

BBKA

Module 5

Podcast

Transcript Notes

Written and Recorded by Janet Preece

Alimentary (Digestive) System

Welcome to the first in a series of podcasts aimed at the BBKA honeybee modules. This first group of podcasts is going to cover module 5 which is honeybee biology. We are going to start in this episode with the alimentary canal.

Before we do that though, we need to consider what food the honeybee is eating and requires. The 3 main food groups are carbohydrates, proteins and lipids. Carbohydrates are the sugars, and these are found in nectar and can be examples such as glucose, fructose and sucrose. Larger sugars can include starch and glycogen if you have heard of them before. Some of these sugars such as sucrose have to be broken down using enzymes into their useable forms and you may have heard of the enzyme invertase, its more common name now is sucrase. This breaks down sucrose into glucose and fructose. Honeybees just like other animals need carbohydrates as an energy source. Any energy demanding activities such as flying would use carbohydrates. Proteins are found in pollen and these can be broken down, again using enzymes, into their smaller parts, these are called amino acids. Proteins are used mainly for growth and repair of tissues. You will find a lot of protein being put into brood food. Lipids, also known as fats are also found in pollen and these need to be broken down as well using enzymes. Lipids are used for energy storage so things like the fat bodies will store lipids and they may also be used in growth and repair to make new tissue.

Moving on to the digestive system itself you should be able to see a schematic diagram of the digestive system in our resources or you can go and have a look at images in Snodgrass or Dade. At the start of the digestive system is the proboscis, the detail of this is found elsewhere in these podcasts. The function of the proboscis is to suck up any liquid food which is nectar. Around the mouthparts are also mandibles. These are toothed organs and they can chew the anthers to collect pollen. Once the nectar and pollen are collected, they enter the mouth area called the cibarium and glands such as the post-cerebral, hypopharyngeal etc may empty their secretions into this area. The cibarium merges into the pharynx which is the back of the mouth. The pharynx then merges with the oesophagus which is a muscular tube leading through the thorax into the abdomen to the crop. This is where food can go in two directions; one to go into the crop and one to go out of the crop to be regurgitated through the proboscis.

The crop is a muscular sac which can expand to accommodate extra volume. It can hold up to 100mg of food such as nectar and pollen but on average it usually holds about 40mg. The crop then has a valve which is called the proventriculus and this valve has 4 flaps with 4 pouches leading off. The flaps are lined with bristles and the valve is there to keep the liquid food in the crop. The pollen can be moved into the pouches and then empty into the next part of the digestive system. The proventriculus is thought to make gulping movements in order to facilitate this.

The ventriculus is the next part of the digestive system and any food that needs to be digested and absorbed by the honeybee enters into here. It's a large structure with a muscular wall. As food moves through, cells from the wall of the ventriculus rupture and secrete digestive enzymes onto the food which breaks it down into smaller substances. Within the ventriculus there is a structure called the peritrophic membrane which is a bit of a jelly-like structure and it surrounds and encapsulates the food and facilitates the enzyme digestion of that food. It also facilitates the flow of food around the ventriculus. Some of the digested substances may be absorbed through the ventriculus wall and into the haemolymph.

The ventriculus then empties into the small intestine, again a muscular tube. At the first part of the small intestine, the Malpighian tubules from the excretory system empty their contents into this. It's called the pyloric area and you will find a pyloric valve just after this point where the Malpighian tubules join. That ensures, just like any other valve, a one-way flow of substances. In the small intestine the inside layer is folded and that increases the surface area for absorption of the digested products and the food will be absorbed into the haemolymph.

Any food or wastes that have not been absorbed will empty into the rectum. Again, this is an expandable bag which can distend to a maximum size especially in a winter bee that may not have been able to go out on a cleansing flight. As the food sits in the rectum there are 6 rectal pads that are in contact with the food. These are partly chitinised so look slightly different from the rest of the rectal wall and are thought to absorb water from the waste products back into the haemolymph to conserve any fluid. Any extra wastes from this such as pollen husks, any undigested material and any excretory products from the Malpighian tubules are then expelled through the anus which opens at the proctiger which empties out through the abdominal segment number 10.

This is a brief overview of the structure of the alimentary canal. What you may need to do now is go back to your text books and put in some extra detail for what happens in each part. I hope you have enjoyed this, and I hope to see you again in the next episode.

Excretory System

Welcome to the second in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure and function of the excretory system of the honeybee. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The excretory system allows waste products to be removed from the haemolymph. Unlike the removal of undigested matter from the digestive system, excretion is defined as the removal of metabolic wastes ie those produced from cellular activity. Wastes produced in this way include chemicals containing nitrogen derived from the metabolism of proteins or nucleic acids (a group of molecules which include DNA). Ammonia is formed from these reactions which is a toxic substance to cells. This is converted into uric acid before being expelled. Other wastes can include water, ions or salts depending on the composition of the haemolymph.

Homeostasis is the maintenance of a constant environment within the haemolymph of the bee. Factors such as pH (which is the acidity or alkalinity) and concentration linked to levels of water and dissolved salts/ions need to be maintained for effective cellular functioning. The excretory system helps to maintain this.

In the larva, only 4 Malpighian tubules are present, these are not connected to the digestive system so simply remove wastes from the haemolymph, distending to a larger size until metamorphosis allows them to empty via the small intestine.

In the adult, around 100 Malpighian tubules are present. These are white, convoluted tubes that are in close contact with the abdominal haemolymph. The distal end of each tube is blind-ending whilst the proximal end connects and empties into the pyloric region of the small intestine.

Looking through a cross-section of a tubule, it is seen to be made up of a single layer of cells fixed to a basement membrane. This provides a very short distance between the haemolymph and the lumen (which is the space within the centre of the tubule). The inner face of the cells lining the lumen is folded into structures call microvilli, providing a large surface area for transfer of substances.

The tubule itself is in close contact with tracheoles from the respiratory system – these supply the oxygen needed for some of the active processes that take place here and remove any waste carbon dioxide that is produced.

Muscle fibres around the tubule contract and relax, allowing the tubule to move around in the haemolymph, constantly mixing the solution for maximum effect.

At the distal end of the tubule, passive filtration of wastes occurs. As waste products are at a higher concentration level in the haemolymph than in the tubule they automatically flow down the diffusion gradient in to the lumen of the Malpighian tubule.

Further along the tubule, cells actively secrete wastes from the haemolymph into the lumen as their concentration changes. Closer to the proximal end of the tubule, selective reabsorption of substances back into the haemolymph occurs. Both of these processes fine-tune the composition of the haemolymph depending on the conditions. Substances that may be actively excreted or absorbed include water and salts/ions.

Any wastes left in the lumen of the tubule then empty into the small intestine to be expelled via the rectum and anus.

Respiratory System

Hello and welcome to the third in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure and function of the respiratory system of the honeybee. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

As with most animals, honeybees require a supply of oxygen to their cells in order to break down food molecules such as glucose to release energy for active processes. During these reactions, carbon dioxide is produced as a waste product and must be expelled. It is the function of the respiratory system to provide the oxygen and remove the carbon dioxide from the body of the honeybee.

The outer openings of the respiratory system are called spiracles and there are 10 pairs of these along the body – each segment from T2 to A8 has a pair of spiracles (T and A refer to thorax and abdomen respectively). Each spiracle (except for T3 which is located under the wings) possesses a valve which, via muscular activity, can open and close to regulate air flow. However, the spiracle on T2 cannot close properly which is why the acarine mite can gain easy access to this part of the system. As a note, the largest spiracle is A1.

Each spiracle leads into the trachea, a tube with spiral thickenings of cuticle called taenidia – these support the trachea, preventing it from collapsing. This part of the respiratory system is synonymous with the outer cuticle and is shed between moults.

The trachea open out into air sacs which lack taenidia. These can be squeezed and expanded to exchange the air with the outside and act as bellows. Their size varies along the body of the bee with the largest air sacs being found in the A2 segment. The air sacs connect to each other by commisures, connecting tubes that link across the segment called transverse commisures and between segments called longitudinal commisures, forming a connected network of pipes. Although there are no spiracles in the head, 3 pairs of air sacs are present and connected to those in the thorax ensuring an efficient air flow to this part of the bee.

The air sacs and commisures branch into smaller and smaller tubes called tracheoles which are thin, delicate tubes. They can get as small as 0.1microns in diameter ie 1 ten thousandth of a millimetre. The tracheoles are open ended and open into the haemolymph, very close to cells. The end of each tracheole contains a small amount of haemolymph, the volume changing as the requirements of the cells change.

