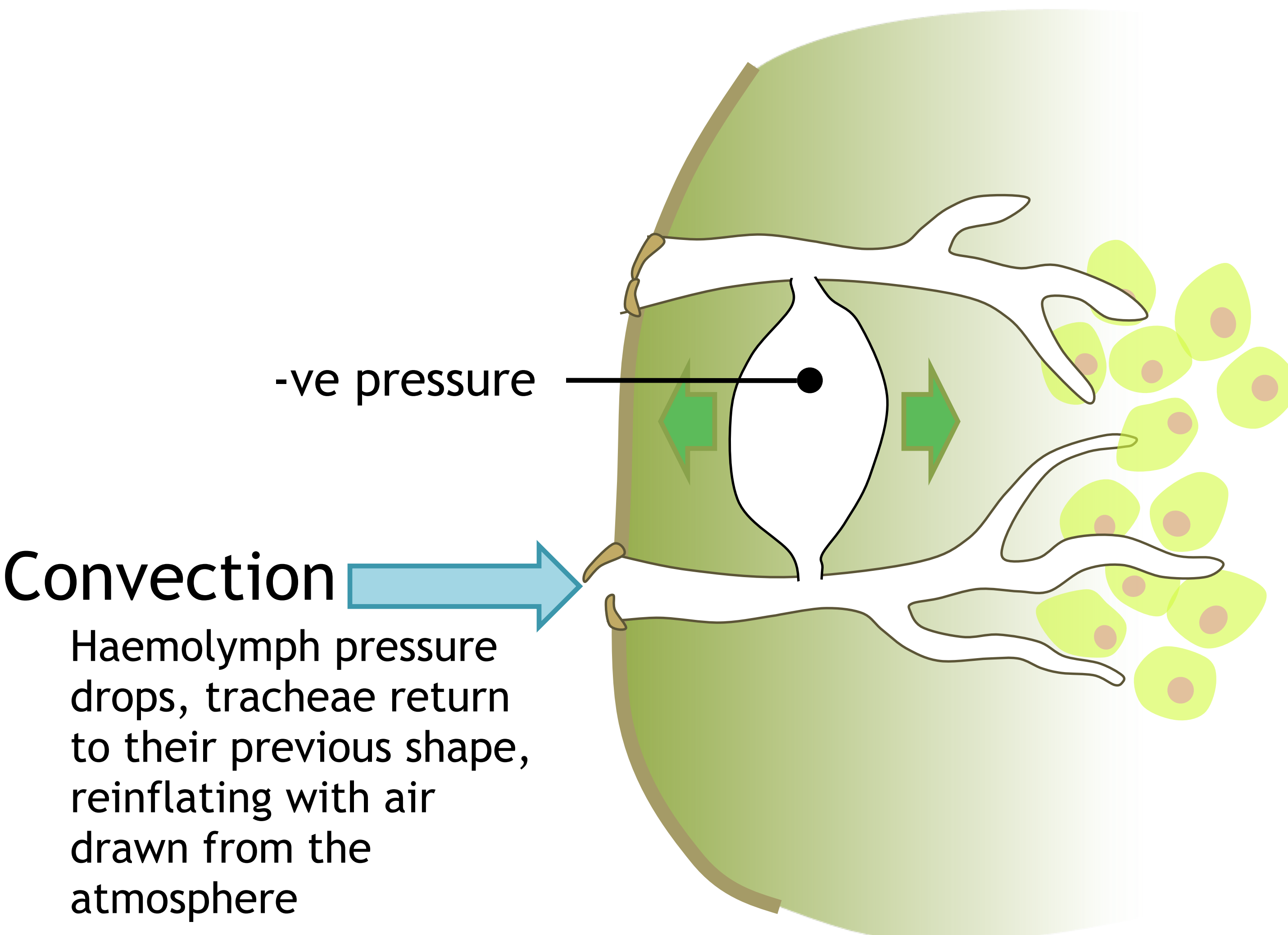
Convection



Increased pressure in the haemolymph exerts pressure on the walls of the tracheae, increasing the pressure of air inside it. Air then flows out to the atmosphere through open spiracles

Insects also breathe in and out using convection, much as we do. They do this by expanding and collapsing regions of their tracheal system much as you expand and collapse your lungs. They do this by increasing pressure in their body cavity through muscular effort: for example, some insects will expand and contract their abdomen. As their abdomen contracts it increases the pressure of their body fluids/haemolymph, which then exert pressure on the walls of their tracheal system. This causes some sections of the tracheal system to collapse, particularly the large, soft-walled air sacks, and the air within these structures is forced out of the trahcheal system through open spiracles

