### Introduction

### References:

The Honeybee Inside Out	Celia F. Davis	
The Honeybee Around and About	Celia F. Davis	
Guide to Bees and Honey	Ted Hooper	
Beekeeping Study Notes (modules 5,6,7&8)	J.D & B.D. Yates	
The Biology of the Honey Bee	Mark L. Winston	
The Anatomy of the Honey Bee	R. D. Snodgrass	
BBKA website		
MBBKA Study Group		
MBBKA Basic Course Notes		

### Contents

The Candidate shall be able to describe in detail and illustrate where appropriate, referring to histological features as necessary:-

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5.2 the excretory system and the substances excreted;5
5.3 the respiratory system, including the muscular ventilation of the air sacs, the structure and operation of the spiracles and exchange of respiratory gases;
5.4 the circulatory system, including the heart, dorsal and ventral diaphragms and the composition and functions of the haemolymph;
5.5The exocrine glands of all castes and sexes of adult bees and larvae, the functions and main compositions of their secretions including pheromones, (hypopharyngeal, mandibular, tergite glands of the queen (Renner-Baumann); Nasonov, sting, Arnhart post cerebal, thoracic salivary, wax glands and wax production)
5.6 the structure and function of the nervous system and sense organs (including the compound eyes, ocelli, organ of Johnston and the sensilla);15
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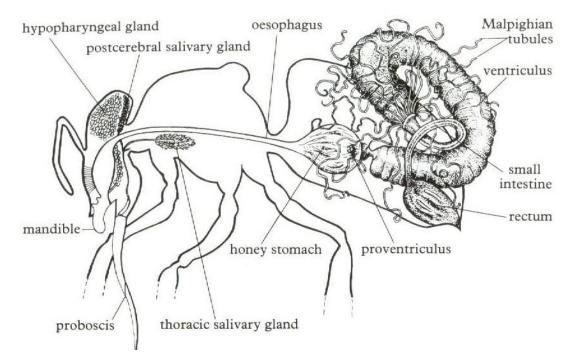
# 5.1 the alimentary system including the process of digestion by enzymes and the absorption and assimilation of products of digestion;

The digestive system of any animal has four distinct functions

- Ingestion taking in of food
- Digestion breaking the food down chemically to simplest, soluble components
- Absorption passing those components through its wall to the blood
- Defecation removing any indigestible material from the body

The honey bee is more complicated due to the need to transport nectar and water.

Food is broken down by the process of digestion and these products are then circulated by the hymolympth (blood) and used to provide energy, bodybuilding substances, and the requirements for carrying out the chemical processes of life. The waste products of these processes have to be collected and eliminated from the insect's body. Digestion and excretion are the functions of the alimentary canal and its associated glands. These are shown in the figure. The mouth is between the base of the mandibles below the labrum and above the labium. Immediately inside the mouth the canal expands into a cavity, formed by the cibarium and pharynx, which has muscular attachments to the front of the head which can expand and contract it, thus providing small amounts of suction to help pass the food from the proboscis and into the oesophagus.



Two pairs of glands empty into the cibarium:

- Postcerebral glands
- Thoracic glands

These glands are collectively called labial or salivary glands. They produce a liquid that passes under the pharynx and opens into the base of the labium and on to the proboscis where it is mixed with incoming food. The saliva contains invertase (from the hypopharyngeal glands) which begins the breakdown of sucrose.

Muscles in the oesophagus provide waves of contractions which work the food back into the dilated crop or "honey stomach", where it is stored for a while. At the end of the honey stomach is the

proventriculus, a valve that prevents the nectar from going any further unless it needs some for its own use.

If the bee is a forager it is here that the nectar is carried back to the colony and regurgitated back to the mouth and fed to other bees. The proventriculus has four lips which are in continuous movement, sieving out solids from the nectar. The solids – pollen grains, spores, even bacteria – are removed from the nectar fairly quickly and passed back as a fairly dry lump, or bolus, into the ventriculus.

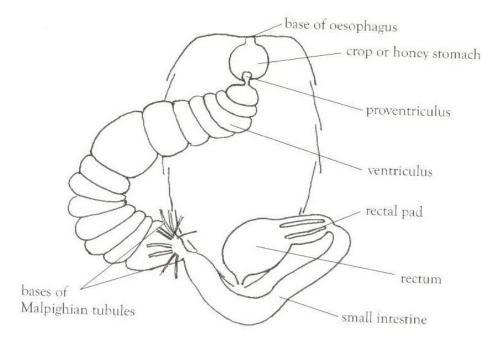
When the bee needs to have sugar the whole proventriculus gapes open and an amount of nectar is allowed through to the ventriculus, where the food is subjected to several enzymes which break it down into molecules small enough to be passed through the gut wall into the hymolympth. The bee appears to only digest two main food types, sugars and proteins. These are digested by enzymes produced in the walls of the ventriculus, assimulated and used to produce energy or to build up the bees own proteins.

The vetriculus is called the mid gut or true stomach, it is lined with epithelium which releases enzymes in order to breakdown fats, proteins and complex sugars into simpler constituent parts. The food is encompassed by a peritophic membrane which again is produced by the epithelium, this film protects the thin wall of the ventriculus during the food passage through it. Non-soluble products pass through to the small intestine.

The small intestine is again lined with epithelium to enable further digestion. The residue is passed into the rectum where it is held, as faeces, until the bee is able to leave the hive and void the contents of the rectum in flight. During long spells of cold weather in winter the rectum can extend almost the whole length of the abdomen before the bee is able to get out for a cleansing flight. At the end of the ventriculus are about a hundred small thin walled tubes. These are the malpighian tubules which have a similar function to our kidneys in that they remove nitrogenous waste (the results of the breakdown of proteins during metabolism) from the hymolympth. The waste products mainly in the form of uric acid are passed into the gut to join the faeces in the rectum.

### 5.2 the excretory system and the substances excreted;

The excretory system is essentially a sophisticated filtration system which not only removes waste substances, which would slowly poison the cells, but also acts selectively, adjusting the amounts of particular substances in the haemolymph so that there is a balance between water and salts and the osmotic pressure and acidity remain within narrow limits.



There are two types of waste produced by active cells:

- Carbon Dioxide produced as a result of respiration and removed by the respiratory system
- Nitrogenous waste resulting from the chemical reactions which go on within the cells involving
  proteins and other nitrogen-containing compounds, this waste is removed by the excretory
  system.

There are four aspects of the excretory system;

- Filtration of the haemolymph by the Malpighian tubules
- Re-absorption from the excretory system of useful substances
- Active secretion of substances into the system
- Complete removal of the end product to the outside of the bees body

Substances in the haemolymph are filtered through the wall of the Malpighian tubule at its upper (distal) end. Muscle fibres cause the tubule to wave about and come in contact with the maximum amount of haemolymph. The substance passes through the single cell wall and travels down the centre (lumin) of the tubule.

As materials travel down the lumin some are re-absorbed, water retention is crucial part of reabsorbtion, depending on the Haemolymph state salts may or may not be re-absorbed.

Finally, other substances are actively secreted by cells. They pull passing molecules in and push them through into the lumin. The Malpighian activity requires a lot of energy hence the proximity of tracheoles for sourcing Oxygen.

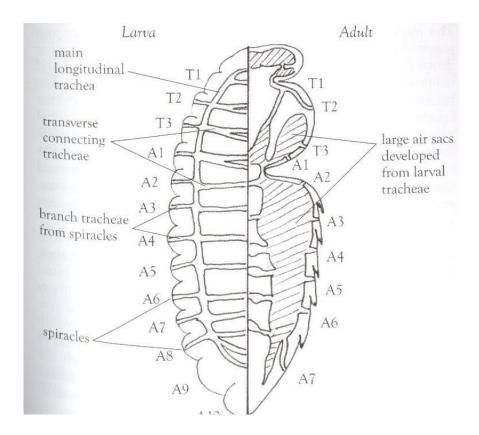
When the material in the lumen of the tubule reaches the intestinal connection, it passes into the digestive system and together with the waste from the digestive system is passed to the outside of the

body through the small intestine, the rectum and finally the anus. During its final passage further water is re-absorbed.

# 5.3 the respiratory system, including the muscular ventilation of the air sacs, the structure and operation of the spiracles and exchange of respiratory gases;

Summary

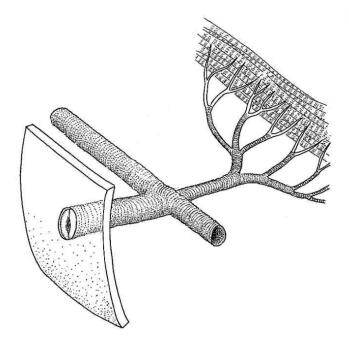
The bee breathes through tubes called trachea which convey oxygen to where it is required within the body of the insect. In all the higher animals oxygen is transported to the tissues by blood, bit in insects the blood is not involved in the transport of oxygen through the body. The trachea is made of cuticle and is prevented from collapsing by spiral thickening. The trachea start quite large but very rapidly divide many times, getting smaller all the while, until finally they end up as single cells, or a loop. The trachea open to the air through holes in the cuticle called spiracles, and in many cases these are provided with a closing mechanism.