The oxygen in the tracheole diffuses into the haemolymph and then into the cells (diffusion is the movement of a substance from a high concentration to a low concentration). As cells become more active, they require more oxygen and so the diffusion occurs faster. Less haemolymph is found in the tracheoles when the cells are very active, this presumably facilitates faster diffusion of oxygen.

Conversely, waste carbon dioxide also diffuses out of the cells and into the haemolymph, eventually moving into the tracheoles and out of the bee.

When the bee is flying, it can establish a 1-way flow of air around the thoracic tubes. Air is drawn into the trachea at T2 and flows out of the thorax at A1 – valves and muscles around the spiracles control this flow. This makes the exchange of gases more efficient. When the bee is not at flight and resting, air flow can go in or out of each spiracle. The structure of a spiracle and its associated valve is shown in the supporting material.

To also aid in energy supply for flying, the indirect flight muscles contain a chemical pigment called cytochrome. This acts as a reservoir for oxygen as it can pick up oxygen and store it until it is required by the cell. This gives the muscles a pink colour.

The network of tracheoles and air sacs can be squeezed and expanded using muscles in the abdomen of the bee – if you have seen a bee returning to the hive and stood pumping its abdomen, it is probably exchanging oxygen and carbon dioxide with the air (it is out of puff!).

When the abdominal tergite and sternite compressor muscles contract, the tergite and sternite plates of the abdomen are pulled towards each other, effectively making the abdomen flatter. This squeezes the air sacs forcing air out of the spiracles. When the dilator muscles contract, the tergite and sternite plates move away from each other, the pressure decreases on the air sacs and air is drawn into them via the spiracles. In essence this is similar to how we breathe.

I hope that this has increased your knowledge of the structure and function of the respiratory system of the honeybee and I hope to see you again for the next episode.

Circulatory System

Hello and welcome to the fourth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure and function of the circulatory system of the honeybee. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

As humans we have a closed circulatory system which means we have blood that flows around the body in vessels such as arteries and veins. A bee has an open system where the blood or more correctly haemolymph is found all around the organs and tissues and is not fully enclosed. However, there are some similarities which we will mention.

The haemolymph has a number of important functions one of which is the transport of substances. It carries nutrients which have been absorbed from the digestive system to all cells of the bee's body. Nutrients can include sugars such as glucose, amino acids which can form proteins, fats, water, salts, vitamins and minerals. It also conversely carries wastes such as uric acid away from the cells and to the Malpighian tubules for excretion.

The haemolymph distributes oxygen to cells from the tracheoles of the respiratory system and removes carbon dioxide. It transports hormones from where they are produced to where they are needed.

As a fluid, the haemolymph can provide hydrostatic pressure to inflate structures. This can include the expansion of the wings just after emergence, an increase in size of the body when moulting and also the eversion of the endophallus in the drone.

As haemolymph bathes all the tissues it is important in a process known as homeostasis – this helps to maintain a constant environment around the cells. Factors such as water and salt levels need to be maintained. It will also distribute heat around the body.

Finally, it can also coagulate so that damaged parts can seal.

Haemolymph itself is made primarily from water – about 90% of it is water with some dissolved salts, nutrients, gases, hormones etc in it. There are also some cells called haemocytes which have a protective role against pathogens. Some of these may also help in the coagulation process.

Haemolymph is pumped around the body by the heart which is a structure found on the underside of the dorsal abdominal wall between segments A2-A6. Fibres which attach it to the dorsal diaphragm keep it in place. It is a lot simpler than our heart in structure and is made of a muscular tube with a blind ending posterior end and 5 chambers linked end to end. Between the chambers are 1-way valves known as ostia. As the heart muscle contracts blood is forced anteriorly and the ostia close. When the heart relaxes, the ostia open, allowing haemolymph from the surroundings to enter the heart.

The heart is connected to the aorta which is the only blood vessel found in the circulatory system of the honeybee. It is found in the thorax running from posterior to anterior and eventually ending in the head. Close to the junction with the heart, the aorta is a convoluted or folded tube which then smooths out. Its purpose is to direct the flow of haemolymph towards the head and associated organs such as the brain.

The antennal pulsatile organ is also found in the head and contractions of this directs haemolymph into the antenna. Movements of the pharynx muscles in the mouth also help pump the haemolymph.

Along with the heart, diaphragms can be found on the inner surface of the abdomen on both dorsal and ventral sides. These are sheets of thin membrane stretched across the segment, attaching to apodeme projections of the tergites or sternites. They have muscle fibres and can pulsate to help direct the flow of haemolymph forward and into the heart, as in the case of the dorsal diaphragms or backwards from the head as with the ventral diaphragms.

Although this flow is not as directed as that found in a closed system, it satisfies the requirements of the bee being such a small animal.

I hope that has helped you understand the circulatory system of the honeybee and I look forward to seeing you in the next episode.

Exocrine glands

Hello and welcome to the fifth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the function of the exocrine glands of the honeybee. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

Exocrine glands are those structures which produce secretions into ducts which empty either on the surface of the bee or into other structures such as the digestive system or sting chamber. This is in opposition to endocrine glands which release their chemicals directly into the blood or haemolymph. Exocrine secretions can act as pheromones in some cases ie signalling to other bees.

There are a number of exocrine glands present in the honeybee and these can vary between the sexes and castes, this will be referred to when looking at each individual gland. Unless stated, the glands are also found in pairs, one on the right side and one on the left.

Exocrine glands associated with the digestive system include the post-cerebral, thoracic, mandibular and hypopharyngeal.

The post-cerebral glands as their name indicates are found in the head behind the brain. The thoracic glands are located in the anterior part of the thorax. Both of these glands are collectively called salivary glands as their secretions empty into the mouth (ie the cibarium and pharynx). Each gland is made of individual units or acini which form small, compact bunches. The secretions from both empty into a common duct and the saliva produced is a watery, slightly alkaline solution that may contain the enzyme sucrase (or invertase). Its primary functions are to moisten food, dissolve substances and washing / grooming. These are found in both sexes and castes.

The hypopharyngeal glands are situated above the pharynx in the head hence the name (hypo means above or high). These are large glands with several hundred small cream-coloured acini which resemble a string of onions. The secretions from these run down a duct and eventually onto the mandibles. These glands are only present in the workers and are larger in younger nurse bees and reduce in size as the bee ages. The secretions change depending on the age of the bee – a young nurse bee will produce protein which contributes to brood food and royal jelly. When older, the secretions contain sucrase to start the process of digestion of sucrose presumably as house bees processing nectar into honey.

Mandibular glands are found above the mandibles and are present in both sexes and castes although they are smaller in drones. These are single-lobed glands, looking very different to the previous glands. Secretions from these runs down grooves on the mandibles. In the queen the secretions from these glands include 9-ODA (oxo decan-2-enoic acid) which is used as a drone attractant. 9-HODA (hydroxy dec-2-enoic acid) is used as a swarm attractant and is also thought to reduce the development of ovaries of workers when in the hive.

In workers the mandibular glands of nurse bees help with the production of brood food by producing 10-HODA which is thought to be a preservative. In older workers, alarm pheromone is produced which include 2-heptanone which can be used to attract other workers in the defence of the hive.

Drones seem to produce the same chemicals as workers ie 10-HODA and 2-heptanone which may be used in marking drone congregation areas and attracting other drones to the area although work on drone pheromones is a little patchy.

An exocrine gland unique to the queen is the tergite or Renner-Baumann gland which are situated in the abdomen and empty into the grooves between segments A3, A4 and A5. It is thought that 9-ODA and 9-HODA are produced from these and suppress ovary development in workers. These may also stimulate retinue behaviour in workers.

Both queens and workers have arnhart glands on the 5th tarsomere of each leg, producing secretions which run onto the foot (pretarsus). This acts as a footprint odour, marking the place where the queen has walked within the hive or where foragers have visited flowers to mark forage. Within the hive it may suppress swarming instinct and indicate queen presence. The composition of the secretions is unknown but is an oily substance.

Around the sting chamber the acid gland in workers will produce an alarm pheromone which includes isopentylacetate among other chemicals. It will initiate a stinging response in other workers.