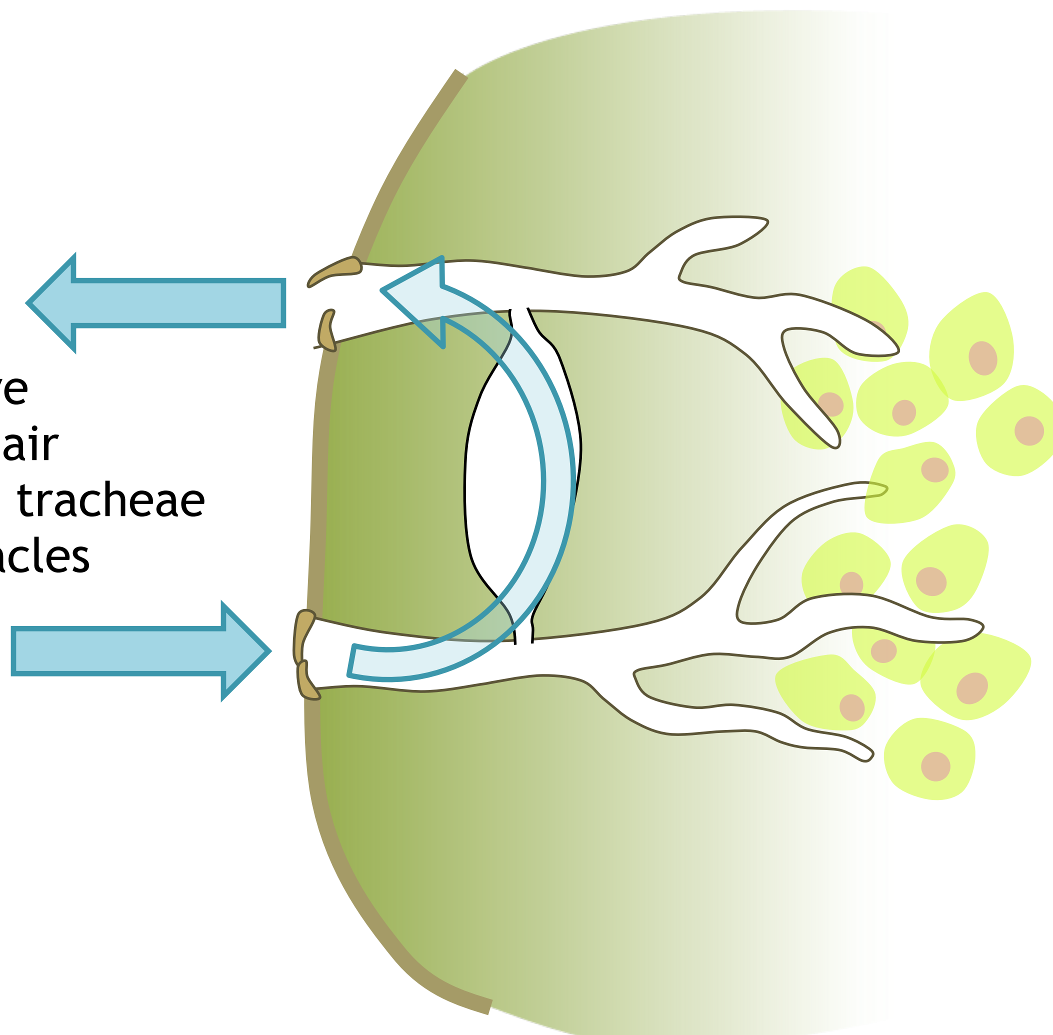
Convection



When their abdomen then relaxes, the tracheae elastically re-expand to their previous shape, and this draws air in through open spiracles.

