9
Respiratory System

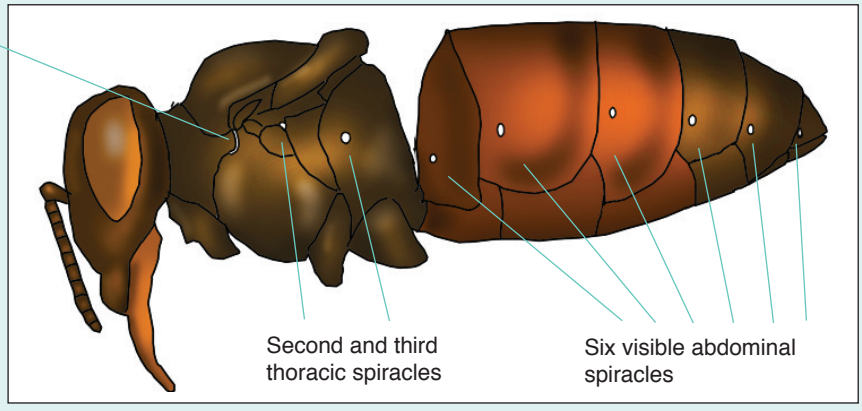


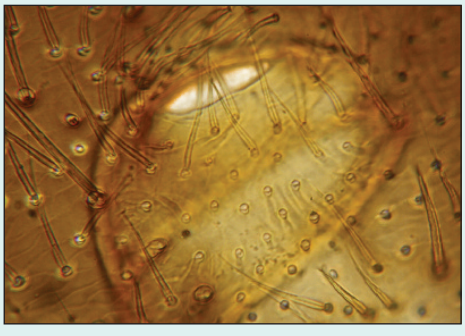
Fig 9.1. The locations of the nine visible spiracles on each side. The tenth, the second largest, is hidden within the sting chamber.

The bee, in common with all insects, has a system for bringing air directly to the tissues. Unlike vertebrates, in which oxygen is transported to the tissues bound to the haemoglobin molecule, and carbon dioxide is dissolved in blood leaving the tissues, insects transport them as gases. It is only at a cellular level that oxygen and carbon dioxide are dissolved.

This gas movement begins with openings in the bee's body wall, the spiracles, through which air is drawn in and expelled out. There are ten spiracles on each side of the bee. Three on each side of the thorax, six visible on each side of the abdomen, and the final pair of spiracles hidden within the sting chamber. There are no spiracles in the head.

The spiracles of the abdomen are all broadly similar, however those of the thorax are not. The first spiracle is hidden beneath the spiracle lobe, a large hair-fringed backward extension of the first thoracic segment. This is the spiracle which is invaded by tracheal mites. The second spiracle is small and lies immediately below the wings, midway between the fore-wing and hind wing just at the top of the second and third pleurites. The third spiracle is the largest, and is easily seen on the sides of the thorax, in the fourth segment. This is strictly the first abdominal segment. The abdominal spiracles are all situated towards the front of the tergites. The first spiracle of the abdomen is a little lower than the others. The final pair of spiracles within the sting chamber have the second largest openings of the ten pairs.

Each spiracle has a valve system to control the flow of air. These operate in a similar way for all the spiracles on the abdomen, although differently for the spiracles of the thorax. The actual opening of each spiracle to the outside is small, from where air enters into a chamber attached to the inside of the abdominal wall. This chamber, known as an atrium, is connected to a large trachea, with an intervening valve, before joining the tracheal system.



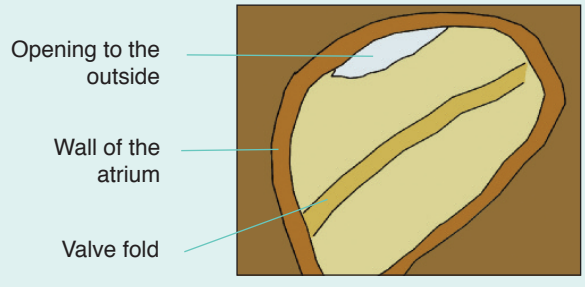


Fig 9.3. Explanation of Figure 9.2.

Fig 9.2. Close-up of the spiracle of the sixth abdominal segment. The walls of the atrium are visible through the abdominal wall. The small opening to the atmosphere is at the top of the image.