Air enters the tracheal system through spiracles and fills the tubes. When the cells in which the trachea end are using up oxygen, this reduces the pressure of oxygen at that point and molecules of oxygen migrate in to make up the deficiency. It is thus by diffusion that oxygen makes its way via the trachea into the body of the bee. Oxygen is used to oxidize substances such as sugar in the cells to release energy for their use, producing the residue substances, carbon dioxide and water, this is cellular respiration. In the honeybee the main tracheal trunks become large sacs which are ventilated by breathing movements of the abdomen, whereby the abdomen is lengthened and contracted in a telescopic type movement.

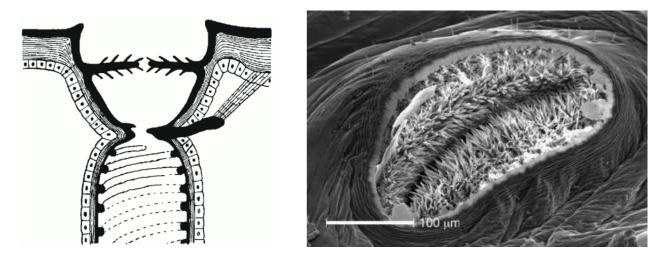
### Definitions:

The respiratory system comprises Spiracles (openings), Trachea (large tubes), tracheoles (smaller tubes) and the total surface through which oxygen and carbon dioxide is exchanged is called the respiratory surface. The respiratory surface must be moist for the gases to diffuse, the tracheoles therefore contain fluid.



### Spiracles

There are 10 pairs, found on each segment from T2 through A8, There is usually a valve surrounded by hairs on each spiracle, exceptions being the small spiracles on T3 and the "lid" on T2 not being able to fully close. The two spiracles on the propodeum A1 are the largest and all the Abdominal spiracles have a widened entrance called an Atrium. The valves are controlled by small muscles.



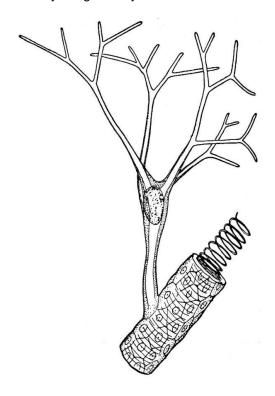
### Tracheae

The tracheae are tubes leading from the spiracles and joining together in the body to give two large lateral tracheae (air sacs in adult bee). The tracheae have thicker areas (made of chitin) like a spiral around the tube which prevent it from collapsing in low pressure. The lining of the tracheae is cuticle and is contiguous with the outer cuticle of the bee (implying it sheds with each molt).



Tracheoles

The tracheae split down to smaller tubes (traceoles) which terminate in very small blind endings with fluid for the diffusion of gases. Whether the end is a single cell, disturbs or splits cells is not known, but they will generally terminate where needed such as close to muscle tissue.



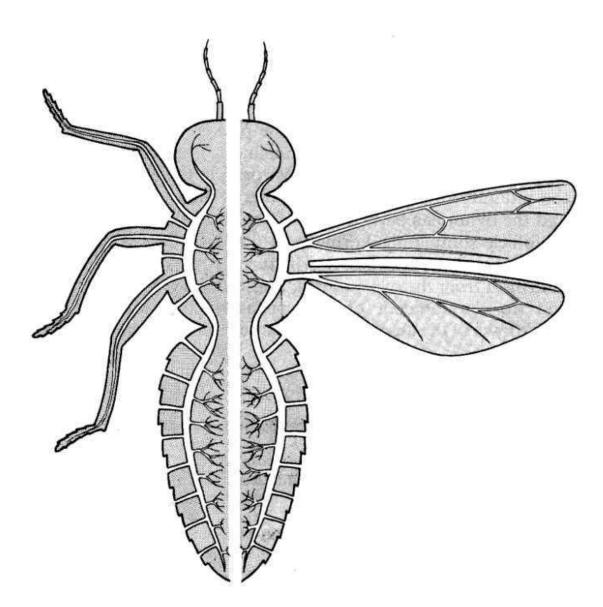
### Air Sacs

Are present in the head, thorax and abdomen of the bee, they are tracheae with no thickening (taenidia) so have thin walls and can expand and contract. This is enables the bee to breath:

Build up of carbon dioxide stimulates the nerves in the ganglia which control the muscles that stretch and contract the membrane linking the sternum and tergum. Build up of carbon dioxide contracts the muscles forcing it out via the spiracles, releasing the muscles causes a vacuum allowing fresh air in. A similar action occurs longitudinally in the abdomen as well as in the thorax.

### Breathing

When resting or working most air flows in and out through the spiracles on T2, when flying which requires large amounts of oxygen, air mainly flows in T2 and out through spiracles on A1.



# 5.4 the circulatory system, including the heart, dorsal and ventral diaphragms and the composition and functions of the haemolymph;

The circulatory system is an Open System, where fluid (Haemolymph) flows throughout the body supporting cells, transporting food and removing the waste products of metabolism.

The elements that control the fluid and effectively comprise the circulatory system are:

- Heart
- Aorta
- Antennal vesticle
- Dorsal diaphragm
- Ventral diaphragm

The heart is tube which is closed at the rear end and has 5 pairs of openings along its length called ostia, haemolymph is drawn into these openings and pumped forward to the aorta. The heart resides within the Dorsal sinus and is connected to the body and the dorsal diaphragm.

The aorta is a narrow tubular extension to the front of the heart which passes through the petiole and opens out at the brain.

At the base of the antennae there is a structure that draws in haemoplymph when relaxed and pumps it up the antennae when tensioned.

The dorsal diaphragm is connected in places to the upper part of the abdomen, above the diaphragm is a gap (sinus) within which the heart resides. The diaphragm has rhythmic undulations from the rear of the abdomen to the front which causes surrounding fluid to travel forwards.

The ventral diaphragm exists within the thorax and the abdomen and is attached to the sternum, again there is a sinus between the diaphragm and the body of the bee. The rhythmic movement of the ventral diaphragm is front to back, moving fluid from thorax to abdomen within the sinus.

The fluid within the space between the diaphragms swirls.

The haemolymph comprises; plasma and haemocytes. Plasma is a colourless liquid (90% water) containing several dissolved substances including salts, amino acids, proteins, carbohydrates, uric acid, lipids, fatty acids and organic compounds. The haemocytes are simple cells suspended in the plasma and are instrumental in coagulation and wound healing.

The functions of Haemolymph can be described as:

**Transport**, of food to cells, waste materials after metabolism, hormones from organ source to point of use

Mechanical support, it fills the cavities of the bee

**Control of water content of the cells**, makes water and dissolved substances available to the cells **Metabolism**, chemicals are broken down into simpler ones in the haemolymph, essential for creation of energy

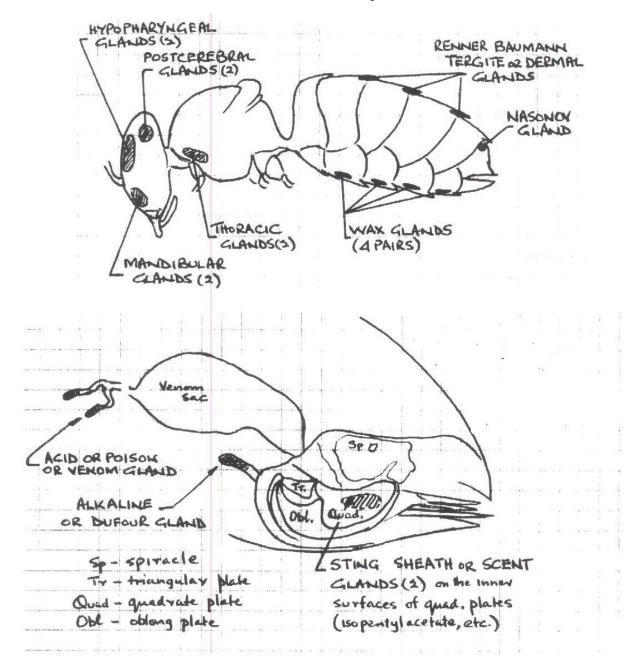
Phagocytosis, some of the haemocytes destroy bacteria and parasites

Wound healing, haemocytes form chain to plug holes until wound repairs.