Nasonov glands, only present in workers are situated at the posterior end of the abdomen and secretions are released in a groove running between the tergites of A6 and A7. The secretion contains a number of chemicals, the most common of which is geraniol. Geranic acid, nerol, nerolic acid, citrate and E-citrate (the last being the most chemically active) are some of the other chemicals found. Nasonov secretions attract other bees such as when marking an entrance, attracting a swarm or marking water or forage.

Four pairs of wax glands are found in the abdomen on the ventral (bottom) side of workers only. They produce wax which is secreted between the segments onto the wax mirrors. Initially as a liquid, it then hardens into flakes and then is passed to the mandibles for manipulation into comb, cappings etc. Wax is made of a mixture of chemicals mainly hydrocarbons including acids, hydroxyacids, alcohols and diols to name but a few.

There are other glands present such as the Dufour's gland which is well developed in queens and is thought to lubricate and mark eggs as they are laid. These can develop in laying workers. The Koshevnikov gland present in the sting chamber of the queen is thought to attract workers although the composition of these secretions are largely unknown.

This has been a whistle-stop tour of the exocrine glands of the honeybee and there are a number of uncertainties in places, but I hope that this has added to your knowledge of this important set of organs and I hope to see you soon for the next episode.

Nervous System

Hello and welcome to the sixth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the function of the nervous system of the honeybee including the eyes and sensilla. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The nervous system of a honeybee, just like ours, has the function of controlling the body. Unlike ours, the central system such as the brain, coordinating responses is a lot smaller than ours. Electrical signals pass along nerve cells that act like electrical wires, transmitting the signal from one part of the body to another. These signals pass along very quickly and so can have an almost instantaneous response.

The nervous system is derived from the ectoderm of the developing larvae. In the larvae there is a single pair of ganglia in each segment – these act as a coordinating centre for the segment. In the adult some of these ganglia have fused into larger structures. For example, the head, which is essentially formed from the fusion of 6 segments has the brain formed from the ganglion of the first 3 segments and the sub-oesophageal ganglion formed from the next 3 segments. A large thoracic ganglion is formed from those found in T2, T3, A1 and A2 ganglia. Similarly, segments A7, 8, 9 and 10 have their ganglia fused into one larger pair of ganglia. Fusion seems to occur where most coordination is required eg in the head where information from sense organs need processing, the thorax to control the legs and wings and the abdomen when controlling the sting or reproductive organs.

Connecting each pair of ganglia is the ventral nerve cord, made up of a pair of nerves running from each paired ganglia to the next. This as the name implies is found running along the ventral wall of the bee.

Radiating out from the ganglia are nerve fibres which connect to various structures such as muscles or glands which need controlling.

The brain is split into 3 areas. The protocerebrum which derives from the first head segment contains the optic lobes and receives information from the compound eyes and ocelli. The deutocerebrum formed from the second head segment receives impulses from the antenna. The tritocerebrum controls the labrum and cibarium. A specialised area known as the corpora pedunculata is thought to be an association centre, coordinating responses from the sense organs into an action. Corpora is latin for body – think of corpse and peduncle is a stalk although most text refer to this as the mushroom body, presumably because the stalked part looks like a mushroom. As a side note this structure is largest in workers and smallest in drones.

The sub-oesophageal ganglion is thought to control the lower mouth parts such as the mandibles and proboscis.

Looking at the sense organs these comprise the 3 ocelli, the 2 compound eyes and the numerous sensilla scattered all over the surface of the bee's body.

The ocelli are found on the top of the head of the bee, pushed forward in a drone due to the size of the compound eyes. They are thought to detect light intensity and the position of the horizon. If these are covered, the bee forages later in the day and stops earlier. A convex lens forms the outer part of the eye. Behind this are transparent cells forming a vitreous layer, probably shaping the lens. Behind these are about 800 light-sensitive cells – these detect the light and pass a signal along nerve fibres to the brain. The whole ocellus is surrounded by pigmented cells, absorbing any stray light that enters the structure.

Each compound eye is made of a number of single ommatidia. The queen has around 3000, a worker 4000-6900 and a drone 8600. Light enters the hexagonal structure through the corneal lens which focuses the light down the centre of the ommatidium. It passes through the crystalline cone and into the rhabdom of the inner section. Each ommatidium is surrounded by pigment cells to avoid light from one entering sideways to other cells. The inner section has either 8 or 9 retinula cells that contain a light-sensitive

pigment. 8 of them are thought to detect wavelength or colour of light 2 for UV, 2 for blue, 2 for green and 2 for yellow. Bees do not have cells that detect red light and so that colour would look black to them. The 9th cell in some ommatidia is thought to detect the direction of plane polarised light. This is light that can indicate the position of the sun even on a cloudy day. Nerve cells from each retinula cell send signals down the optic nerve to the brain.

As the brain receives this information the picture seen will have less detail than that of humans – the image would look more like a mosaic pattern with about 1/100th the acuity or detail of what we see. However, as the signals come from successive and adjacent ommatidia, the brain can sense movement at a far faster speed than humans. We can process around 30 images a second, a bee can process about 300 – this is called the flicker fusion frequency and means a bee is 10 times quicker at detecting movement than we are.

Both the ocelli and compound eyes can therefore provide information to the bee about light intensity, the position of the sun, the colour of their surroundings and any movement.

Insects such as honeybees are encased in a hard exoskeleton of chitin so how do they sense the world around them such as smell, taste, wind speed etc. This is the function of the numerous sensilla located on the surface of the honeybee body. Just as we have different sense organs to detect smell, taste, touch, temperature etc so the honeybee has different sensilla.

Sense plates known as placodea or plate cells are circular structures with radiating pits through which chemicals can pass. This provides the bee with a sense of smell. There are around 30,000 of these on a drone antenna, especially at the tips, indicating their importance at smelling chemicals such as queen pheromones.

Hairs or setae called trichodea can be found all over the body even between the ommatidia of the compound eyes. These are single hair cells which, when deformed or moved, stimulate a nerve cell which is connected to a thin part of the membrane called the scolopale. This acts as a sense of touch. These can be found all over the body but especially at joints to feed back the position of the body. The tormogen cell produced the thin membrane around the hair.

The Organ of Johnstone which is found in the antenna between the scape and flagellum also detects vibrations of the antenna and can also indicate wind speed.

Peg organs also known as basiconica can also detect chemicals and are thought to act as taste. They are found primarily on the antenna and around the mouthparts but also on the legs and look a little like a short, stubby cone projecting from the cuticle of the bee.

Sunken pits or sunken pegs called coeloconica can be of different types and can detect various environmental factors such as temperature, carbon dioxide levels or relative humidity.

Bell organs or campaniformia are dotted around the body and provide the bee with information about how much stress the cuticle is under. These may be small bumps in the cuticle under which a nerve cell is located and as the cuticle stretches and bends, it sends signals. These are mainly found around the mouthparts, bases of the antenna and wings, sting and legs.

I hope that has helped you understand a little more about the nervous system of the honeybee and I look forward to seeing you in the next episode.

Endocrine Glands

Hello and welcome to the seventh in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the function of the endocrine system of the honeybee. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

We have previously reviewed the exocrine system in episode 5 of this series of podcasts and these are structures that empty their secretions into ducts or channels. The endocrine also produces chemicals and these are called hormones. These are secreted directly into the haemolymph just as our hormones enter our blood system. They travel around the bee and target specific cells to stimulate a response. They are usually used for coordinating long term development such as growth, moulting, determining caste in the females and also determining the age of duties in the workers.

There are 3 main endocrine glands, the corpora allata, the corpora cardiaca and the prothoracic glands. Corpora is Latin for body as we see in the word corpse. There are also other structures called neurosecretory cells which form a link between the nervous system such as the brain and ganglia and the endocrine glands so that there is some overall control and coordination between the two.

The corpora cardiaca is a pair of glands located behind the brain, on either side of the aorta (hence the name cardiaca referring to the cardiovascular system). They are connected to the brain by neurosecretory cells and store hormones from these cells.

In the larva the corpora cardiaca produces a hormone called prothoracicotropic hormone or PTH for short which enters the haemolymph and stimulates the prothoracic gland to produce ecdysone which is the moulting hormone.

The function of the corpora cardiaca in the adult is currently unknown.

The prothoracic glands are a pair of glands are between the pro and meso thorax close to the oesophagus in the thorax.

They produce ecdysone in response to stimulation from the corpora cardiaca hormone .PTH Ecdysone stimulates epithelial cells in the cuticle to produce moulting fluid so that the cuticle can be shed. The prothoracic glands degenerate after pupation and are absent in adults.