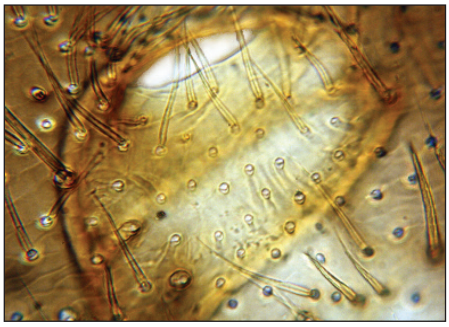


Fig 9.5. The opening into the atrium, and the atrial walls are visible in this focal plane.

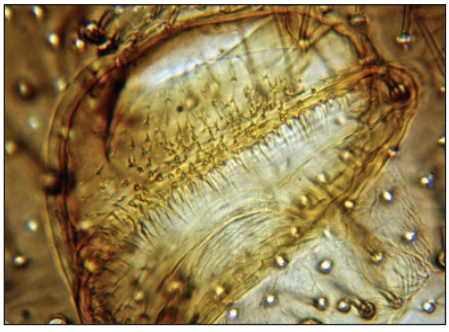


Fig 9.6. A little deeper the hairy edge of the valve fold comes into focus.

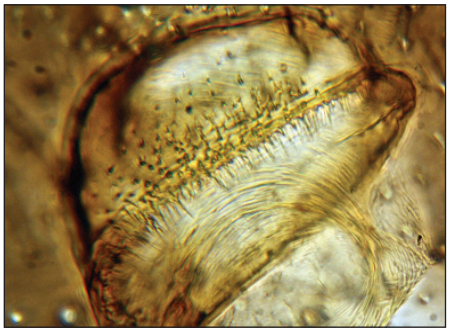


Fig 9.7. Deeper still the main trachea leading from the atrium begins to become visible.

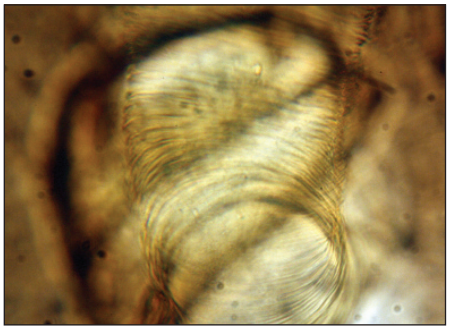
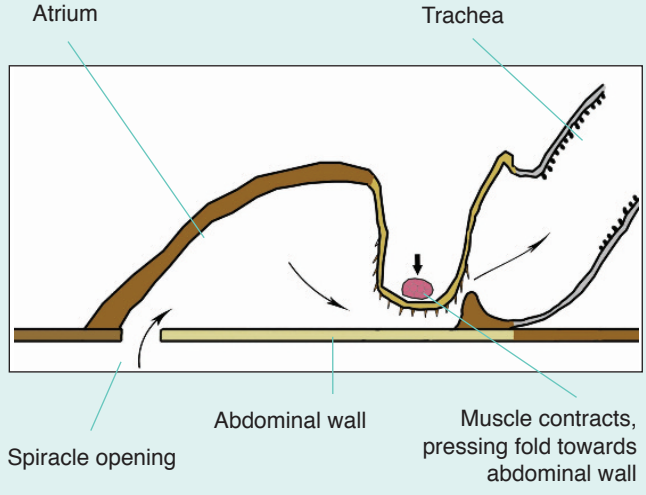


Fig 9.8. Finally the tracheal rings of the main trachea are clearly seen.

Figure 9.4. is a cross-section through an atrium with the wall of the abdomen at the bottom of the picture. The flow of air passing through the small opening into the atrium and hence to the tracheal system is controlled by the fold with its covering of small hairs. This can be brought closer to the abdominal wall by the action of a muscle. This muscle runs across the back of the fold, and is attached at one end to the abdominal wall, when the muscle is contracted it presses the fold down, closer to the abdominal wall, reducing air flow.



Figures 9.5 to 9.8 are images of the same spiracle as in figure 9.2, taken with transmitted light. With each successive image, the focal plane has been moved progressively deeper.