5.5The exocrine glands of all castes and sexes of adult bees and larvae, the functions and main compositions of their secretions including pheromones, (hypopharyngeal, mandibular, tergite glands of the queen (Renner-Baumann); Nasonov, sting, Arnhart post cerebal, thoracic salivary, wax glands and wax production)

Gland	Located	Function	Composition	Caste
Hypopharybgeal	Front of head	Produces element of brood food in younger worker and enzymes in older worker	Young worker protein in form of clear liquid for making broo food Sucrase and glucose oxidase in older/foraging worker	
		Gorging on pollen can cause gland to revert to food production		
		Young worker, production of brood food and royal jelly	In young worker 10-HDO (10-hydroxydec-2-enoic acid) which is principle fatty acid in brood food and acts as preservative Older worker 2-heptanone which is the alarm pheromone	
		Mature worker, alarm pheromone issued		
		by guard bees to ward off robbers and	Queen produces :	
		initiate stinging response from other bees	9-oxodec-2-enoic acid (drone attractant when mating) 9-hydroxydec-2-enoic acid (holds swarm together)	
		Queen, produces pheromones used in		
		mating or part of queen substance		
Tergite (renner-	Edges of	Queen recognition, contributes to Queen	Composition unknown	
Baumann)	abdominal	Substance, emitted through Queen		
	tergites A3-5	grooming and retenue palpating her		
		abdomen with their antennae		
Nasonov	Tergite A7	Location scent used when flying in swarm	Terpenic alcohols Geraniol, Nerol and (E,E)-Farnesol	W
		to attract other bees, marking the	Terpenic aldehydes (E)-Citral and (Z)-Citral	
		entrance to hive, marking source of water	Terpenic acids Geranic and Nerolic acid	

Sting scent gland	Quadrate plates	Alarm pheromone, (Z) attracts bees to sting site and stabilises Isopentyl which along with 2-heptanone elicits stinging response	(Z)-11-Eicosen-1-ol Isopentyl acetate		W
Sting acid (poison or verom gland)	Abdomen	Production of venom to be used in sting	Major ones: Mellitin (50% of dry weight), Phospholipase A, Hyaluronidase, Acid phosphatise, Allergen C		QW
Sting Alkaline (Dufour)	Sting Chamber	Generally unknown but assumed to: lubricate sting mechanism, neutralise remaining acid and in queen protective coating to eggs or egg adhesive for cell floor	Unknown, white in colour and alkaline in nature		QW
post cerebal	Behind brain	Salivary, no reservoir, secrete directly into outlet ducts Only vestigial in drone, equal development in Queen and Worker	Water of Alkaline nature		QWD
Thoracic	In the thorax	Salivary, developed from silk gland in larvae, have resevoir	Water of Alkaline nature		QWD
Arnhart (tarsal glands)	5 <sup>th</sup> tarsome of each leg	Location (footprint odour) in worker bee Constituent part of Queen Substance, queen emits factor x13 of rate of worker	Unknown except different in the two castes		QW
Wax glands	Sternites A4-7	Wax production	Downing (1961) 16% hydrocarbons 31% straight-chain monohydric alcohols 3% diols 31% acids 13% hydroxyl acids 6% other substances	MBBKA 2009 esters 70% alcohols 1% acids 10% hydrocarbons 13%	W
Wax production	Sternites A4-7			W	



# 5.6 the structure and function of the nervous system and sense organs (including the compound eyes, ocelli, organ of Johnston and the sensilla);

The nervous system comprises:

- The brain and sub-oesophageal ganglion
- 7 ganglia connected together in the ventral sinus and to the brain by nerves
- Sense receptors throughout the body

The brain sits above the oesophagus and is composed of three parts; the protocerebrum, deutocerebrum and the tritocerebrum which is not a distinct division of the brain like the other two parts. Below the oesophagus resides the sub-oesophageal ganglion (really 4 fused ganglia) and is directly attached to the brain causing the pair to operate as one.

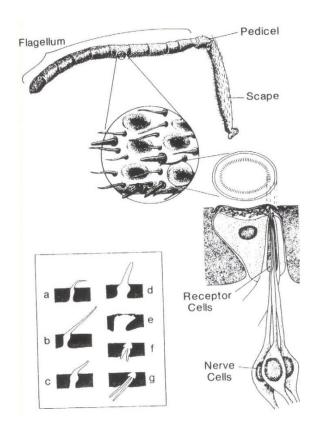
The protocerebrum supports two large optic lobes and manages the compound and simple eye, the deutocerebrum supports two large antennal lobes connected to the antennal nerves and the tritocerebrum manages the lower part of the face and the labrum and is connected to the frontal ganglion via nerves. The sub-oesophogus ganglion manages the mandibles, hypopharynx, first and second maxillae (labium is 2<sup>nd</sup> maxillae).

The larva has 11 ganglia (T1-3, A1-7, plus one in A8-10) these fuse during metamorphosis to 7 in the adult bee T1, (T2+T3+A1+A2), A3-6, (A7+A8+A9+A10). The ganglia are in fact fused pairs of ganglia connected via a nerve cord.

The first two ganglia in the Thorax manage the legs and wings as well as the Thorax and propodeum. The ganglia in the Abdomen supply the nerves to the appropriate segments in the abdomen.

The major receptors are called sensilla (sensillum – singular) have a specially constructed cell or group of cells in the cutilcle together with sensory nerve axons connected to an associated synapse. The table summarises the list of major sensilla:

Name	Role	Description	Location
Sensilla trichodea	Touch	Nerve cell attached to	All over body, legs and eyes
(hair or seta)		base of a hair	
S. basiconica	Taste	Similar to trichodea	Mouthparts, antennae and legs
(peg or cone)		except stunted hair	
S. coeloconica	Carbon Dioxide,	Same as basiconica	Mainly on antennae
(pit)	temp and	except peg in pit below	
	humidity	surface of exoskeleton	
S. campaniformia	Stress and	No hair, covered by thin	Groups in wings, legs and sting
(bell)	strain on cuticle	layer of cuticle	
S. placodea	Taste,	Flush with surface of	On antennae, used pheromone
(plate)	permeable to	cuticle, elipticle plate,	sensing.
	chemicals	pores allow molecules of	
		gas through	
S. scolopophora	Muscle tension	Subgenual organs and	Tibia and antennae respectively
	and vibration	organ of Johnston	
Ocelli	Simple eye	See below	3 on top of head, lower in drone
Compound eye	Sight	See below	Side and top of head



- a. Small thick-walled hair S. Trichodeum
- b. Thick-walled peg S. Trichodeum
- c. Slender thin-walleded peg S. Trichodeum olfactorium
- d. Large thin-walled peg S. Basiconicum
- e. Pore plate S. Placodeum
- f. Pit organ S. Coeloconicum
- g. Pit organ S. ampullaceum

### Organ of Johnston

Found at the distel end of the pedicel of the antenna. Some of the dendrites are embedded in the wall of the pedicel and others are connected to the membrane between the pedicel and the first segment of the flagellum. Movement of the flagellum cause nerve impulses.

Its role seems to be a wind speed indicator, for recognising speed of flight, and possibly for detection of airborne vibrations.

Ocelli Compound Eye Antenna Mandible Proboscis

Compound Eye

The Compound eye is so-called because they are made up of many parts. Each part is called a ommatidium which operates as a complete eye in itself. The bee creates a picture of its surroundings by joining together all the images.

The ommatidium comprises two parts the lens and the receptor.

Lens

The corneal lens is the surface of the eye, it is transparent, looks hexagonal when eye viewed as a whole and is slightly convex at the sides.

The crystalline cone is behind the lens and is a hard and transparent cone

Two primary pigment cells surround the cone to prevent light entering from adjacent ommatidia

### Receptor

The retinula cells are elongated nerve cells, there are 8 long ones and one short one, they are twisted around each other forming a core.

- 2 cells sensitive to green light
- 2 cells sensitive to blue light
- 2 cells sensitive to ultraviolet light
- 2 cells sensitive to green or blue light
- 1 cell sensitive to ultraviolet polarised light

The core is called the rhabdom and is made up of the right angle projections (microvilli) from the retinula cells called rhabdomere and combined they make up the rhabdom.

#### Operation

The lens and cone concentrate the light striking its surface into a beam directed to travel down the rhabdom.

Light reaches the rhobdomeres and strikes the microvilli, within which there is a photopigment called rhodopsin.

Rhodopsin changes structure based on energy and colour of light, it then changes back

Each retinula cell has a nerve fibre leading from it and impulses are created with each rhobdopsin change.

All nerve fibres lead back to brain where an image is composed.

Image will be a mosaic in nature and between frames of images it will be dark, but frames are at 100 per second.

### Ocelli

The ocelli has the same structure as the ommatidium employed in the compound eye but the lens does not focus on the retinula cells, so no image is formed. The ocelli seem to be concerned with the intensity of light, but work in conjunction with the compound eye in a stimulatory effect. Cover the ocelli does not stop the perception of light intensity in the bee but the coverse (cover the compound eye and the bee is blind.

5.7 the endocrine glands and the functions of their secretions particularly the neurosecretary cells, the corpora allata, corpora cardiac and the prothoracic glands;

The endocrine system contains a number of ductless glands producing secretions called hormones which are released directly into the haemolymph and have a profound effect upon growth, development, moulting, caste determination, age polyethism and glandular development.

It works in combination with the nervous system, the latter controlling the rapid minute-by-minute activities of the organism while the hormones are more concerned with slower, long-term effects.

The glands of the endocrine system although quite distinct work together and sometimes hormones from different glands may produce contradictory effects.

There are four major parts to the system

- The neurosecretory cell
- The corpora cardiaca
- The prothoracic gland
- The carpora allata

#### **Neurosecretory cells**

Found in groups in the brain and other ganglia. They are special nerve cells, identical in shape to other cells, which have processes to conduct impulses but as a result of stimulation secrete chemicals which can travel down the nerve fibres to various organs or other endocrine glands.

#### **Corpora Cardiaca**

These two glands are found behind the brain one on either side of the aorta connected to the brain by the fibres of the neurosecretory cells. The chemicals produced by these cells are stored in the corpora cardiac and when conditions are right they are released into the haemolymph, so the corpora cardiaca acts as a conduit for the chemicals produced by the brain. It also produces its own hormone.

#### **Prothoracic gland**

These two glands one found between the pro- and mesa- thorax near the first spiracle and they produce and secrete ecdysone (moulting hormone). The production of ecdysone is essential for moulting but it is only released in response to another hormone produced in the neurosecretory cells, stored in the Corpora Cardiaca and subsequently released by them into the haemolymph. This illustrates well the connection between the nervous and endocrine system because the brain hormone seems to be released as a result of the reception of impulses in the brains possibly related to size and stretching in parts of the cuticle.