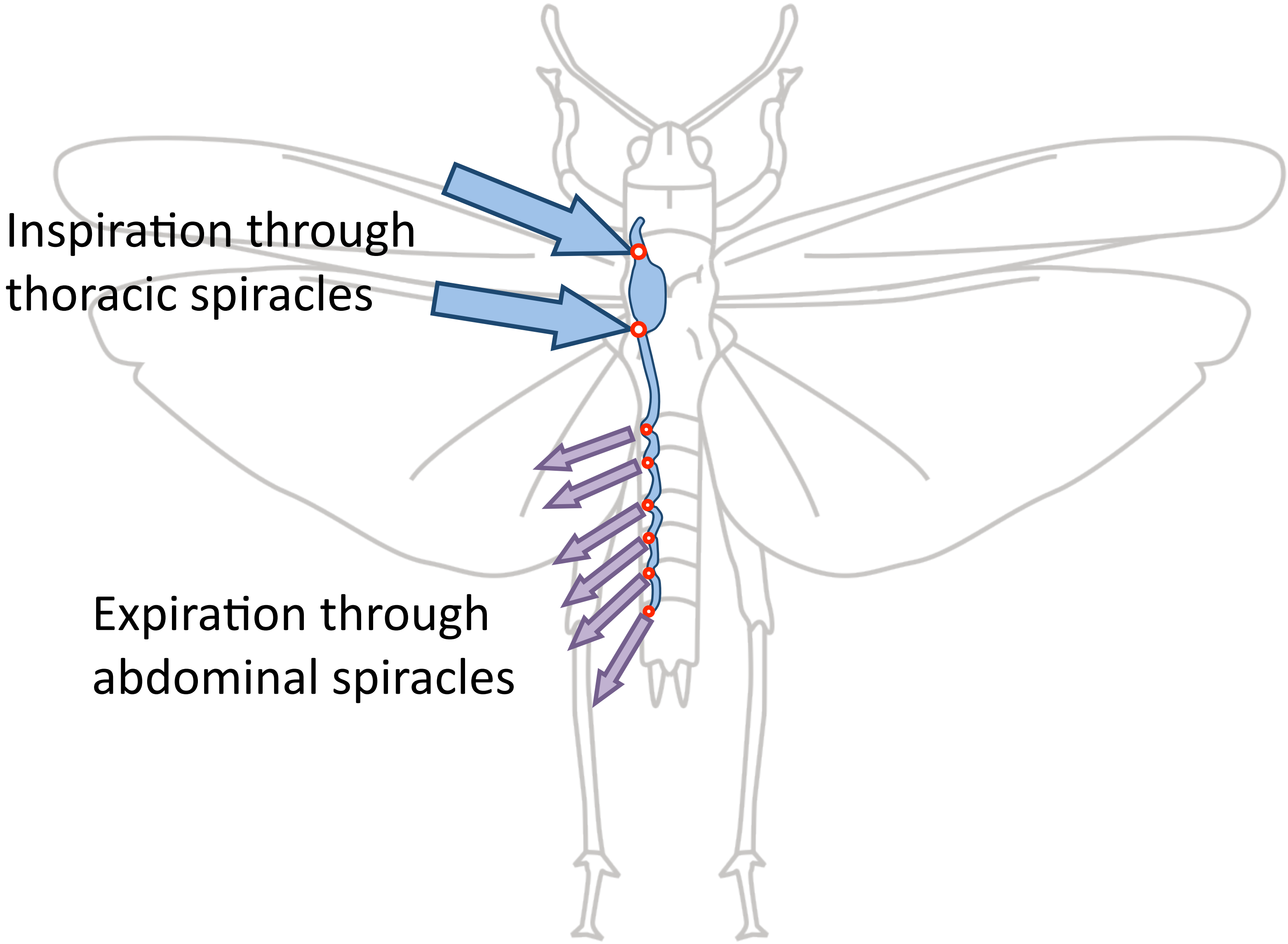
Convection

The convective movement of air ventilates the tracheae between spiracles



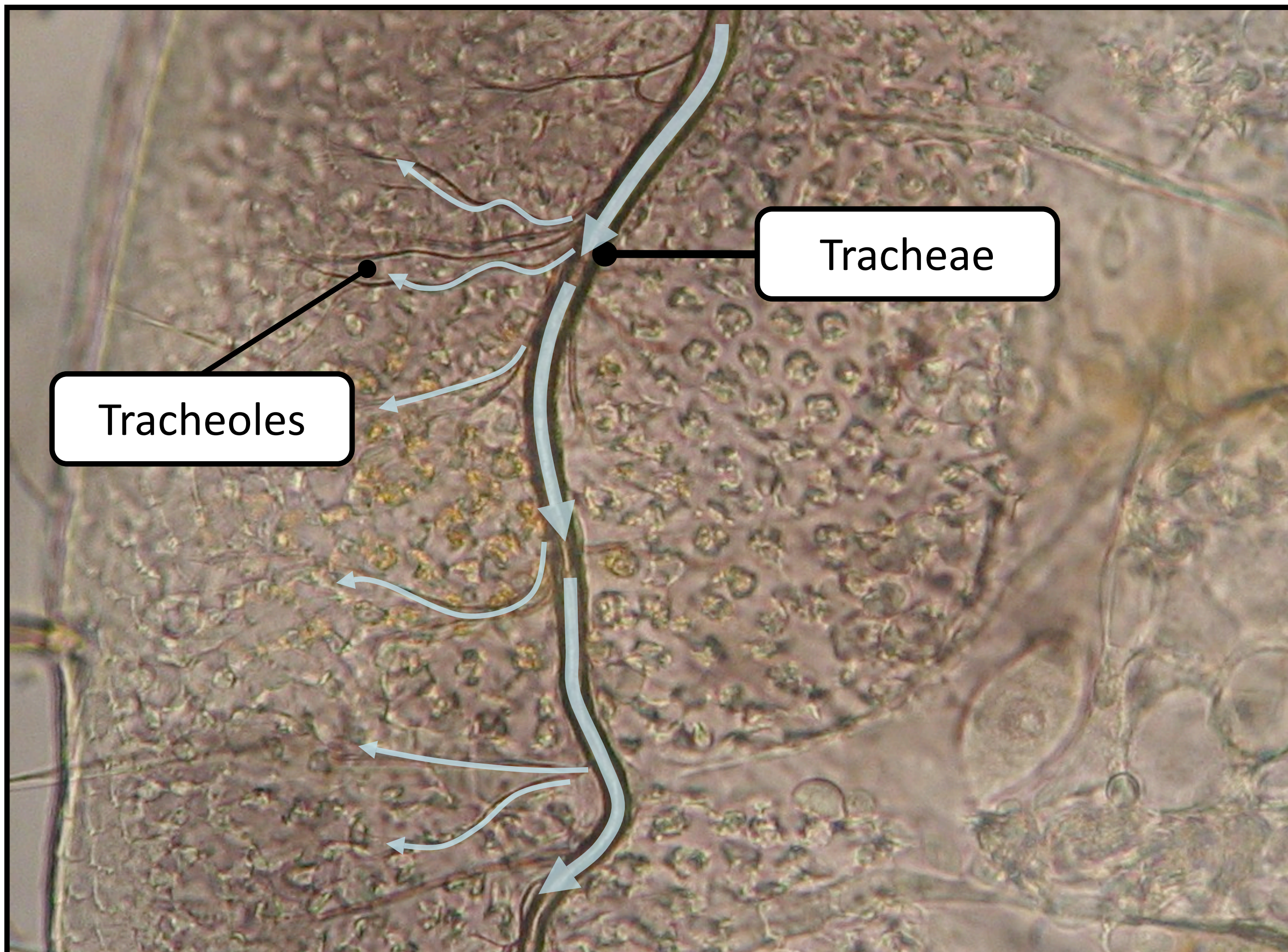
So by periodically compressing their tracheal system and insect can convectively ventilate some portions of their tracheal system. You should also note that the blind-ending tracheoles cannot be ventilated convectively, as they do not deform, and air cannot flow in through one branch and out the other, as they are dead-ends. So diffusion remains the only process by which oxygen and carbon dioxide can move through the tracheoles. I have put a video on the blackboard website which shows convective ventilation actually occurring in a beetle. The video was made by placing the beetle in a machine called a syncrotron which produces a powerful, focussed x-ray beam. This allowed researchers to see, for the first time, that almost all the large tracheae can be expanded and collapsed, allowing the beetle to convectively ventilate much of its tracheal system.

Unidirectional convective ventilation



Many insects can also channel the convective flow of air through their trachel system by timing the opening and closing of their spiracles. For example, the locust Schistocerca gregaria generates a unidirectional flow of air while it is at rest by opening its thoracic spiracles during the inhalation phase, while keeping its abdominal spiracles shut. It then closes its thoracic spiracles and opens its abdominal spiracles while compressing its tracheal system, thus forcing air out through its abdominal spiracles. So by timing the opening and closing of the spiracles on the different body segments with convective pumping movements, insects can direct the flow of air through their tracheal system.