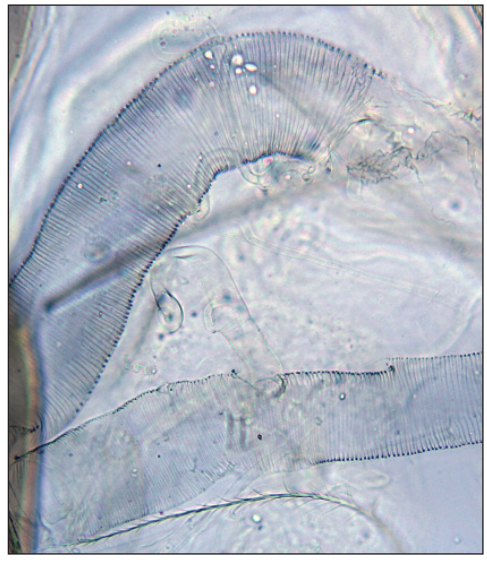


Fig 9.9. This image is of two large tracheae which have arisen from the last pair of spiracles from the eighth abdominal segment, hidden within the sting cavity.

The tracheae leading from the spiracles form a network of interconnecting airways throughout the body. The longest and thickest tracheae pass forward from the thorax into the head, providing air for the metabolically highly active structures in the head, the brain, the eyes, the antennae, muscles of the mouth-parts etc. The thin-walled tracheae are exposed to tissue pressure changes within the haemolymph in the body chambers. In order to prevent collapse of the tracheae their walls are supported by rings of cuticle known as taenidiae.

Fig 9.10. Section through main trachea in thorax, showing taenidiae and a branch point.

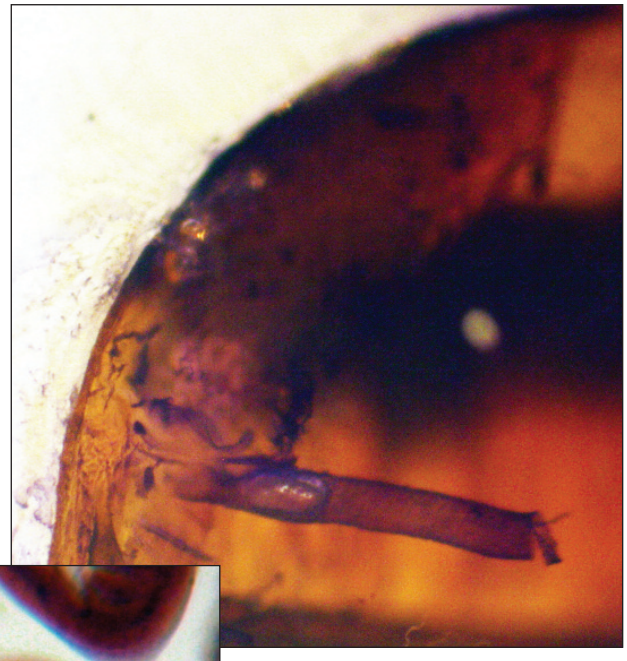


Fig 9.12. This image shows a main trachea passing into the body from a spiracle in the abdominal wall of a drone. It has been stained to show up more clearly.

Fig 9.11. This higher power view of the wall of a trachea shows the taenidiae in section. These thin cuticular strengthenings of the trachea spiral along the lining of each trachea like a delicate spring. The large round structures are cells of the thoracic salivary glands.

The spiracles are connected by fairly wide tracheae to tracheal sacs. These sacs are expanded and contracted by fluid pressure changes due to the movement of the plates of the abdomen caused by the muscles connecting them. As the abdomen expands the pressure in the tracheal sacs falls, and air is drawn in through the spiracles. Similarly contraction of the muscles connecting the abdominal plates increases the pressure within the abdomen forcing air out again. In this way the air within the sacs is continually replenished by fresh air drawn through the spiracles.

From the tracheal sacs tracheae branch out towards the tissues. They branch to progressively smaller and smaller tracheoles, penetrating all tissues and organ systems until the final tracheoles, less than a micro-metre across, reach to a cellular level. The tracheoles end blindly, and often contain a small quantity of liquid.

Within the head there are generally three main pairs of tracheal sacs. One around the inner aspects of the compound eyes and optic lobes of the brain, one pair above the bases of the mandibles, and a pair join together behind the frons (forehead) and over the top of the brain. These communicate with the rest of the tracheal system through the two large tracheae entering through the upper part of the neck.