#### The corpora allata

These are found on either side of the oesophagus. Connected to the brain by the fibre of the neurosecretory cells which have come via the corpora cardiaca and also connected to the suboesophageal ganglion. They produce the vital hormone called juvenile hormone (JH). (Also known as neotenin). High levels of JH in the larva maintain the larval characteristics and it is only when levels of JH fall and ecdysone is released that moulting occurs and growth and development changes are able to take place. This is one example of the interaction of two quite separate hormones from different glands having an effect on one development process. JH also plays an essential part in the determination of the female caste.

All except the prothoracic gland, which degenerate at pupation, persist in the adult.

### How do they work??

Hormones circulate in the haemolymph and are broken down by enzymes. They are not stored in the glands so there must be continuous production where a sustained effect is required. When a hormone reaches a target cell it causes biochemical changes, usually resulting in the production of enzymes which allow specific reactions to take place and/or enable production of particular proteins. One hormone may have different effects on different parts of the insect at different stages of its life.

The endocrine glands work in combination with the nervous system. The neurosecretory cells are part of the nervous system a long processes connect these groups of cells with the corpora cardiaca and the corpora allata. Nerves also connect the corpora cardiac with the thoracic glands and with the corpora allata so there is an intimate connection between the two systems.

### 5.8 the fat body and its storage of metabolites;

The fat body is not a thing rather a collection of cells distributed in different parts of the body for the storage of food reserves to be used by the bee in different manners at distinct stages of the life cycle.

There are three types of cells within the fact body:

- Trophocytes, these form the major part of the fat body and are present in all stages of the bees life
- Oenocytes (oil cells), again in all stages larva, pupal and adult life, the cells are destroyed at the larval stage and new ones formed in the adult stage. Large concentration are formed over the wax glands in adult bee, peaking at same time as wax production. Cells larger in queen and contribute to the egg yoke.
- Urate (excretory cells), found only in larva and pupa. They store nitrogenous waste in the form of uric acid in larva and pupa, once the Malpighian tubules are formed they disappear.

### Fat Body and Larva/Pupa

In the larval stage the fat body, consisting of small polygonal cells, increases in size and number with each stage of development. At time of the cell being sealed the fat body occupies 65% of body weight. During the pupal stage the fat cells release their contents into the haemolymph. The white colour of the larvae is the density and colour of the fat body (occupying the body cavity) pressed against the translucent larva skin.

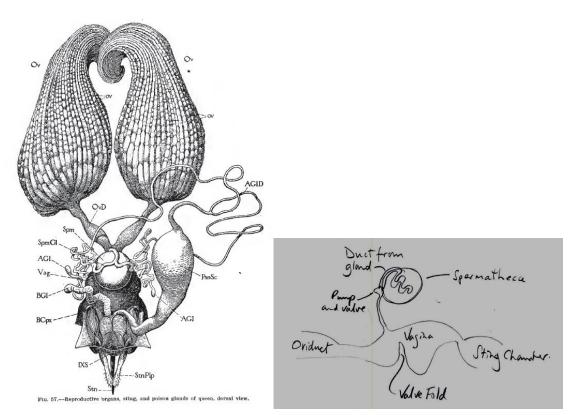
### Fat Body and Adult Bee

The contents of the fat body storage varies by bee age and season:

- Young bee, fat globules (required for food production) and little protein
- Older summer bee, protein and glycogen (rapid breakdown for energy) stored in fat cells
- Winter bees, large amounts of protein, little fat

# 5.9 the reproductive system of queen and drone and the production of sperm and eggs;

Queen Reproductive System



The reproductive system of the queen not only produces eggs it stores sperm and unites it with eggs prior to laying.

The key elements of the system are:

- ovaries, there are two ovaries, one on either side of the abdomen and attached to the ventral wall. The each ovary consist of 150-180 egg producing ovarioles (worker 2-12). The ovarioles produce up to a million eggs over the lifetime of the queen.

oviducts, these are tubes that lead from each ovary to the median oviduct

- vagina, the median oviduct feeds into the vagina along with the spermatheca duct. Within the vagina is the valve fold which coordinated with the pump in the spermatheca duct unites sperm and egg.

- bursa copulatrix, this is the sting chamber from where the egg is laid within a cell

- spermatheca, is a spherical structure above (dorsal side) the vagina, within here the sperm from mating is held. The sperm travels down the spermatheca duct into the vagina. At the entrance to the vagina the valve fold presses an egg to the duct for fertilisation.

### Egg Production

At the tip of each ovariole germinal cells divide and produce:

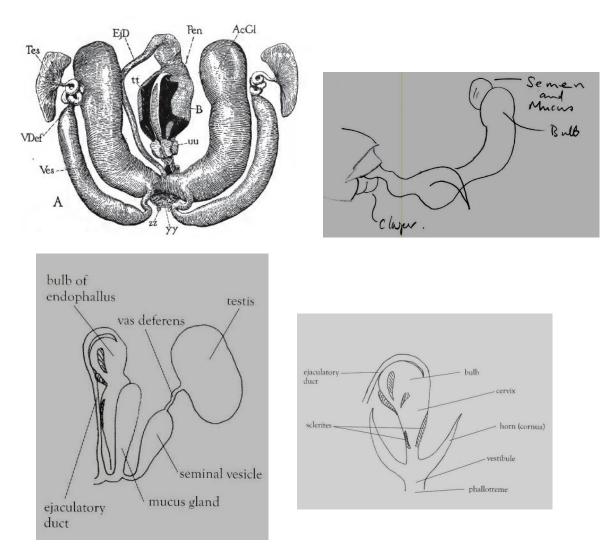
- Oocytes which become the eggs

- Trophocytes which provide nourishment to the oocytes, there are 48 trophocytes per oocyte.

The oocyte passes down the ovariole gaining size through the supply of nourishment from the trophocytes which diminish and finally disappear, yolk is added in the later part of the ovariole, the follicle cells surrounding the egg form the covering (chorion). As the egg leaves the ovariole the final meiotic division occurs.

The egg emerges from the oviduct, is pressed to the entrance of the spermatheca duct by the valve fold, if sperm worker egg results, if no sperm drone egg results.

Drone Reproductive System



The drones reproductive system comprises:

- Testes, there are two testis which peak in size prior to drone emerging from cell, they shrink until the drone reaches full maturity at 12 days
- Vasa deferentia, small tubes that lead from each testis and lead to the seminal vesicles
- Seminal vesicles, the sperm reside here and are nourished until they are required

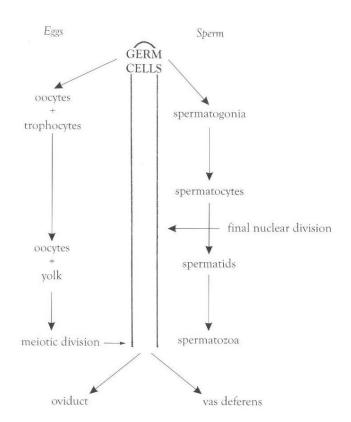
- Mucus glands, two small tubes enter the gland from the seminal vesicles, the mucus produced by the glands is not involved in the production of the semen rather the delivery. The mucus forms a thick mass when in contact with air.
- Ejaculatory duct, runs from the base of the mucus gland, near the entrance from the seminal vesicle to the bulb of the penis
- Penis, the penis (endophallus) resides within the abdomen of the drone, opening to the outside on A9 (the phallotreme) from the vestibule which is connected to the bulb by the cervix. Two horns (cornua) are attached to the phallotreme. The surface of endophallus has several plates (sclerites) on the surface

### Sperm Production

The testis comprises a large number of tubes, the tip of which form the sperm cells, as they travel down the tube they divide to form spermatogonia, then form groups called spermatocytes which grow and divide into spermatids and finally change shape to form spermatozoa which emerge into the vas deferens.

The drone mates once and dies, so all sperm (spermatozoa) are released in one explosive moment. After the mounting of the queen the contraction of the abdominal muscles causes the penis to evert (go inside out). The muscle lining of the seminal vesciles and mucus gland causes the sperm and then the mucus to be expelled.

The endophallus breaks off, the drone dies, the sperm remains within the queen until endophallus is removed by next drone or worker on return to colony.