The corpora allata are found in the head just behind the corpora cardiaca either side of the oesophagus. Again, these are connected to the brain and sub-oesophageal ganglion by neurosecretory cells. The corpora allata produces juvenile hormone (in some older texts this is known as neotenin). In the larva, the levels of juvenile hormone and ecdysone coordinate growth and moulting – high levels of JH from the corpora allata inhibit the activity of the prothoracic gland, lowering the levels of ecdysone produced from the corpora cardiaca – this promotes growth in the larva. Lower levels of JH remove the inhibition of the prothoracic glands and therefore higher ecdysone levels are seen and moulting occurs. This means there must be some coordination between the brain, corpora cardiaca and corpora allata to fine tune this rhythmic process of growth and moulting.

In the females JH and another hormone called vitellogenin will control caste determination – in queens there is a high level of JH around day 3 of larval development compared to a worker which promotes queen development. In the adult queen JH will promote ovary development whilst in workers it will reduce ovary development. It is also thought to increase development of drone reproductive organs, but this is not known for certain.

JH has other functions in the adult bee. JH levels increase in an adult, peaking around day 15. In general, as JH increases it stimulates age polyethism ie a movement from hive duties to more entrance and guard

duties increasing defensiveness to eventually promoting the worker to a forager. It will help with the development of glands such as the hypopharyngeal in order to produce brood food and royal jelly.

As you can see there is a lot of coordination between endocrine glands, the nervous system and as yet unknown mechanisms in the honeybee to control these quite complicated processes. I hope that this brief overview has increased your knowledge and understanding of the endocrine system and I hope to see you for the next episode.

Fat Bodies

Hello and welcome to the eighth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the function of the fat bodies of the honeybee. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

Fat bodies are found in the larvae, pupae and adults of the honeybee and other insects. They have different roles and cellular structure depending on the stage of the lifecycle.

There are 3 types of cells found in the fat bodies – fat cells (or trophocytes), oenocytes and urate cells.

In a larva the fat bodies can make up to 65% of the weight of the larva. They are white which gives the larva its white colouration. The trachea anchor them in place. As the larva grows in size, the fat bodies also increase in size.

In a larva the fat cells can contain proteins, fats and carbohydrates, which are absorbed from the food it receives. A fat cell contains vesicles or sacs containing albuminoid granules which are made from protein (albumen is the main protein found in egg whites and is also present in our own blood). It also contains fat droplets and glycogen which is a type of carbohydrate. The fat cells are smaller in size than the oenocytes. Urate cells collect and store nitrogenous wastes and they can be found to contain crystals of uric acid.

In the prepupa and during metamorphosis, the fat cells increase in size equal to the oenocytes. They do this by absorbing the nutrients from the breakdown of the tissues that once formed the larva. Eventually, the fat cells themselves separate and breakdown to release their contents, this provides the nutrients necessary for the tissues in the pupa to form and take on the adult structures. Once the Malpighian tubules fully develop, the urate cells are no longer needed and so disappear – these are not found in the adult bee.

In the adult, fat bodies are found on the floor and roof of the abdominal cavity. They can change in size and composition depending on the time of year and the age of the bee. The fat bodies are now made up only of fat cells and oenocytes. Fat bodies are largest in a winter bee and smallest in a summer bee. As stated previously, the fat cells contain proteins, fats and carbohydrates but during summer, the protein content of these will decrease as it is turned into brood food to feed the developing larvae. In a foraging worker bee, the glycogen or carbohydrate stores of the fat body also decrease and are used up providing a source of energy for flight. In winter, the protein content will increase as the bee builds up stores to aid its survival during winter. It is also not feeding brood.

The oenocytes are thought to be closely involved in wax production. They are found in higher numbers around the wax glands and are thought to produce the fats necessary for wax formation. It would be logical therefore, to assume the size and number of these are at a maximum when the worker is around 12 days old and producing wax and then decrease as the worker ages.

There is still a lot of research needed on fat bodies as not all of their functions are fully understood. However, I hope that this brief overview has increased your knowledge and understanding of the fat bodies in honeybees and I hope to see you for the next episode.

Reproductive System

Hello and welcome to the ninth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the function of the reproductive systems of the queen and drone honeybee and the production of sperm and egg cells. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

In the queen there are 2 ovaries which are smaller in a virgin queen and increase in size after mating when eggs or ova are produced. In a laying queen these can fill the abdominal cavity and are dorsal to or above the digestive system. Each ovary consists of between 150-180 ovarioles which are tubes within which the eggs develop. Ovarioles lead into lateral oviducts which then merge to form the median or common oviduct which serves both ovaries. The median oviduct passes the valvelfold close to the entrance to the spermatheca and then leads into the vagina. Eggs will eventually pass through the bursa copulatrix and through the sting chamber before being laid. The spermatheca holds the sperm from the drones and the spermathecal gland nourishes them. If needed for fertilisation, the sperm are released through the spermathecal duct which has a pump and valve to regulate their flow.

Eggs develop in the ovarioles from germinal cells. As they grow in size they form around 48 trophocytes and an oocyte which has been formed by a special type of cell division called meiosis which halves the number of chromosomes. The whole ovum or egg is surrounded by follicle cells. The trophocytes absorb nutrients from the haemolymph and pass these to the oocyte which increases in size. Once fully developed, the follicle cells form the chorion of the egg and the trophocytes disappear, leaving a large oocyte or egg containing a large yolk.

When the egg is about to be laid, it can pass through the reproductive system without being fertilised (this will produce a drone) or it can more often than not, be fertilised by sperm from the spermathecal gland. The egg passes over the muscular valvelfold which presses the egg against the entrance of the spermathecal duct. The pump and valve pass sperm onto the egg – more than one is probably released at a time but only 1 is needed to enter the egg for fertilisation to occur.

A worker possesses ovaries but these are a lot smaller, made only of around 2-12 ovarioles. A worker does not possess a spermatheca.

The drone has 2 testes, these are extremely large in an immature drone and can fill the abdominal cavity. After emergence they begin to decrease in size and are smallest at around day 12 when the drone is sexually mature. Their role is to produce sperm cells. Just as in the ovaries of the queen, sperm are produced in tubes starting life as germ cells. These divide to produce spermatogonia. Bundles of these cells form spermatocytes which then grow and divide by meiosis to produce spermatids which are immature sperm. These mature and change shape to the characteristic tadpole form and are now known as spermatozoa (or sperm for short). Once mature, the sperm move down the muscular vas deferens tubes into the seminal vesicles in preparation for mating. The sperm will stay in the seminal vesicles and be nourished by them until mating. When mating takes place, the sperm travel through the ejaculatory duct passing the mucus glands which add mucus to the sperm. This is thought to harden on contact with air and prevent the sperm from leaving the queen. During mating the endophallus bulb everts through the phallosome due to pressure from the abdomen and enters the queen's bursa copulatrix. The sclerites may help to support the bulb as it everts. The sperm is then deposited in the queen's reproductive tract by muscular contractions of the seminal vesicles and mucus glands. The horns or cornua were thought to hold the drone in place during mating but this is not the case. Their function is currently unknown although they are highly visible to other drones in UV light and it is hypothesised that they may act as mating guides to other drones.

The sperm enters the queen which such force that it ends up in her oviducts. Eventually, after a day they will have moved to the spermatheca and reside in there until needed. Many sperm are lost from the queen during this time but around 5-6 million sperm are stored as she will have taken part in 15-20 matings.

As you can see, reproduction in the honeybee is a complex process requiring a number of specialised structures in both the queen and drone. I hope this has increased your knowledge of this fascinating aspect of bee biology and I hope to see you again in the next episode.

Egg structure, embryo development and hatching

Hello and welcome to the tenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure of the egg, the development of the embryo and the hatching of the larva. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

A honeybee egg is around 1 and a half mm long and about 0.33mm wide. It is slightly curved and weighs 0.13mg. The head or anterior end is wider than the posterior end and the dorsal side is convex which the ventral side is concave. The dorsal side of an animal is the uppermost and the ventral the lower (in humans the dorsal side would be your back and the ventral your chest and tummy).