The thorax has the lowest volume of tracheal sacs of the three body segments. As described earlier two large tracheal trunks run forwards from below the spiracles lobes. As well as giving branches through to the head these give large branches which run downwards to the front legs, and backwards to the main indirect flight muscles, with connections to the tracheal sacs in the back of the thorax. The second and third spiracles of the thorax communicate directly with a pair of large tracheal sacs in the upper part of the back of the thorax. From this upper pair of sacs there are connections to a transverse sac within the scutellum. These sacs also have connections down to a lower pair of sacs in the back of the thorax which connect with the middle and back legs. This lower pair is also connected across the midline by a smaller sac. These sacs within the back of the thorax connect by two large tracheae through the petiole with the tracheal sacs of the abdomen.

The abdomen has two large sacs on either side running backwards in the lower part of the abdomen and gradually becoming narrower. These sacs are connected by broad tracheae with all the spiracles along each side of the abdomen. These large sacs are connected with each other across the floor of the abdomen by a series of connections. Some of these are simply broad tracheae, others are distended as small sacs themselves. In the upper part of the abdomen the large tracheal sacs have a series of large branches passing towards the midline. These branches include a number of saccular enlargements, before ending in fine branches which enclose the heart.

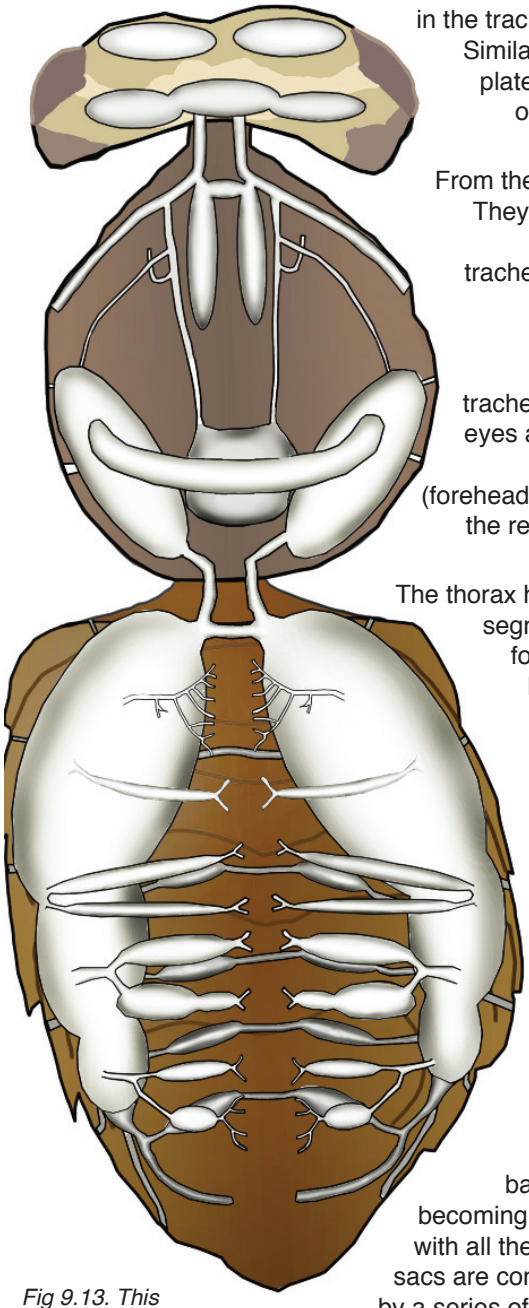


Fig 9.13. This image is a simplified illustration of the tracheae and tracheal sacs. In practice each bee is different, and wide variations around this norm may occur.

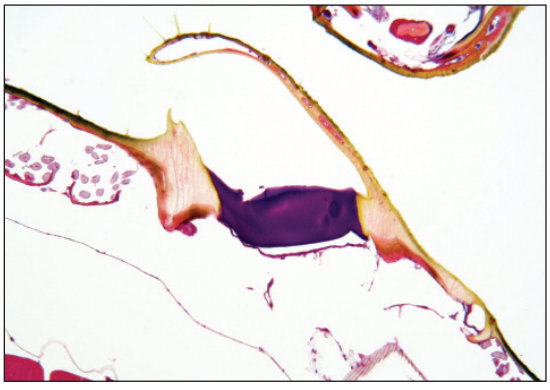
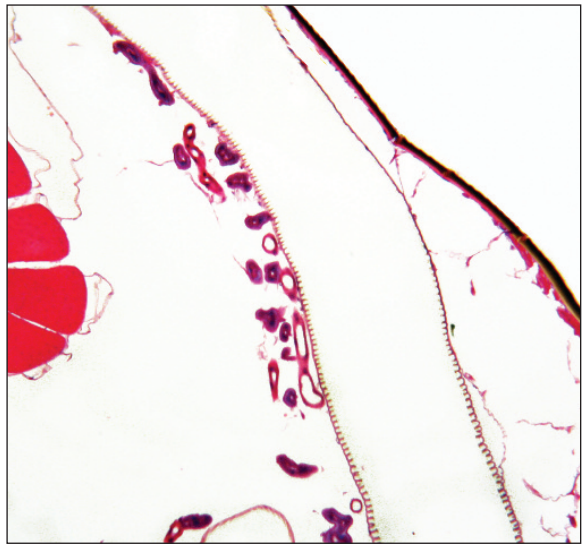