# 5.10 the structure of the egg, development of the embryo within the egg and the hatching of the larva;

Structure of the egg:

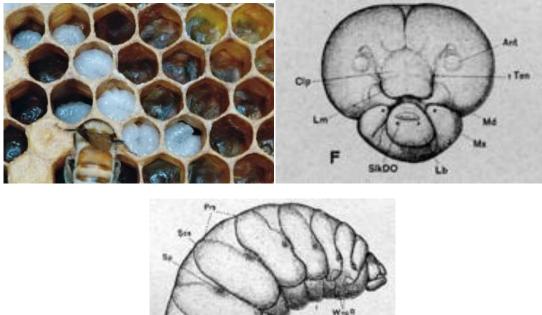
- Chorion, is the outer layer of the egg
- Vitelline membrane, is the egg wall
- Cytoplasm, lining inside vitelline extending to strands throughout the egg
- Yolk, globules entwined throughout the egg with the cyptoplasm strands
- Nucleus, contains all the genes for the development of the bee

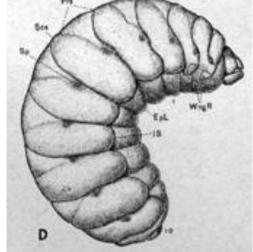
Stages of egg development to the emergence of larva:

- Cleavage, single nucleus divides forming many cells throughout the yolk
- Blastoderm formation, the cleavage cells form layer inside vitelline membrane
- Formation of germ band (layers of cells), thickening of the blastoderm on ventral side becomes the germ band
- Division of germ band, longitudinal fissures which run the length of egg divide germ band into three areas, two side lateral plates and median plate on ventral side
- Median plate moves inwards towards the yolk to form the mesoderm (which later will develop into muscles, circulatory system, part of reproductive system). The lateral plates grow, enclosing the mesoderm and forming the ectoderm (which will become the cuticle and its appendages, tracheal system, foregut and hindgut, nervous system and sense organs, part of reproductive system, oenocytes)
- The endoderm (evolves into the midgut) form from two ingrowths of the blastoderm, they join enclosing the yolk.
- Pits and ingrowths form on the ectoderm which will mature into physical elements in the larval development.
- After 3 days the larva is complete and enclosed within a membrane which splits to allow the emergence of the larva.

### 5.11 the external and internal structure of the honeybee larva;

### External Structure





The body is divided into a head and 13 segments comprising T1-T3 (Thoracic) and A1-A10 (abdominal).

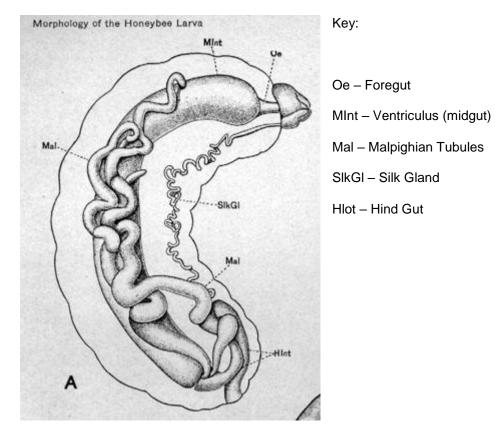
The main body does not have external structures, at one end it has the beginnings of the head with mouth and spinneret and at the other end the anus.

### Internal Structure

All the main elements of the mature honeybee exist within the larva:

- **Digestive System**, a large part of the body is occupied by the midgut (ventriculus), at this stage it is not connected to the hindgut. Liquid food is sucked in through the mouth.
- **Excretory System**, the waste products of the body are stored with the malpighian tubules which swell with their contents.
- Respiratory System, there are 10 permanently open pairs of spiracles on segments T2-A8 (reflecting adult bee structure) which connect into tubes that run the length of the body.
- Nervous System, brain, sub-oesophageal ganglion and ganglia associated with each segment are formed, A8-10 are fused.
- Circulatory System, the heart is present from A9 through T2 with 11 chambers and 10 pairs of openings terminating in a short aorta and both Ventral and Dorsal Diaphragms are present.

- Fat Body, fills most of the space within the body giving the creamy white colour to the larva. The fat body contains urate cells for further storage of waste.
- Silk Glands, long coiled structures that appear to the outside world at the spinneret on the labium.
- Testes and Ovaries, worker and queen larvae have ovaries (the queens ovaries larger than those of worker) and the testes in drone larger still than queens ovaries, located between A4 and A6.



5.12 the metamorphosis of the larva with outline accounts of ecdysis, larval defaecation, cocoon spinning, the external anatomy of the pro-pupa, its change to a pupa and then to an imago;

"Ecdysis" correctly is the actual emergence of a new form of the insect from an old cuticle.

The "correct" term for the process of moulting is apolysis (Davis).

There are six instances of moulting between the egg hatching and the emergence of the imago.

### General description of moulting

The process is initiated by hormones.

During the stadia (periods between moults), the level of juvenile hormone in the haemolymph is high.

The moult is initiated by a rise in the level of moulting hormone ecdysone, corresponding with a drop in the level of JH.

Ecdysone is secreted by the prothoracic glands.

The secretion of ecdysone is initiated by the neurosecretory glands in the brain which give a chemical signal to the corpora cardiaca which in turn signals the prothoracic glands to release ecdysone.

JH is secreted by the corpora allata, also under the control of neurosecretory cells in the brain via the corpora cardiaca.

At the start of the moult the epidermal cells divide and multiply.

- The cuticle separates from the epidermis.
- Epidermal cells secrete ecdysal fluid which fills space between the epidermal cells and the old cuticle.
- Enzymes in the ecdysal fluid digest the old cuticle and a new cuticle grows over the epidermal cells.
- Digestion products assist growth of the new cuticle.
- The larva (or (pro)pupa?) swallows air, expands and ruptures cuticle.
- The old epicuticle and exocuticle are sloughed off.

Produticle separated by fluid from epidermis
The by find from
moulting fund
Beauting funct produced by epidemak cells
From: C. DAVIS Gridermis cells d'unde
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to promite many move

### **Propupal Moulting**

When the worker larva is six days old (day 9) and fully grown, the cell is capped possibly with some food remaining which it may or may not eat (Winston).

The larva stretches out in the cell on its back, head nearest the capping.

The connection between the hind gut (proctodaeum) and ventriculus is made and the contents of the four Malpighian tubules and the ventriculus is discharged into the cell as larval faeces.

The cocoon is spun with silk originating from the silk glands via the spinneret (the silk glands later become the adult thoracic glands).

The faeces become mixed up with the cocoon silk and possibly reinforce the cocoon.

In the next 24 hours many external features form as the larva changes into a propupa (or prepupa).

### Anatomy of Propupa

- Head and mouthparts are remodelled
- Compound eyes develop
- Thoracic segments change shape
- The petiole forms
- Abdominal A8 A9 and A10 are combined into A7.
- Rudimentary wings and legs
- The sting starts to form.
- Also the ventriculus starts to reduce in size.

Almost two days after capping (worker) the 5th moult starts, and lasts about two days during which the propupa changes into the pupa. Completed day 12 -13.

#### Pupa characteristics

The new pupa is white, not hairy, has small wings and mostly adult appendages.

Many internal changes then take place:

- The alimentary tract develops, the musculature and the reproductive system develops.
- Some nerves die and new nerves form
- Reproductive system changes to adult form
- The drone's testes shrink as sperm is transferred to the seminal vesicles

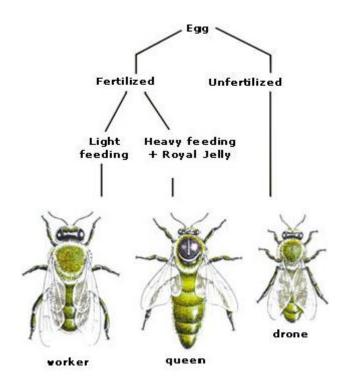
#### Externally:

- Cuticle hardens.
- External hairs grow.
- Wings develop.
- Exoskeleton colour darkens white to brown
- Eyes change colour pink to purple.

#### Sixth moult

Final moult occurs (day 20), then after waiting several hours while the cuticle hardens, the imago chews through the wax capping and finally emerges (eclosion).

5.13 the effect of feeding and other factors on caste determination including discussion about the differences between brood food and royal jelly;



The type of feeding of a larva is determined by the type of cell in which a larva resides (worker/drone or queen cell), worker and drone cells will be fed brood food and queen cells copious amounts of royal jelly. Sticking to the differences in feeding and food between worker and queen, there are three elements within brood food and it is the mix of elements as well as the feeding programme that determine the caste.

Larval food comprises:

- White, produced by the mandibular gland
- Clear, produced by the hypopharyngeal gland
- Yellow, derived from pollen

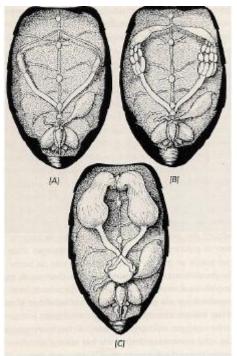
Composition of feed:

- Queen larva (Royal Jelly)
  - First three days mostly white
  - Last two days ratio white to clear 1:1
- Worker (Brood Food)
  - o white:clear:yellow in ratio 2:9:3 average

Points to note:

- queen is fed 10 times volume of worker, queen "swims" in royal jelly, worker fed as needed
- larva up to 3 days old transferred between cell types and hence feed change will mature to appropriate caste i.e. queen cell produces queen, worker produces worker.
- Larva transferred 3-4 days old will mature to appropriate caste but may exhibit traits of other caste e.g. pollen baskets on queen.
- Sugar composition in royal jelly is 47% and in brood food 12% for first three days. Brood food rises to 47% after 3 days with addition of honey to mixture. Sugar stimulates to consume more.
- Higher levels of Juvenile Hormone in larva triggers queen development, royal jelly stimulates JH production by the early development of the endocrine system

5.14 the physiological and structural differences between laying workers and normal workers and the role of pheromones in bringing about these differences;



### Reproductive organs of a normal worker [A], A laying worker [B] and a virgin

A laying worker [B] and a virgin queen [C].