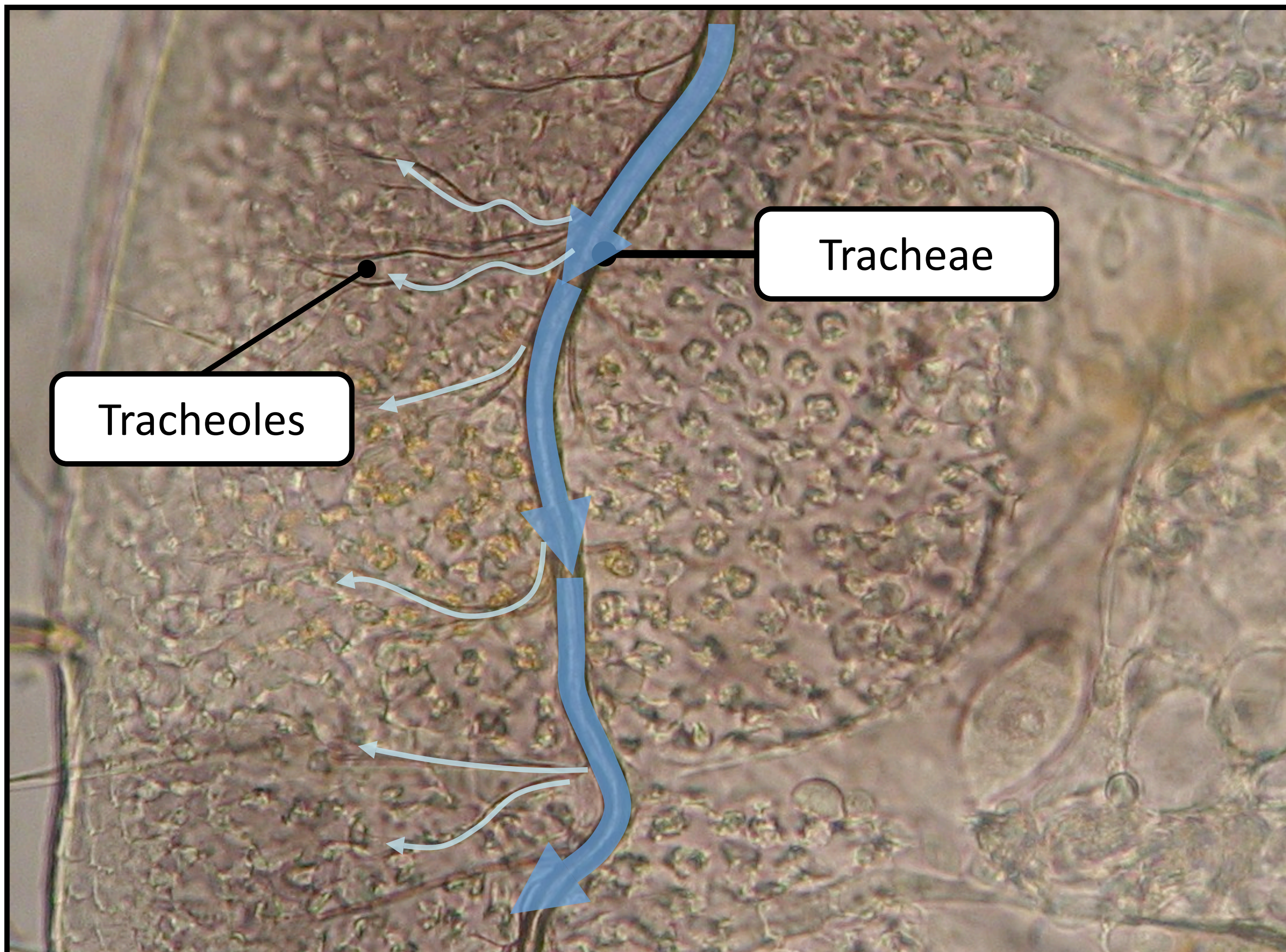
Diffusion only



Water boatman 1st instar: *Agraptocorixa eurynome*

The advantage of convective ventilation is that it moves fresh air through the insects tracheae, which means that diffusion only occurs over very short distances in the tracheoles. So if you look at this diagram, you can imagine that in the absence of convective ventilation oxygen would need to diffuse in through a spiracle, along the tracheae, through the tracheoles, and then into the tissues. Diffusion would occur quite slowly over this distance

Convection + diffusion



Water boatman 1st instar: *Agraptocorixa eurynome*

But with convective ventilation, fresh air can be moved en mass through the tracheae, so diffusion only needs to occur over the much shorter distance of the tracheoles alone. This means oxygen and carbon dioxide can be moved in and out of the insect much more rapidly.