Fig 9.14. A section through the spiracle lobe. This hair fringed cuticle plate conceals the opening into the first thoracic spiracle.

Figure 9.14 shows the main trachea from where it arises beneath the spiracle lobe of the thorax. This spiracle does not have an atrium like those of the abdomen, instead the trachea opens directly out of a membrane beneath the spiracle lobe. However it does have a valvular system to control the degree of opening, like the other spiracles.

Fig 9.15. The main trachea arising from the first thoracic spiracle is particularly large and long, leading forward to the neck and head in addition to its branches into the thorax.



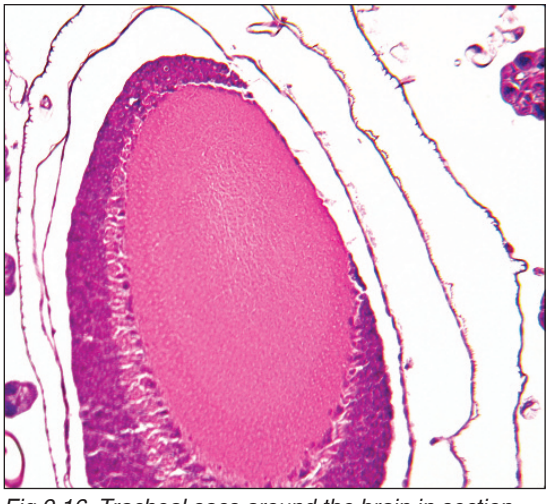


Fig 9.16. Tracheal sacs around the brain in section.

Figure 9.17 shows the tracheal sacs within the head, after removal of the cuticle from above the brain. The three brown circular areas are due to pigment in the retinae of the simple eyes (ocelli). The brain is hidden beneath this tracheal sac, just beneath the ocelli. The clusters of cells of the hypophrayngeal gland are visible beyond this sac, and beyond these another tracheal sac bulges out from beneath the cuticle of the forehead (frons).

Fig 9.17. The top of the head after removal of the cuticle. The front is at the top. The image has been taken under water, and the tracheal sacs can be seen bulging upwards.