The egg is covered in an outer layer known as the chorion which forms a continuous protective layer around the cell. A hole called a micropyle is found in the anterior part of the chorion and is the passageway for a sperm to enter if the egg needs to be fertilised. Underneath the chorion is a vitelline membrane which surrounds a liquid called the cytoplasm (if you have any knowledge of cell structure this would be familiar to you). The central part of the egg contains a large yolk and suspended in this is the nucleus of the egg cell which contains the DNA or genetic material (remember this only has 1 set of chromosomes due to the meiosis cell division which formed the egg cell in the queen).

Whether a cell is fertilised or not, once it is laid, it begins to change to form the embryo. If fertilised the sperm will fuse with the nucleus of the egg. This will then divide by a different form of cell division called mitosis which produces cells identical to each other within the yolk. This process is called cleavage and the cells formed are called cleavage cells. These migrate outwards forming a layer of cells called a blastoderm (derm refers to skin or layer in biology).

One area of the blastoderm on the ventral side thickens by producing more cells and this then becomes a germ band – this forms the embryo.

From this point onwards, any new cells formed start to change and specialise into different structures. The embryo forms structures called plates – there are 2 different types of plate – the lateral and median plates. The ectoderm will form from the lateral plates and eventually form structures such as the trachea, nervous system, endocrine glands, external reproductive parts and all of the external structures of the bee such as the cuticle, wings, legs etc. The median plates will form the mesoderm which will eventually go on to form structures such as the muscles, heart and inner reproductive organs. The final part the endoderm forms from the remaining blastoderm and migrates inwards to form the digestive system. Invaginations or folds that form from both anterior and posterior ends will fuse eventually to form this tube running through the bee which is the digestive tract. This 3-layered body plan is exactly the same as all higher animals including us.

The whole of these structures which eventually form the larva are still enclosed within the chorion of the egg and surrounded by the amnion another structure formed from the lateral plates of the germ band.

Towards the end of the egg period, the embryo which now has a number of recognisable features also forms segments from front to back and is now similar to a larvae. After 72 hours, the now formed larvae begins to wriggle, the chorion splits and the egg hatches into a new larva.

I am sure you have seen eggs in your own colonies and sometimes found it difficult to see these tiny structures. However, this shows that underneath the thin shell, a lot of activity is going on in this first stage of the lifecycle of the honeybee. I hope that has given you more of an insight into this period and I hope to see you again for the next episode.

The External and Internal Structures of a Honeybee Larva

Hello and welcome to the eleventh in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the external and internal structures of the larva. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The larva emerges from the egg about the same size of the egg – 1.5mm long and 0.33mm wide and weighing around 0.13mg. It is segmented but the first 6 segments have already fused to form the head. The remaining segments comprise of 3 thoracic and 10 abdominal. The letters T and A will be used here to refer to these segments.

The head is small and inconspicuous and there is evidence of rudimentary legs and wings on the thoracic segments although these are almost like small bumps on the surface.

Ten pairs of spiracles, small openings which form part of the breathing system, are found on segments T2 and T3 and A1-8.

Inside the larvae the digestive system starts with the mouth and then stomodaeum which form the foregut. A simple, oesophageal valve which prevents regurgitation, leads on to the ventriculus which forms the midgut. 4 Malpighian tubules lead off from the ventral part of the ventriculus and these absorb any waste material which remains undigested. The ventriculus is blind-ending – the Proctodaeum which is the hind gut is not connected to the ventriculus until after the cell is sealed and metamorphosis begins. The anus then forms the last part of the digestive system.

The labium and spinneret are found just below the mouth and lead into a pair of silk glands. These are employed once the larvae starts metamorphosis to spin the cocoon.

The immature ovaries or testes are found dorsal to the digestive system and occupying the space around segments A4-6.

The heart of a larvae is similarly placed dorsally covering T2-A9 but it has more chambers – 11 in total and 10 ostia. The respiratory system does not contain air sacs, but the spiracles lead onto 2 main longitudinal trunks (running along the length of the larva. Fat bodies are large and white, giving the larva its pearly white colouration. The nervous system includes the brain and sub-oesophageal ganglion along with paired ganglia in all 3 thoracic segments and in segments A1-8 of the abdomen (ganglia from A9 and 10 have fused with that of A8).

During the larval stage, the nurse bees will feed the larvae and the larvae will go through 4 moults before the cell is sealed, growing in size between each one. Insects and other similar animals have to shed their outer skin or cuticle to grow in size and this is known as moulting. Once the larvae has grown sufficiently in size and undergone 4 moults it is now ready to pupate.

Although simple in structure compared to an adult bee, the larvae has an important role – it is an eating growing machine, getting the bee ready to undertake metamorphosis. I hope this has helped you understand more of the structure of the larvae and I hope to see you again for the next episode.

Metamorphosis

Hello and welcome to the twelfth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the process of metamorphosis of the larva. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

After hatching from the egg the larva undergoes 4 moults whilst being fed by the nurse bees.

Moulting involves detaching the old cuticle from the underlying tissues and then forming a new cuticle beneath this. Epidermal cells beneath the cuticle will secrete moulting fluid which detaches the old cuticle from them. At the same time new cuticle is formed by the same epidermal cells. The lower layer of the cuticle, the endodermis is digested using enzymes and the products re-absorbed into the larva, the outer layer the exocuticle is shed by the larva swallowing air and increasing in size until the cuticle splits and is sloughed off.

2 days after the 4th moult the cell which houses the larva is sealed. The larvae eats the remaining food and stretches out lengthways in the cell with the head end closest to the capping. 24 hours after being capped the ventriculus and hind gut (proctodaeum) fuses and the larvae defecates for the first time into the bottom of the cell. At the same time, the larva spins a cocoon using its paired silk glands. The silk emerges from the spinnerets just beneath the mouth. It then enters a state of quiescence.

After another 24 hours, the pupa starts the 5th moult and forms a propupa. The moult is not completed at this time, the old skin is still attached to the new cuticle being formed beneath it. During this moult, the external features of the larvae develop into the adult form. These structures include the mouthparts, eyes, antenna, legs, wings to some extent, fore and hind gut, trachea. Segments A8-10 telescope into A7. Around 2 days after starting, the 5th moult completes and the pupa now resembles the adult form at least in shape if not in colour or detail.

There now occurs a massive remodelling of the internal organs of the pupa which is fuelled by the fat bodies which have absorbed food from the nurse bees and the products from the breakdown of the tissues within the larva. Eventually the fat cells separate and rupture, ejecting their nutrients into the body cavity of the pupa – this now provides the fuel to form new tissues which will form the adult.

The brain enlarges due to the development of the sense organs and some of the ganglia fuse so that only 7 ganglia are found in the adult – two in the thorax and 5 in the abdomen. Nerve connections are remodelled as the body systems such as the muscles change and develop.

The muscles will be re-modelled and grow in size especially the flight muscles. They have an external cuticle to attach to and nerves will grow to control them and connect them to the ganglia or brain.

The heart reduces in size from 11 chambers to 5.

The respiratory system develops airsacs and more branches of tracheoles to penetrate all the new tissues.

The 4 Malpighian tubules have disintegrated and in their place form around 100 tubes.

The digestive system is re-modelled into the adult form, for example, the crop, proventriculus rectum etc are formed.

The reproductive system continues developing as the testis and ovaries were already present in the larvae. The testes will become very large in the drone during this stage as this is when the sperm are formed. Once emerged, these will shrink.

This internal change takes around 8 days on average in a worker after which the pupa will undertake its 6th and final moult, turning into an imago – this is a fully formed adult bee, but it needs around 24 hours for its cuticle to harden and for external structures such as the wings and hairs to dry out after the moulting

process. The cuticle hardens by a chemical process known as tanning and it darkens during this process. The bee will then chew its way out of its cell and emerge as an adult honeybee.

Complete metamorphosis in any animal is an amazing and almost magical process, happening behind closed doors and completely changing the individual into a new form. The honeybee is no exception and there is still a lot we don't understand about this complex process. However, I hope that this account has given you a small insight into this fascinating process and I hope to see you again for the next episode.

Effect of Feeding on Caste Determination

Hello and welcome to the thirteenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the effect of feeding and other factors on caste determination. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

There are 2 genders of honeybee – females and males produced from fertilised or unfertilised eggs respectively. However, there are 2 castes of female – the worker and the queen and as they are both formed from a fertilised egg, other factors must be involved in determining the path the bee takes. It is known that the type and amount of food fed to the larvae are the main factors in determining this.