Relative importance of diffusion and convection

2 mm long

Unknown clown beetle: Histeridae

Insect gas exchange best described by a mix of both diffusion/convection

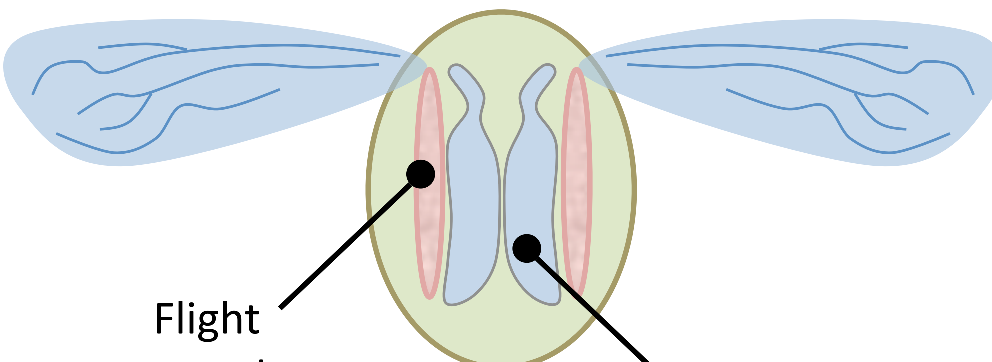
>50 mm long

Rhinoceros beetle *Xylotrupes ulysses*

So which is more important to an insect: diffusion or convection? Well that depends on how large you are. A small insect like a fairy wasp doesn't have much distance between its respiring tissues and the outside atmosphere. This means that its respiratory requirements will be easily met by diffusion. But what happens when you are much bigger, like a rhinoceros beetle? Diffusion cannot occur rapidly enough over the longer distances between their spiracles and the tips of their tracheoles. So bigger insects tend to rely more on convective ventilation to maintain gas exchange, and you will often see large beetles and grasshoppers actively pumping their abdomens in order to ventilate their tracheal systems.

Autoventilation

Gram for gram, flying insects have the highest rates of oxygen consumption in the animal kingdom: 3-fold greater than a hovering hummingbird, 30-fold greater than a human athlete



Flying Cetoniid flower beetle, *Cetonischema aeruginosa*

While convection becomes increasingly important with size, it also becomes increasingly important with high metabolic rates which demand large fluxes of oxygen to the tissues. This is particularly true for flying insects which can have phenomenally high rates of aerobic respiration, the highest in the animal kingdom. To ensure that their flight muscles receive enough oxygen, many insects use autoventilation: This is basically where air sacks near the flight muscles are compressed and expanded with the wing stroke. This means that the flight muscles not only move the wings, but incidentally pump air into the insects tracheal system and keep themselves supplied with oxygen.

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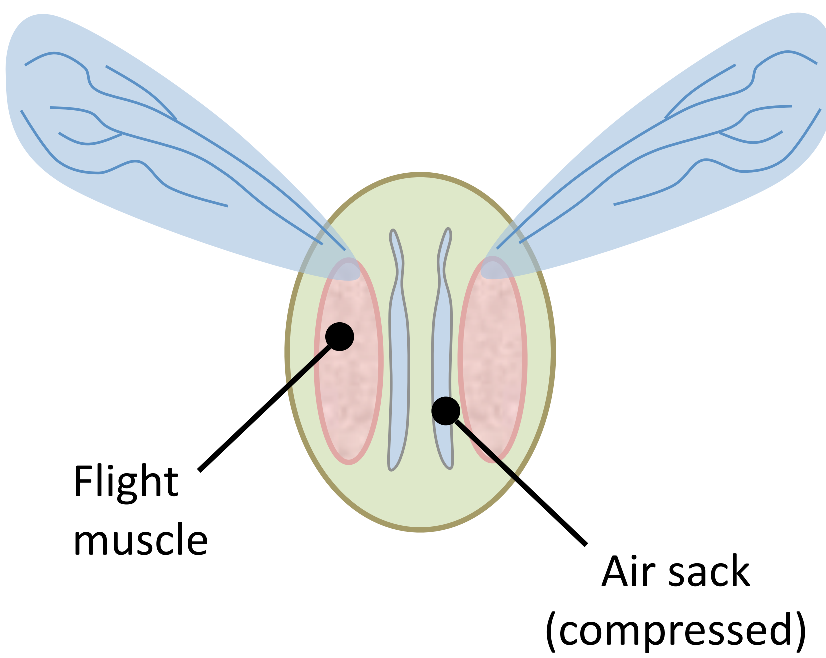