### Development of laying worker bees

In a honeybee colony, under normal conditions female worker bees' ovaries are inactive as their development is prevented by brood pheromone (a 10-component mixture of methyl and ethyl fatty esters) and Queen Mandibular Pheromone (9-ODA). However, when a colony loses its queen and there are no fertile eggs or worker larvae of an appropriate age to raise a new queen from, one or more worker bees will partially activate their ovaries and commence to lay eggs as a result of the absence of queen and brood pheromones. The process of developing a laying worker usually takes weeks (3-4 weeks) after the loss of the queen, and by the time all the brood has emerged.

The eggs will be laid in worker cells with several in the same cell and produce eventually undersized drones. Drones produced from laying workers are sexually viable.

The laying workers take the place of the proper queen, they emit a pheromone, which mimics that of the queen scent which along with the brood pheromone inhibit other workers to lay eggs.

	Laying Worker	Normal worker
Ovarioles	10 – 12	Nil or vestigial
Laying rate	50 eggs per day	Nil
Spermatheca	Nil	Nil
Hypopharyngeal gland	Enlarged	Atrophied in older bees
Fat bodies	Increased	Low in summer
Age	Extended	Circa. 6 weeks
Pheromones	Mimic queen substance	Nil
Colony	Disorganised	Orderly
Behaviour	May attract court	Maul laying workers

### 5.15 the differences between summer and winter worker honeybees;

A key difference between summer and winter bees is their lifespan, the summer bee will survive around 6 weeks whereas the winter bee will survive several months in order for the colony to see through the winter.

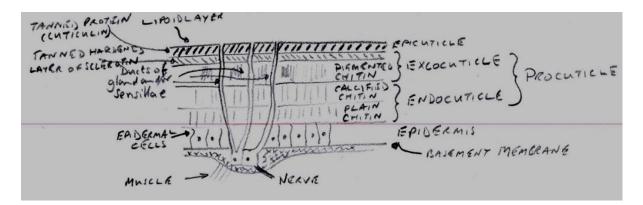
The summer bee the employs the hypopharyngeal gland to produce brood food, this gland decreases as the bee becomes older. Going into winter there is less brood and the worker is less likely to be required to produce brood food. Older workers who have not produced brood food when younger can produce brood food after consumption of pollen, this is necessary when the queen begins to lay again in the spring.

Summer bees lifespan is shorter also because their bodies basically wear out, after approximately 800 km of flying they run out of glycogen which is required for the energy to power the flight muscles.

So key differences are:

- Winter bees contain large amounts of stored glycogen and fat in the fat bodies
- The hypopharyngeal gland is plump and full of brood food in the winter bee
- Metabolic rate of winter worker is lower than summer worker
- Winter bees do less work i.e. no foraging
- The life span of winter worker is months compared with summer worker of circa 6 weeks.

5.16 the structure and main constituents of the cuticle with an outline account of its invagination within the body to form linings of the gut and tracheae;



The cuticle comprises the procuticle and the epicuticle. Through the cuticle there are ducts carrying pheromones or sensillae. The functions of the cuticle are:

- Waterproof protective covering
- Provide anchor points for muscles
- Make hard parts
- Provide lining for some internal structures

The cuticle sits on the epidermis, a layer of living cells that secrete substances including:

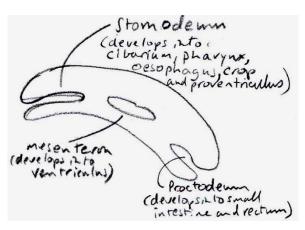
- Chitin, long thread like molecules of nitrogenous polysaccharides
- Anthropodin, protein injected between the chitin threads
- Polyphenols, for tanning the anthopodin and eventually forming sclerotin
- Cuticulin, tanning protein
- Cuticular lipids, paraffin hydrocarbons used for waterproofing the epicuticle

The thickness of the cuticle is circa 0.2µm.

Endocuticle - contains a large amount of chitin which is tough but flexible

Exocuticle - contains a large amount of sclertotin which is hard and dark in colour

Epicuticle – is primarily a thin layer of hard sclerotin and cuticulin but no chitin



Invaginations are internal folds, within the larva they are the stomodeum and proctodeum which are lined with cuticle and develop within the adult bee to become:

Oesophagus - slender tube lined with thick cuticle and surrounded with circular muscles

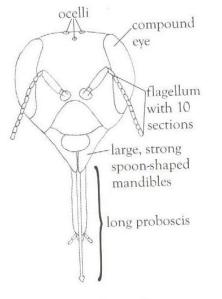
Crop - an extention of the oesophagus which is capable of stretching in order to take a heavy load

Proventriculus - walls are lined with dense cuticular intima

Rectum - has an epithelial wall lined with thin cuticular intima

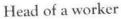
Trachea - epidermal layer of cells with delicate cuticular intima

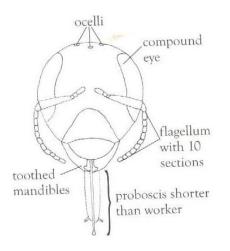
### 5.17 the external anatomy of the queen, worker and drone;

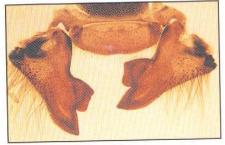




Worker mandibles are spoon-shaped

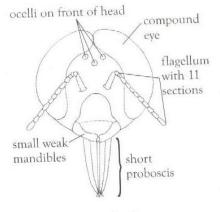




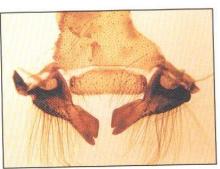


Queen mandibles are strong and toothed

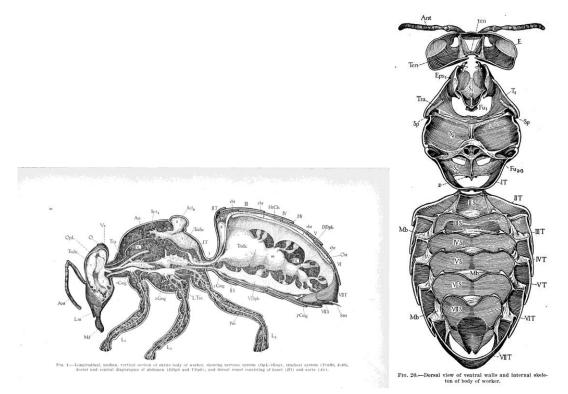
### Head of a queen



Head of a drone



Drone mandibles are small and not well co-ordinated



The honey bee comprises three external elements, Head, Thorax and Abdomen. The above diagrams give an outline to their structure.

The head comprises the eyes, mouthparts and antennae.

The Thorax and Abdomen are covered in a series of plates (tergum and sternum) which are linked via smaller pleuron plates connected via membranes.

The Thorax comprises three main plates:

- prothorax (T1), the first segment behind the head carrying one pair of legs
- mesothorax (T2), middle segment with one pair of legs, pair of wings and a pair of spiracles
- metathorax (T3), rear segment with a pair of legs, pair of wings and a pair of spiracles

There are no Sternum on the Thorax.

There are 10 Abdominal plates although A1/S1 (propodeum) reside on the thorax and linked to the Abdomen via a narrowing of the body called the petiole. Segments A8-A10 are hidden under A7. On the Abdomen there is a sternum associated with each tergum.

The castes differ externally in the following ways:

- Queen has a longer abdomen in order to house her reproductive system
- Drone has larger eyes and a larger rounded Abdomen

# 5.18 the function and structure of the wings, legs, feet, antennae, mouth parts and setae (hairs);

Wings

Function:

- to enable the bee to fly
- Used within the hive to fan
- The muscles associated with the wings used to generate heat

### Structure:

- Two pairs of wings
  - Forewing attached to T2
  - o Hindwing attached to T3
- Hind wing has series of hooks (hamuli) along leading edge of wing, in flight they hook into a fold on the trailing edge of the forewing creating a single wing for flight
- There are indirect muscles that act upon the forewing causing the up and down movement of the wing
- There are direct muscles that act upon each wing to
  - To produce rocking and rolling of the wings
  - To trim the wings for yaw, roll and pitch
  - For furling and unfurling the wings
- The flight action is for the leading edge of the wing to make a figure of eight movement
- There are two sets of indirect muscles
  - Longitudinal stretching from the front of T2 to the rear of T3
  - Dorsoventral muscles are connected between the thoracic segment and the scutum
- The wings attach to the appropriate Thoracic segment in a groove called a notum

WINGS NP 4(1)

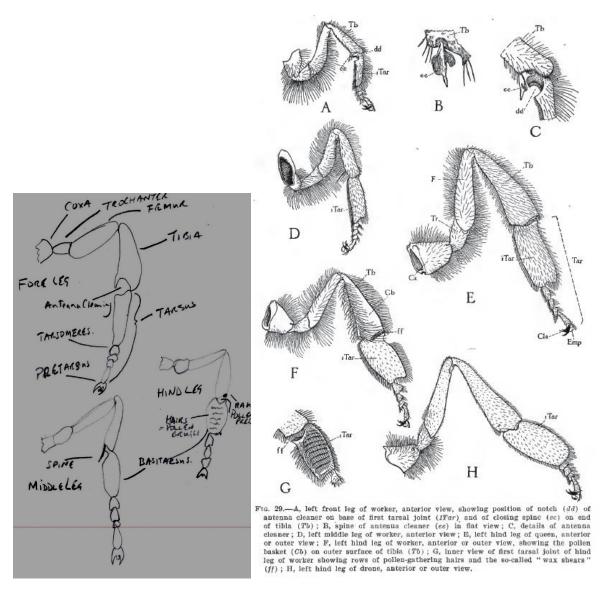
DORSOVENTRAL MUSCLES TIGHT LONGITUDIAL MUSCLIES RELAXED

WINGS DOWN

DV OOD

DORSOVENTRAL MUSCLES RELAXED LONGITUDIAL MUSCLES TIGHT \* Note ABDOMIN CHANGEI SIZIEJSHAPIE WITH WINGMONLMENT

Legs and feet



The honey bee has three pairs of legs all attached to the thorax, facts:

- The legs are hollow with a hard outer coating
- Part names; coxa, trochanter, femur, tibia, tarsus (5 tarsomeres), pretarsus
- Function as two tripods when walking at normal speeds (front, rear and opposite middle)
- Fore legs have notch between Tibia and basitarsus which is used for antenna cleaning
- Middle leg has spine which is of unknown use
- Rear leg differs between castes, in worker it is highly developed for pollen collection, in drone and queen it is not
- Foot has claws (ungues) for use on rough surfaces and suction pads (arolium) for smooth surfaces

### Antennae

The antennae function as highly developed sense detectors as well as playing an integral communication role as part of trophallaxis.