Food produced by the nurse bees comes in three types:- the white portion is produced by the mandibular glands and it is this secretion which makes up the majority of royal jelly. White food is high in biotin and pantothenic acid both of which promote faster growth in the larva. The clear portion of food comes from the hypopharyngeal glands and the crop (which will contain some honey from the stores). The yellow portion is mainly made of pollen and its derivatives. These latter two types make up the majority of brood food.

Both brood food and royal jelly are high in proteins such as major royal jelly proteins, essential amino acids ie the building blocks of proteins that cannot be made by the larva and lipids, especially 10 hydroxy-2-decanoic acid. A number of these substances are antimicrobial and antibacterial. However, the sugar content and type differs between the two. Royal jelly has 34% sugar which is mainly glucose whilst brood food alters from 12% during the first few days to 47% and changes from glucose to more fructose.

Nurse bees do not directly feed the larvae but deposit food into the cell for the larvae to feed on. The caste of the resulting bee is determined by the mix and quantity of this food.

A queen larva will receive royal jelly which is mainly white secretions from the mandibular glands for the whole of the larval stage. She will also have had 12-1600 visits from the nurse bees to supply her with a large quantity of this food which is why you can see the larva floating in food in a queen cell (worker larva do not float in the same quantity of food). The high level of sugar in this diet acts as a phagostimulant which encourages the larva to feed.

A worker larva will receive about 20-40% white and the rest clear food over the first 2 days and then this will change to almost 100% clear with some yellow food – you may have heard of this mix being called bee bread due to it being a mixture of pollen and honey. As you can see, a worker receives a higher proportion of clear secretions from the hypopharyngeal glands compared to the queen over the feeding period. The worker larva will also only receive around 140 feeding visits and therefore have less food than the queen.

It is thought that after days 2-3 of the larval stage, the corpora allata gland in the queen increases in size due to more sugar being present in the diet. It is at this point that the path seems to be set on the resulting caste produced which is probably why grafting older larvae produces poor or no queen. By days 4 to 5 the level of Juvenile Hormone in the queen larva has reached around 10 times the levels seen in that of a worker larva. You may remember that the corpora allata produces juvenile hormone which is responsible for queen development such as increase in ovariole number.

So how does this difference in food cause all these changes in a larva? The difference alters the activity of genes in the larvae, switching some on and some off so that for example in the queen the corpora allata growth gene will be switched on earlier than that of the worker causing the increase in JH. In response to the higher levels of JH, genes for ovary development switch on. Other genes for the formation of a corbicula or wax glands not present in a queen would switch off.

There is still a lot to find out about how nature turns a single fertilised egg into either a queen or worker bee simply by the food it eats but I am sure you agree this is a fascinating area of honeybee biology. I hope to see you for the next episode.

Laying and Normal Workers

Hello and welcome to the fourteenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the physiological and structural differences between normal and laying workers and how this is brought about by pheromones. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The queen is usually the only reproductive female in a colony of honeybees. However, due to certain factors, laying workers can develop and this account will look at how this comes about and what the differences are between a normal and laying worker.

The queen produces a number of pheromones within the hive which suppresses the ovary development of the workers. Pheromones produced by the tergite gland, mandibular gland and hypopharyngeal glands are all thought to be involved in this process.

Pheromones also come from the brood itself. Both open and capped brood produce brood pheromone which is thought to suppress worker ovary development and may even play a more important role in this than the queen pheromones. In the absence of a queen and brood, laying workers will develop.

The reproductive system of a laying worker will begin to develop. Although workers have a reduced number of ovarioles in their ovaries – around 2-20, which are vestigial (this just means they are under-developed) a number of these, thought to be around 6-12 will begin to mature and produce eggs. The laying worker will then be able to lay around 50 eggs a day – a far cry from the 1500-2000 that a queen lays. Workers have never mated and do not possess a functioning spermatheca so all of these eggs will be unfertilised and develop into drones. The abdomen of a worker is shorter than that of a queen and so eggs will be laid onto the side walls of the cells. As a number of laying workers may be present, more than one egg is deposited into a cell. The pattern of laying is also haphazard with brood being patchy.

Physiologically, the laying worker will also have an enlarged Dufour's gland which is small in the normal worker. This will produce queen-like pheromones, indicating to the colony that a queen is present. It is thought that it may also label the eggs preventing workers from destroying them, which would normally happen during policing in a queen-right colony if a worker lays eggs. The mandibular gland enlarges in the laying worker and produces 9 oxododec-2-enoic acid which again, acts as a queen-like pheromone, suppressing worker ovary development.

As more drone brood is produced by the laying workers, the brood pheromone from these will suppress the development of any other laying workers, reducing the number of these in the hive. The laying workers will have an extended lifespan compared to the normal workers, although the lower level of brood in the hive will also extend their lifespan to some extent.

It may take up to 3 weeks for a colony to produce laying workers, a shorter time if there is less brood when the queen is lost. However, at this point a colony is usually hopelessly queenless – in other words it has no means with which to produce a new queen - and re-queening is difficult if not impossible. The colony can be more defensive at this point and acts disorganised. It will eventually collapse.

This account indicates how finely tuned a queen-right colony is and how disruptions to this normal balance can alter the colony irrevocably. I hope that has given you more of an insight into the difference between laying and normal workers and I hope to see you again for the next episode.

Difference Between Summer and Winter Worker Bees

Hello and welcome to the fifteenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the differences between summer and winter workers. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The lifespan of a worker bee depends on a number of factors including the season, available forage, activities undertaken and the race of the bee. On average, a summer worker will last between 15-38 days and a winter worker around 140 days. One of the main factors for this difference is the amount of brood and hence the amount of work the worker has to undertake. Feeding brood, keeping it warm, capping the larvae, foraging for food etc will all take its toll on the house bees and shorten their lifespan. It is noticeable that lifespan is extended when there is little or no brood to rear, even if this occurs in the summer for example when swarming or when a colony becomes hopelessly queenless.

Due to less work being undertaken, the metabolism of a winter bee is reduced whilst that of a summer bee is high. This means the nutritional composition of a worker will change. Winter bees have less fat stores but a lot more protein. A winter bee will have larger fat bodies to accommodate this extra protein along with higher glycogen stores (this is a form of carbohydrate which is used up during metabolism and flying). The hypopharyngeal gland of a winter bee will be larger than its summer counterpart.

All newly emerged workers consume pollen. In a summer worker this will allow the hypopharyngeal glands to develop in size so that it can take on nursing duties converting protein consumed into brood food hence the lower protein levels in a summer bee. As the HP gland produces its secretions and the bee ages, it will eventually reduce in size. A newly emerged worker going into winter will also consume pollen and develop its HP glands. However, as these are not used to feed brood, they remain large and in the young state. Any excess protein is then stored in the fat bodies.

However, a winter bee may not be able to leave the hive very often for cleansing flights and so will have a larger, more distended rectum than a summer bee. However, on a warm, sunny winter day, this can be voided on a cleansing flight so the size of the rectum will be variable in a winter bee.

Once brood rearing starts in late winter / early spring, the physiology of the winter bee will change to that of the summer bee and they will age quickly tending the young.

I hope that this has given you an insight into the main differences between summer and winter workers and why their lifespans are very different and I hope to see you again for the next episode.

Structure of the Cuticle

Hello and welcome to the sixteenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure and functions of the cuticle. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The cuticle is the structure that forms the outer covering of all insects including honeybees. Similar to our own skin it has a number of layers with different chemical compositions that allow it to perform the many functions it has. Unlike us, this cuticle needs to be shed in order for the bee to grow in size, a process called moulting, which is covered in the metamorphosis podcast.

The cuticle provides a waterproof layer which reduces the loss of water from the bee, decreasing the chance that it will dehydrate. It provides protection for the delicate, internal organs. Synonymous our own skeleton, it provides attachment points for muscles so that the bee can move. These attachment points are known as apodemes. Some areas of the cuticle need to be harder than others, for example the sting which may need to penetrate tissue, the mandibles which need to cut or chew structures and the endophallus of the drone. In other areas, the cuticle provides a lining structure to some of the internal organs. Invaginations or depressions in the cuticle form areas such as the trachea, the mouth, oesophagus, crop, proventriculus and rectum – not surprisingly, even these areas are shed when the bee moults.