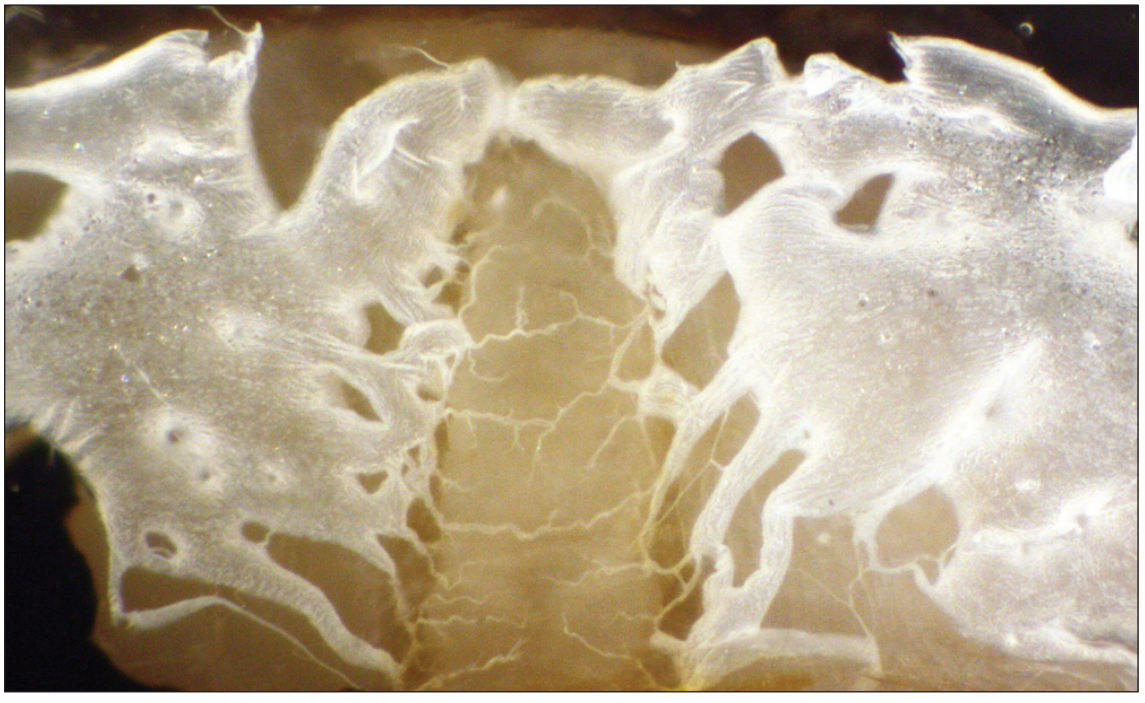


Fig 9.18. The back of the abdomen with the dorsal plates (tergites) removed. The structure down the centre is the heart. Tracheal sacs can be seen on either side of the heart, with tracheole branches penetrating into the heart tissue.

Fig 9.19. Tracheal sacs around the sting. The bulb of the sting is at the centre of the image.

Fig 9.20. Tracheal sacs just beneath a tergite of the abdomen.

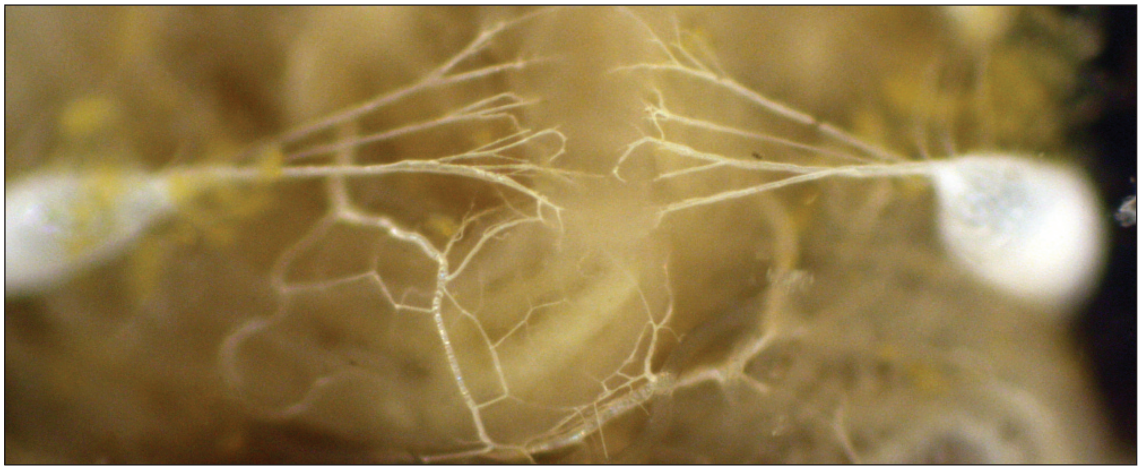


Fig 9.21. Tracheoles branching into part of the intestine.

Fig 9.22. A drawing of tracheal sacs in one worker abdomen, illustrating the variability in the arrangement of the respiratory system between bees.

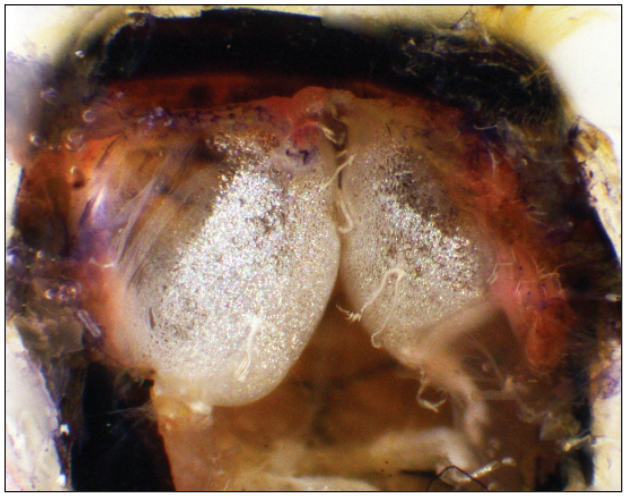


Fig 9.23. Two large tracheal sacs at the front of the abdomen, the usual arrangement.