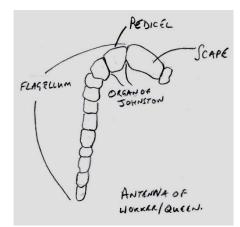
The larval antennae develop in pockets of the epidermis, they complete their development during the propupal stage and are exposed on the pupa after the 5<sup>th</sup> moult.

There are two antennae attached to the front of the head in a flexible manner so that they can move in all directions. The antennae are the noses of the bee, each consisting of a 10 or 11 segment flagellum attached to a scape via a pedicel.

Each antenna is a hollow tube containing the large antennal nerve, minute extensions of the tracheal system and small muscles which enable the antennae to move in all directions.

The scape is connected is set into a membranous socket and pivoted on a single articulated process, the antennifer, thereby all allowing movement in all directions and controlled by 4 muscles. The proximal segment of the flagellum is the pedicel, it contains the Organ of Johnston, this is employed to determine wind speed and airborne vibrations (sound).

The joint between the pedicel and scape is controlled by 2 muscles facilitating vertical movement. The flagellum on the drone comprises 12 segments and on the worker/queen there are 11 (including the pedicel). Within the



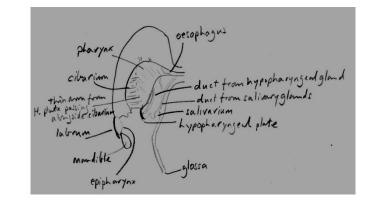
The function of the antennae are as sensory organs, mainly for touch (tactile) and smell (olfactory), they are key elements in the communication within the colony especially with the distribution of queen substance. The sensors within the antennae include:

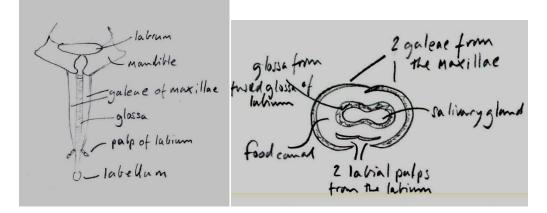
- Olfactory
- Tactile
- Temperature
- Humidity
- Gas (CO<sub>2</sub>)
- Vibration
- Muscle tension
- Cuticle strain

### Mouth

The mouth parts are generally common to other insects:

- Labrum, the upper lip is an extension of the face
- Mandibles, the jaws in a worker are spoon shaped and smooth, their uses include
  - Taking in of pollen, shaping and chewing wax, fighting, grooming, dragging out of debris from the nest, brood feeding, gathering and using propolis and to support other mouth parts.
- Proboscis, 5.3-7.2 mm dependent upon race, is basically a tube within a tube, the central tube called the glossa surrounded by another made up from the galeae of maxillae and labial palps (2 of each fused together). It is terminated in the labellum.





The proboscis main function is to ingest liquid (water, nectar and honey) but it also functions in trophallaxis and in the licking of pheromones and exchanging them with other workers. The proboscis can be folded in a Z shape within the mouth when the bee is resting. liquid is sucked up the glossa by the cibrarial pump (the walls of cibarium expanding and contracting). The epipharynx forms an airtight seal at the top of the glossa in order to enable the suction to occur.

The glossa is very hairy and an important use is in the collection of pollen that sticks to the hairs and is removed by the fore legs.

The proboscis is able to protrude and retract and used to:

- Tongue lashing, the worker regurgitates liquid (water or nectar) spreads it on comb or side of hive in a thin layer and repeatedly beats it with her tongue.
- Tongue stropping, hesitant bees when entering the wrong hive and are challenged by a guard, pull their proboscis through their front feet.
- Honey ripening, nectar is regurgitated and held in a fold of proboscis exposing it to air

To liquefy solid foods saliva travels down the glossa tube and the labellum is employed to rub it into the solid food to create a liquid to be drawn up.

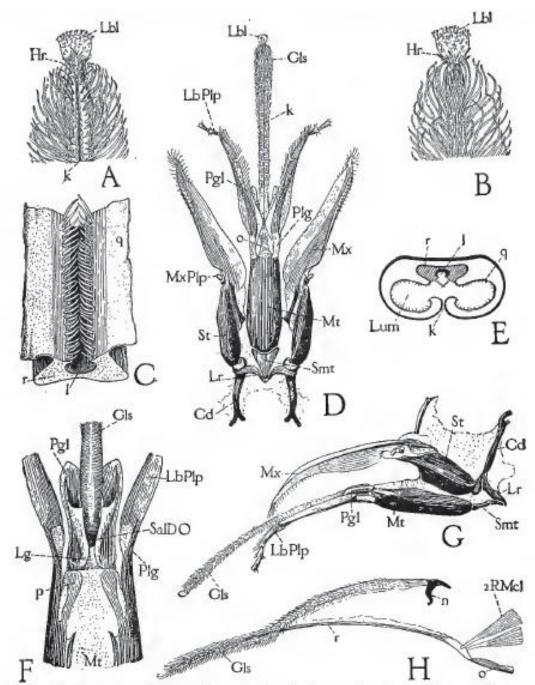
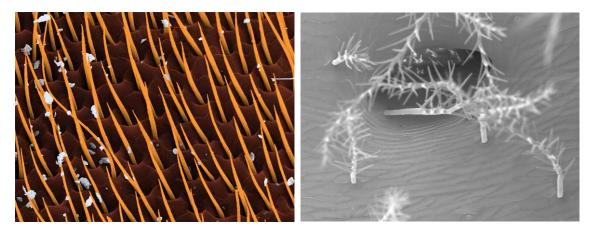


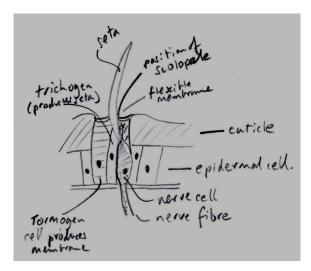
FIG. 15.—Mouth parts of the worker: A, tip of glossa, showing labellum (Lbl), guard hairs (Hr), and ventral groove (k); B, same, from above; C, small piece of glossal rod (r) with adjoining parts of walls (q) of glossal canal attached, showing ventral channel (l) guarded by rows of hairs. D. parts forming the proboscis, labium in middle and maxillæ at sides, flattened out, ventral view; E, cross section of glossa showing its invaginated channel (Lum) and position of rod (r) along its dorsal wall, and likewise position of channel (l) of rod along median line within the glossal channel; F, end of mentum (Mt) and bases of ligula (Lq) and labial palpi (LbPlp), showing opening of salivary duct (SalDO), dorsal view; G, lateral view of proboscis showing parts on left side; H, lateral view of glossa (Gls) with its rod (r) torn away at base showing attachment of retractor muscles (2RMel).

Setae (hairs)



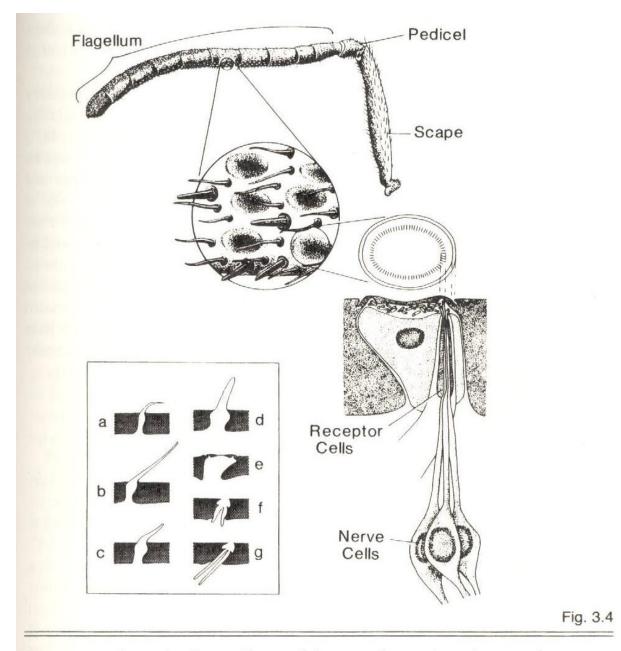
Setae are small hairs that are found all over the body (including on the compound eye) that are used for sensory purposes and the collection of pollen. There are branched hairs and smooth hairs. The branched hairs capture pollen whilst the smooth hairs generally have specific functions:

- The specialised hairs on the legs are used for collection and packing of pollen and include the corbicula, rastellum and pollen brushes
- Interfacetal hairs located in the compound eyes act as mechanoreceptors measuring wind speed and direction
- Tomenta hair on the abdominal tergites whose function is unknown but varies in length, volume and colour on bees of different races.
- Lack of hair is also a sign of age and disease e.g. hairlessness with CBPV
- Sensilla trichodia is a seta providing tacticle information.