The cuticle sits on a basement membrane and the first layer is known as the epidermis and is made of epidermal cells. These are metabolically active and are responsible for producing the new cuticle during the moulting process. Above them is the endocuticle (endo in biology means inside so this is one of the inner layers of the cuticle). The exocuticle sits on the endocuticle (exo meaning outside as in exit) and the final and outer layer is the epicuticle which is an extremely thin structure made of many even thinner layers.

There are 2 main chemicals that form the cuticle – chitin and sclerotin. Sclerotin is a substance which darkens and hardens during a process known as tanning, hence why pupae eventually darken from a white colouration as the sclerotin matures. This produces the hardness to the cuticle. Chitin is a tough substance but more flexible than sclerotin so provides flexibility to the cuticle.

Moving from the inside to the outside of the cuticle, in general the levels of chitin decrease and the levels of sclerotin increase. For example, the endocuticle is mainly made of chitin with a small amount of sclerotin whereas the exocuticle has a small amount of chitin but lots of sclerotin. The epicuticle contains no chitin but it does contain wax along with the sclerotin to make this outer layer waterproof.

The composition of the cuticle changes depending on which area we look at. For example, the hard plates of the tergites, sclerites and pleurites have all the layers mentioned above. However, the joints between them lack the epi and exocuticle layers. This is so that these areas are highly flexible. The taenidia or spiral thickenings in the trachea will have thicker and more sclerotised cuticle than the surrounding areas for extra support.

As you can appreciate from this account, the cuticle of the honeybee is a complex structure but highly adapted to its functions. In future podcasts you will find out that there is even more complexity to this external skeleton of the bee, but that's another story that I hope you can join me on.

The External Anatomy of the Queen, Worker and Drone

Hello and welcome to the seventeenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the external anatomy of the queen, worker and drone. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list. Further information about the detailed structure and function of some of these parts can also be found in other podcasts in this series.

The basic body plan of all insects consists of 3 regions, the head, thorax and abdomen. The head contains the main sense organs. In honeybees a single pair of antenna are found on the front of the head. One pair of compound eyes and 3 ocelli are also found. The drone has the largest compound eyes to those of the queen or worker with on average 8600 facets or ommatidia. The worker has between 4000-6900 and the queen has around 3-4000. The compound eyes are so large in the drone that the ocelli normally found on the top of the head are pushed forward onto the face.

The front of the face is known as the clypeus and the cheeks are called gena. The paired mandibles are located just below the upper lip which is known as the labrum.

The thorax is made of 3 segments. Each segment has a tergite / tergum as the dorsal plate, a sternite / sternum as the ventral plate and a pleurite / pleuron as the lateral or side plates. Confusingly a tergite of the thorax is also known as a notum. However, the notum can be split further in the thorax making a series of interlocking sections which are highly modified. The second thoracic plates are the largest – the area that a queen is marked on is the second thoracic tergite or notum. To see these in more detail, it would be useful to look at the diagrams found in Dade or Davis. Each thoracic segment has a pair of legs – fore, mid and hind. The second and third segments house a pair of wings – the fore and hind wings. Covering each forewing is a flap known as the tegula.

The first abdominal segment, also known as the propodeum, is found anterior or forward of a constriction in the bee's body, the petiole – this is commonly known as the 'wasp waist'. This first abdominal segment forms part of the thorax section and is thought to increase the volume of the thorax in order to house the large flight muscles. The remaining abdominal segments are found posterior or behind this structure. The abdominal segments, including the propodeum, comprise of tergite and sternite plates but lack pleurites. The last 3 abdominal segments, 8, 9 and 10 are telescoped into the posterior end of the abdomen and house the sting, reproductive structures and the anus.

There are a number of similar and different external anatomical features between the queen, worker and drone and the next podcast will look more closely at the structure and function of some of these and hopefully fill in any gaps you may have from this general overview.

The Function and Structure of the Wing, Legs, Feet, Antennae, Mouthparts and Setae (hairs)

Hello and welcome to the eighteenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure and function of some of the main parts of the bee including the wings, legs, feet, antennae, mouthparts and setae or hairs. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list. Further information about the detailed structure and function of some of these parts can also be found in other podcasts in this series.

In honeybees there is a single pair of antenna originating from the head of the bee which are split into segments. The first area originating from the head is the antennifer. This forms a ball and socket joint with the head which is controlled by 4 muscles. The majority of movement of the antenna originates from here – this joint is similar to the hip or shoulder in humans. The first proper segment is the scape which is also the longest. The scape forms a hinge joint with the next segment the pedicel – this allows the antenna to flex or extend (similar to the elbow or knee in humans). The joint between the scape and pedicel also houses the Organ of Johnston previously covered and which is thought to determine wind speed or speed of flight. The subsequent segments are called flagella or flagellum if you are referring to a single one. There are 10 flagella in the worker or queen, the drone has 11. These have no muscles and cannot move independently.

The surface of the antenna is covered with sensilla such as placodea or basiconica which are covered in the nervous system podcast in this series. However, they allow the antenna to detect chemicals through taste and smell which are important senses for the bee. The drone has a lot more of these on their antenna especially on the terminal flagella. To give you some numbers, a drone antenna has around 30,000 placodea where as a worker has around 3-6000 and a queen only 1600. This indicates the importance of the antenna in the detection of queen pheromones at drone congregation areas. Other sensilla may detect touch or other chemicals such as carbon dioxide levels.

The mouthparts of a honeybee are complex, made of a number of separate parts. The upper lip is the labrum and this covers the proboscis and a pair of mandibles. The mandibles have a variety of functions including chewing anthers for pollen or wax for manipulation, grooming of other bees, nibbling or biting sick or invasive bees. The ends of the mandibles differ in shape between the queen, worker and drone. The queen mandibles have a toothed appearance and are used for biting other queens. They also have deep grooves which allow mandibular secretions to run down, forming part of the queen substance. Worker mandibles are more spoon shaped possibly for holding regurgitated nectar or mixing brood food. Secretions from the mandibular glands will also run onto these. Drones have the smallest mandibles probably because they have little to use them for.

The proboscis is formed from a series of interlocking structures, details of which can be seen on the supporting diagrams. The cardines or spines at the top of the mouthparts are attached to muscles and act as a lever swinging the proboscis outwards when needed and backwards when not. The galea lock with the labial palps to form a tube down which the glossa runs. Saliva can run down the middle of the glossa and by performing 'sucking' movements using dilator muscles in the cibarium or mouth cavity, liquids such as nectar can be pulled up the tube. The flabellum at the end of the glossa is spoon shaped and used to start the process of sucking up liquids such as water or nectar. The whole proboscis is shorter in drones and queens compared to workers, possibly due to workers collecting nectar from flowers.

The lower lip or labium completes the mouthparts.

There are 2 pairs of wings in honey bees known as the fore and hind wings. The fore wings are larger than the hind wings. They originate from thoracic segments 2 and 3. There is a flap of cuticle covering the fore wing joint called the tegula. When needed in flight, the fore and hind wings at each side are locked together to form a single unit. This is done using around 20 hooks or hamuli which are found on the anterior or forward face of the hind wing. They hook onto a channel present at the posterior or rear of the

hind wing. This provides a larger surface over which air can flow making flight more efficient. The wings themselves develop during the 5th moult and are extended by pumping haemolymph through the veins – expanding them into their final shape. The haemolymph drains out leaving hollow veins which support the thin cuticle of the wings. The wings are covered in setae or hairs and controlled by the flight muscles which will be discussed in the next podcast. When not in use, the wings are folded back over the back of the bee and the hamule are unlocked.

The wings are obviously used for flight but can also be used within the hive for temperature regulation, fanning of the wings can create air currents through the hive to cool the interior. They can also be used to disperse hormones such as those produced by the nasonov gland.

A honeybee has 3 pairs of legs, fore, mid and hind originating from the 3 thoracic segments, T1, T2 and T3. The legs are made of segments and between each segment is a joint which makes them highly flexible. Starting from where they originate from the thorax the segments are called coxa, trochanter, femur, tibia, 5 tarsus segments (the first of which can be known as the basitarsus) and the pretarsus or foot. A mnemonic to remember the order of these could be 'can trains follow time tables perfectly'. The legs are adapted for various functions both in an individual bee and between workers and queens or drones.

The fore leg has a groove formed from the tibia and basitarsus which is covered by a flap known as the fibula and straight hairs. The groove is just the right size to fit the antenna in and this structure is therefore known as the antenna cleaner – you may see your bees drawing their antenna through this structure when cleaning.