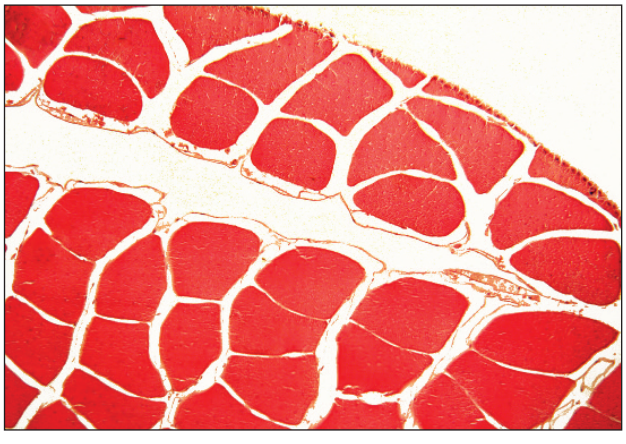


Fig 9.24. Tracheoles branching within an indirect flight muscle.

Figures 9.25 to 9.28 show tracheae passing into more peripheral structures.

Fig 9.25. Trachea entering coxa (first segment) of front leg.

Fig 9.28. Two tracheae in a section through the mid part of the scape of the antenna. The antennal nerve is the large central structure, surrounded by a number of muscle fibres.

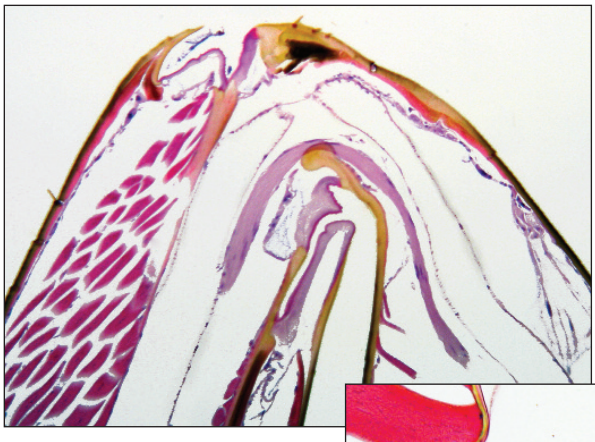


Fig 9.27. Trachea passing through knee (femur to tibia joint) of middle leg.

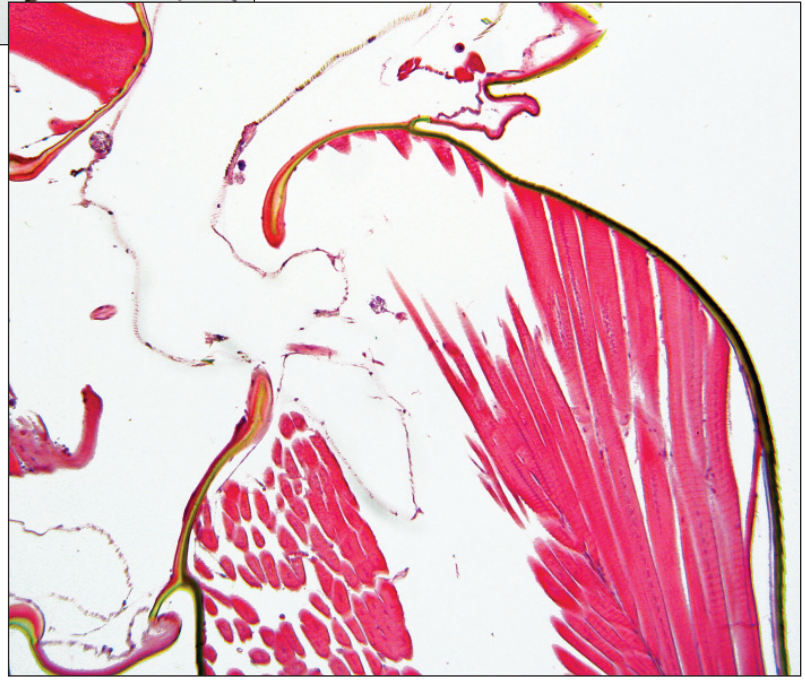


Fig 9.26. Trachea entering coxa of rear leg.