The diagram shows a sensillum trichodeum which reacts to touch:

- Seta is the receiving stimuli, when touched it bends within the flexible membrane
- The trichogen cell produces the seta
- The tormogen cell produces the membrane and fills the space beneath it
- The nerve cell produces an impulse when activated
- The scolopale is a thin cap which contains the nerve ends in order to pick up the movement

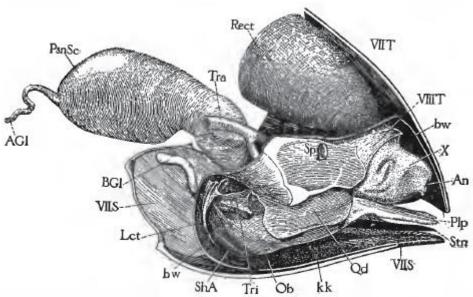


The antenna of a worker bee, with one of the pore plates enlarged to reveal the odorant receptor apparatus. The insert shows the seven types of sensory structures found on antennae: (*a*) small thick-walled hair (sensillum trichodeum), (*b*) thick-walled peg (s. trichodeum), (*c*) slender thin-walled peg (s. trichodeum olfactorium), (*d*) large thin-walled peg (s. basiconicum), (*e*) pore plate or plate organ (s. placodeum), (*f*) pit organ (s. coeloconicum), and (*g*) pit organ (s. ampullaceum). (Nomenclature is from Lacher, 1964. Redrawn from von Frisch, 1967a, based on Lacher, 1964, and Snodgrass, 1956. Copyright © 1956 by Cornell University. Used by permission of Cornell University Press.)

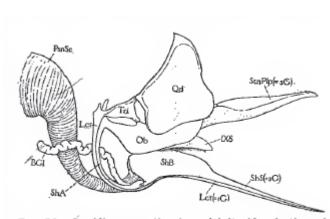
# 5.19 the structure of the sting mechanism and how this mechanism operates to penetrate human skin and deliver the venom;

The worker sting is a highly modified ovipositor which has evolved for defensive functions. Unlike most stinging insects the bee loses its sting after use, resulting in the bee's death shortly afterwards. The advantage of losing the sting is that the victim is injected with additional venom. The sting chamber is formed by the reduced and modified 8<sup>th</sup>, 9<sup>th</sup> and 10<sup>th</sup> abdominal segments attached to the bee by a thin membrane.

It is this delicate membrane that enables the sting along with the three segments, the poison glands and the terminal end of the alimentary canal to easily become detached once the bee has stung. The sting of the queen is more strongly attached and there are fewer bards on the lancet (see later) meaning the chamber does not become detached after stinging.



F16. 41.—Tip of abdomen of worker with left side removed, showing right halves of seventh tergum (VIIT) and sternum (VIIS), containing the sting chamber (kk) cut open along the line *bw*, exposing the eighth tergum (VIIIT), the rudimentary tenth segment (X) carrying the anus (An), and the sting and accessory parts shown by fig. 36.



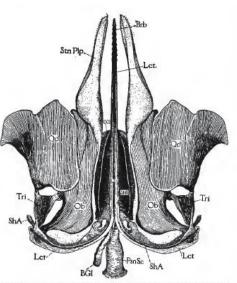


FIG. 36.—Semidiagrammatic view of left side of sting of worker, accessory plates (*Tri*, *Ob*, *Qd*), sting palpus (*StnPlp*), alkaline poison gland (*BGI*), and base of large poison sac (*PsnSc*) of acid gland.

FIG. 37.-Ventral view of sting of worker and accessory parts, flattened out.

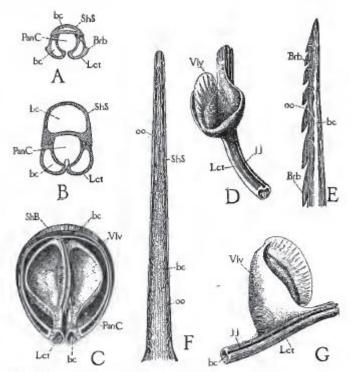


FIG. 40.—Details of sting of worker: A, section through tip of sting showing lancets (*Let*) and shaft of sheath (*ShS*) surrounding central poison canal (*Psn(*), and each containing a prolongation of the body-cavity (*bc*); B, section of same near base of bulb; C, section of sting through basal bulb, showing poison canal as large invaginated cavity (*PsnC*) In bulb of sheath (*ShB*) containing the two valves (*Vlv*), dorsal view; E, tip of lancet showing pores opening on bases of barbs (*oo*) coming from body-cavity (*bc*) of lancet not from poison canal; F, dorsal view of shaft of sheath showing lateral series of pores (*oo*) from prolongation of body-cavity (*bc*); G, lateral view of left valve and part of lancet.

The elements of the sting are:

- Three plates (per lancet) which along with muscles drive the associated lancet and valve to the bulb
- The shaft comprising the lancets and a stylet which expands into the bulb via an umbrella valve for each lancet, the valve opens when the lancet is extended and closes when it is removed from the victim
- Venom sac which holds the venom and is connected to the bulb
- Poison glands (acid glands) which secrete the venom into the sac
- Dufour gland (alkaline gland) which opens to the sting chamber to lubricate the stylet and to possibly neutralise any leaked venom

Before stinging the bee positions itself perpendicular to the victim by contracting ventral sclerites and extending dorsal sclerites.

The working of the sting mechanism comprises three main elements:

- Sting
- Plates and muscles
- Poison glands and venom sac

The sting is made up of two barbed lancets which slide on the tracks of the stylet or sheath. These open out into a large swelling called the bulb via umbrella valves. The bulb is full of venom from the venom sac and releases it into the poison canal formed by the linking if the lancets and sheath.

When the worker stings the first one lancet is extended by a series of plates and muscles which drive the lancet into the victim as well as opening the valve to the bulb releasing the venom. As the first lancet is withdrawn the second lancet is driven into the victim, this continues until the lancet becomes stuck and the sting is detached. The action of withdrawing the lancet causes a vacuum within the bulb drawing more venom into the bulb. On extending venom is forced into the lancets and sheath causing it to enter the victim via small pores in the lancets and sheath.

The three plates are Oblong, Triangular and Quadrate, there is one set for each lancet and each side functions alternately. The plates drive a Ramus which extends to the lancets and thus the action of thrusting and withdrawal is controlled by muscles connecting the oblong and quadrate plates which connect via joints to the triangular plate. The thrusting action opens the lancet valve within the bulb and venom is poured into the sting.

The poison glands (acid and alkaline) continually produce venom which is stored in the venom sac. The venom sac does not have a muscular wall, rather the flow of the venom is controlled by the expansion and contraction of the bulb. The pulsing of venom after the bee has detached itself is the continued action of the plates.

The Dufour gland releases alkaline solution into the sting chamber at the base of the sting, the purpose of which is not clear, it is thought to lubricate the sting and neutralise any venom that has seeped into the chamber. Snodgrass talks of both acid and alkaline poison elements making up the venom.

Main components of venom are:

- Melittin which makes up 50% of dry weight. It causes the rupture of blood and mast cells and depresses blood pressure and respiration (mast cells release histamine and heparin when ruptured)
- Phospholipase A which causes cell breakdown and pain
- Hyaluronidase acts like a cement holding cells together so as to facilitate better passage of other substances

### 5.20 the role of the direct and indirect muscles in flight.

The thorax to which the wings are attached at the notum is effectively a box that can change shape. Rather than have muscles directly connected to the wing drive the actions for flight, the wing movements are driven by indirect muscles changing the shape of the Thorax at over 200 cycles per second.

There are two pairs of indirect muscles that occupy the majority of the space within the Thorax:

Dorsoventral muscles, are connected to the lateral parts of the scutum (anterior part of the notum) and to the lower wall of the appropriate thoracic segment. When the muscles contract the notum is pulled downwards which causes the wings to move upwards, the muscles are also known as the elevator muscles. There is are Dorsoventral muscles in the mesothorax (T2) and metathorax (T3) so each pair of wings have their own pair of muscles.

Longitudinal muscles, are attached to the front of the thorax on the curved part of the mesoscutum. The other end is situated in the propodeum on the hind part of the mesothorax. When contracted they cause the wings to be pulled downwards. These muscles are also called depressor muscles. Both pairs of wings are depressed by a single pair of these muscles.

Apart from flight these muscles are employed by workers for other functions, all of which employ the fact that the act of flying creates heat in the muscles:

- Warming the nest, with wings furled the bee is able to exercise its flying muscles to create heat in winter and to maintain the brood temperature in the summer.
- In preparing a swarm next to fly scout bees will heat bees on the outside of the nest by jumping on them and activating their flight muscles to heat the other be in preparation for flight
- A bee must be warm to fly so the muscles are activated before the bee takes off
- Fanning the nest to keep it cool, the wings are flapped whilst the bees are stationary in order to cause air to be circulated