The mid leg has a large spine originating from the distal end of the tibia. The function of this is unknown but it has been speculated that it may be used in pollen packing. However, this would suggest it should only be present on workers but it is found on all types of honeybees.

The most modified leg in workers is the hind leg. This is very different from the structure of the queen or drone hind leg as it contains the pollen basket, pollen comb and pollen press. As you can infer from this, the hind leg is used to pack and carry pollen back to the hive.

The inner surface of the basitarsus is covered with 9 lines of straight hairs or setae which form the pollen brush. This can be drawn over the thorax and abdomen to collect pollen. The joint between the tibia and basitarsus forms the auricle or pollen press, a flat surface where pollen can be compacted. Short, stout hairs forming the rastellum surround this surface to prevent pollen from being lost. The pollen is then passed up to the outer face of the tibia which forms a concave surface called the corbicula or pollen basket. The pollen, moistened with saliva/nectar and compacted is carried back to the hive on the corbicula or pollen basket. Naturally, the queen and drone lack these specialised structures.

The foot or pretarsus of the leg ends in a pair of claws which are used to cling to surfaces. If the surface is smooth, an adhesive pad or arolium is used. The claws are spread and the arolium muscles pull this part of the foot downwards to make contact with the surface.

Setae or hairs have been mentioned before but these can be found all over the bee's body and they can be straight or branched. The branched hairs known as plumose hairs are thought to trap pollen but could be used to prevent particles from entering openings such as the spiracles. Straight hairs can be sensory providing the bee with a sense of touch. Others may not be linked to nerve cells and may simply be there for physical reasons for example, those of the pollen press. These are found covering the surfaces of the head, thorax and abdomen even between the ommatidia of the compound eye.

This has been a brief overview of some of the structures of the honeybee linked to their functions. Differences between queens, workers and drones has been highlighted and it shows that some of the tools of the trade can be highly specialised. I hope you have enjoyed this subject and I hope you can join me for the next episode.

Structure of the Sting Mechanism and its Operation

Hello and welcome to the nineteenth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the structure and operation of the sting mechanism and composition of venom. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

The sting in honeybees is used as a defensive mechanism and is found in workers and the queen – drones lack a sting. Queens usually only use their sting against other queens although they will sting a beekeeper if mishandled. Unlike a worker, a queen will survive after using her sting, probably an evolutionary adaptation to prevent queens from being lost during queen replacement in colonies.

The sting itself is housed in the sting chamber formed from the abdominal segments A8 and A9 which are telescoped within segment A7. The venom gland (sometimes known as the acid gland) produces the venom which is ejected when the sting is employed. Hormones from the Dufour's (or alkaline) gland also empty into the sting chamber in the queen.

Each side of the sting is an identical mirror image and is made from 3 plates which interlock and articulate with each other. It would be useful for you to see the supporting diagram at this point. The oblong plate is fixed whilst the quadrate and triangular plates can move relative to each other. When a bee prepares to sting it curves its abdomen using sclerite muscles so that the sting will enter the skin at 90 degrees to the surface. The lancets and stylet are forced out of the opening of the A7 segment by the contraction of protractor muscles (some literature call these the A198 muscles). These pull on the quadrate plate and the quadrate plate swings upwards along with the triangular plate. This forces a 'rod' like structure, the ramus, along a groove and downwards. This ramus eventually forms the lancet which is a barbed and pointed structure and this is forced into the skin. At this point the retractor muscles (or A199) contract which moves the plates in the opposite direction. The barbs on the lancet prevent the sting from being removed from the skin. The opposite side of the sting works in tandem causing an alternating push and pull of the paired lancets into the skin and the sting is forced even deeper. The umbrella valve in the bulb opens and venom runs down the groove formed from the paired lancets and stylet.

Eventually the bee attempts to pull the sting out, but the backward pointing barbs coupled with loose connections between the sting plates and other abdominal plates cause the sting, proctiger which is the remnants of abdominal segment 10, oblong plate, ganglia and the end part of the digestive system including the anus to separate from the bee. The ganglia continue to send nerve impulses to the venom sac and bulb muscles to pump further venom into the skin. The bee itself will die within a few days and cannot sting again.

The sting of the queen possesses fewer barbs and firmer connections with other abdominal structures and so she can remove the sting without damage to herself. Her sting is also curved probably to help her insert it at 90 degrees even with a longer abdomen.

Venom consists of a number of chemicals but in general these cause an inflammatory response. Melittin, which makes up around 50% of the venom is a protein and it causes blood cells and cells known as mast cells to rupture. This releases histamine and heparin which initiates the inflammatory response and also prevents clotting of the blood. An enzyme known as phospholipase A works alongside melittin and breaks down cell membranes at the sting site, destroying cells – this causes the pain we perceive. Another enzyme called hyaluronidase or hyaluronic acid causes the glue that holds cells together to break down – this causes tissue damage. Other substances are also present including substances that prevent the melittin or enzymes from being broken down, histamine which enhances the inflammatory response and together these cause the reactions humans have to stings. People with a high sensitivity to these can experience anaphylaxis or severe allergic reactions to the chemicals which can be life threatening. Sensitivity can also

increase without warning or some people develop a reduced sensitivity to bee venom. Each sting injects about 0.1mg or one thousandth of a gram of venom.

The sting of the honeybee is one of the main reasons why few people become beekeepers but as you can see from this account it is a highly modified structure that forms a protective defence mechanism for the colony. I hope that you have enjoyed finding out more about this sometimes painful part of the bee and I hope to see you for the next episode.

Role of the Flight Muscles

Hello and welcome to the twentieth in a series of podcasts looking at BBKA Module 5, Honeybee biology. This episode looks at the role of the direct and indirect flight muscles. Supporting diagrams can be found alongside this podcast and further information can be added using the sources listed in the BBKA reading list.

Muscles in bees are similar to those found in all animals, that is they are structures which can contract and pull on hard structures and relax and be pulled back into their original shape. Muscles, however, cannot actively lengthen and so they are normally found in pairs which work opposite to each other. These are called antagonistic pairs and a good example to consider in humans is the bicep and triceps muscles of the upper arm. In simple terms, when the biceps contract and the triceps relax the elbow is bent or flexed. When the triceps contracts and the bicep relaxes, the elbow is straightened or extended. This dual action allows the movement of the elbow in both directions.

Just as in other animals the sets of muscles involved in flight of the bee are also found in these antagonistic pairings. The indirect flight muscles comprise of the depressor and elevator muscles, both of which will lower or raise the wings respectively with their antagonistic actions. They are known as indirect muscles as they are not attached to the wings, but their action causes the deformation of the thorax which then causes movement of the wings and provides the main power for flight.

The first set of indirect muscles are found in thoracic segments T2 and T3 and are attached to the inner surface of the upper and lower thoracic segments, that is the notum at the top or dorsal surface and the sternite at the bottom or ventral surface. Therefore, they are known as dorsoventral muscles. When these muscles contract they effectively pull the upper and lower parts of the thorax closer to one another and the wings are elevated. The second set of indirect muscles are found in second thoracic segment and run from upper front to lower back of the segment, overlapping inside the propodeum formed from the first abdominal segment. These muscles are known as longitudinal muscles and when these contract, the notum forms a domed shape and the wings lower or depress. They are therefore also known as depressor muscles. The antagonistic action of these two sets of muscles cause the upwards and downwards movements of the wing which is why they are so large and almost fill the thorax.

The wings make a figure of eight movement when flying and this is caused by the direct muscles. These are so called because they are attached to the sclerites at the base of each wing and are used to articulate the wings to allow the bee to fine tune its flight and manoeuvre in the air such as when taking off or landing or when flying in windy conditions or changing direction. They are far smaller than the indirect flight muscles.

The large, indirect flight muscles can also be used to keep the hive and brood nest warm when the bee is in the hive and not flying. The bees rapidly contract and relax these muscles whilst their wings are decoupled which is similar to humans shivering. As these muscles are large, they can generate a large amount of heat when contracting and working. However, the literature doesn't describe how the wings uncouple from the muscles or thorax connections and so this will have to remain a mystery for now.

As you can see, flight is not a straightforward process and relies on two main groups of muscles for power and direction. The thorax and its structure also play an important role in this. It is also fascinating to see a dual role for the indirect muscles in the production of heat in the hive.

This is the last in the present series of podcasts for module 5 but I hope you have enjoyed this extraordinary journey into the biology of the honeybee and I hope you have learned more about this intriguing animal.