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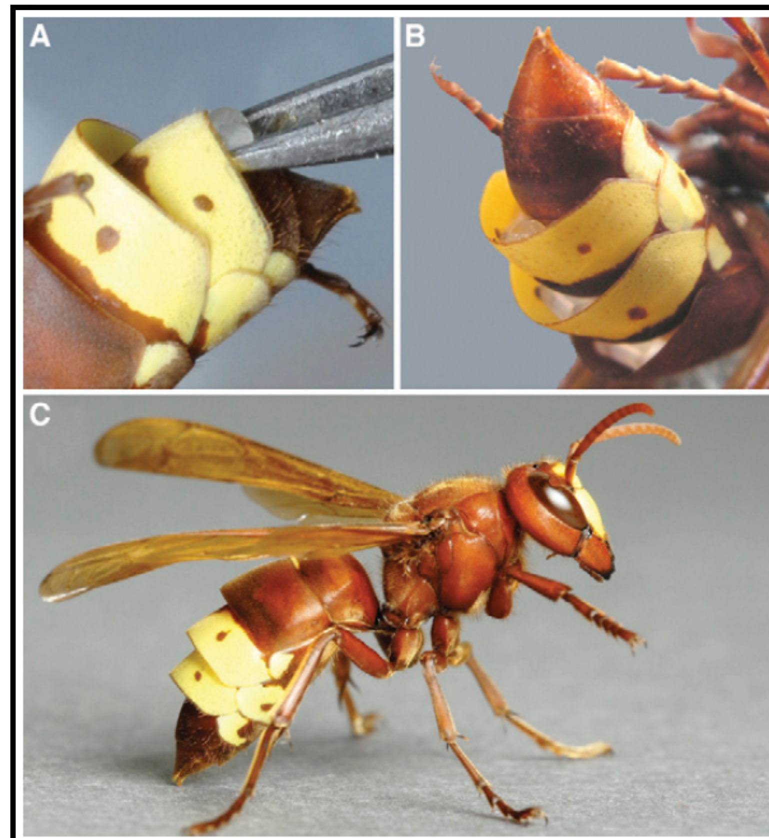
Convection: the hornet's Achillies' heel

Honeybees swarm a hornet in a 'bee ball'

Photo by Takahasi, Wikipedia commons

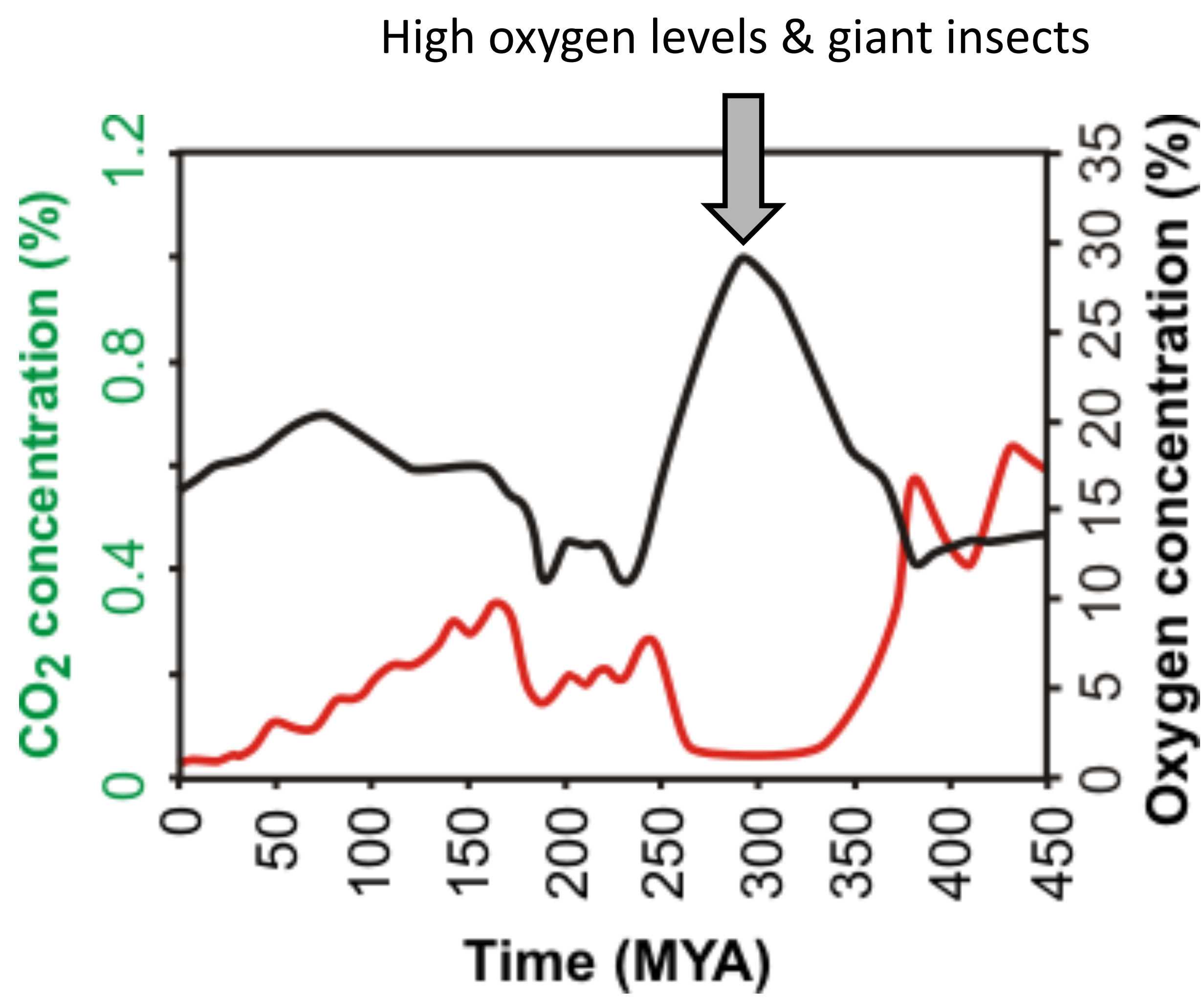
Hornet with braced abdominal tergites



Papachristoforou, Rortais *et al.* 2007 *Smothered to death: Hornets asphyxiated by honeybees* Current Biology 17 R795-R796

The importance of convective ventilation in insect respiration can also be seen in how cyprian bees deal with an attacking hornet. Hornets prey upon honeybees, raiding their hives and eating the workers. But on the island of Cyprus, the honeybees have developed an effective defence against their attack. Researchers noticed that when Cyprian hornets attack a honey bee hive, the bees would swarm the hornet. But instead of stinging it they would cluster all over it, particularly around its abdomen, and after an hour the hornet would be dead. It turns out that what the bees were doing was suffocating the hornet. Hornets must pump their abdomens to convectively ventilate their tracheal system, and what the bees were doing was grabbing on to the hornets abdomen and keeping it compressed, preventing the hornet from convectively ventilating. Eventually, this caused the hornet to suffocate. The researchers also showed that if plastic blocks were inserted between the abdominal tergites of the hornet, which is what the picture on the right is showing, the bees were unable to compress the hornet's abdomen, and so the hornet could survive being mobbed by the bees for far longer. So this is just a neat example of how convection is important, especially among the bigger insects.

Is insect size limited due to diffusion through the tracheal system?



So while larger insects tend to use convection more to ensure they can deliver enough oxygen to their tissues quickly enough, there are some parts of the insect which cannot be ventilated by convection, and where diffusion must suffice. For example, insect legs don't contain air sacks, or loops of tracheae that would allow air to be pumped down one tracheae and out through the other. This means insect legs must receive an adequate supply of oxygen by diffusion alone. It has been suggested that the diffusion limits the length that these diffusion-only sections of the insect can be, and so this constrains the upper maximum size of the insect. This partly explains why most insects are small, and only a very few insects exist which are larger than 10 centimetres or so in length. This idea of diffusion limiting insect size is partly backed up by evidence from the geological record. Some 300 million years ago in a period called the carboniferous, levels of atmospheric oxygen were much higher than today. At the moment the earth's atmosphere is around 21% oxygen, but in the carboniferous it was probably close to 30%. And during this period we find fossils of enormous insects – proto-dragonflies with wingspans of over 70 centimetres. From this correlation it has been argued that these giant insects could grow so large because the gradient driving the diffusion of oxygen into the insect was much larger, and thus diffusion could occur rapidly enough in this high oxygen atmosphere to sustain the insect's respiration.

Summary

- The tracheal system is effective because:
  - Oxygen and carbon dioxide are exchanged directly with the atmosphere – a circulatory system is not required
  - Tracheoles provide a diffusion pathway directly to respiring tissues
  - Gas exchange occurs due to both diffusion and convection. Convection increasingly important in larger insects. Diffusion important in blind-ending tracheoles
  - Compression and expansion of tracheal system combined with coordinated spiracular opening/closing generates directional convective flows of air