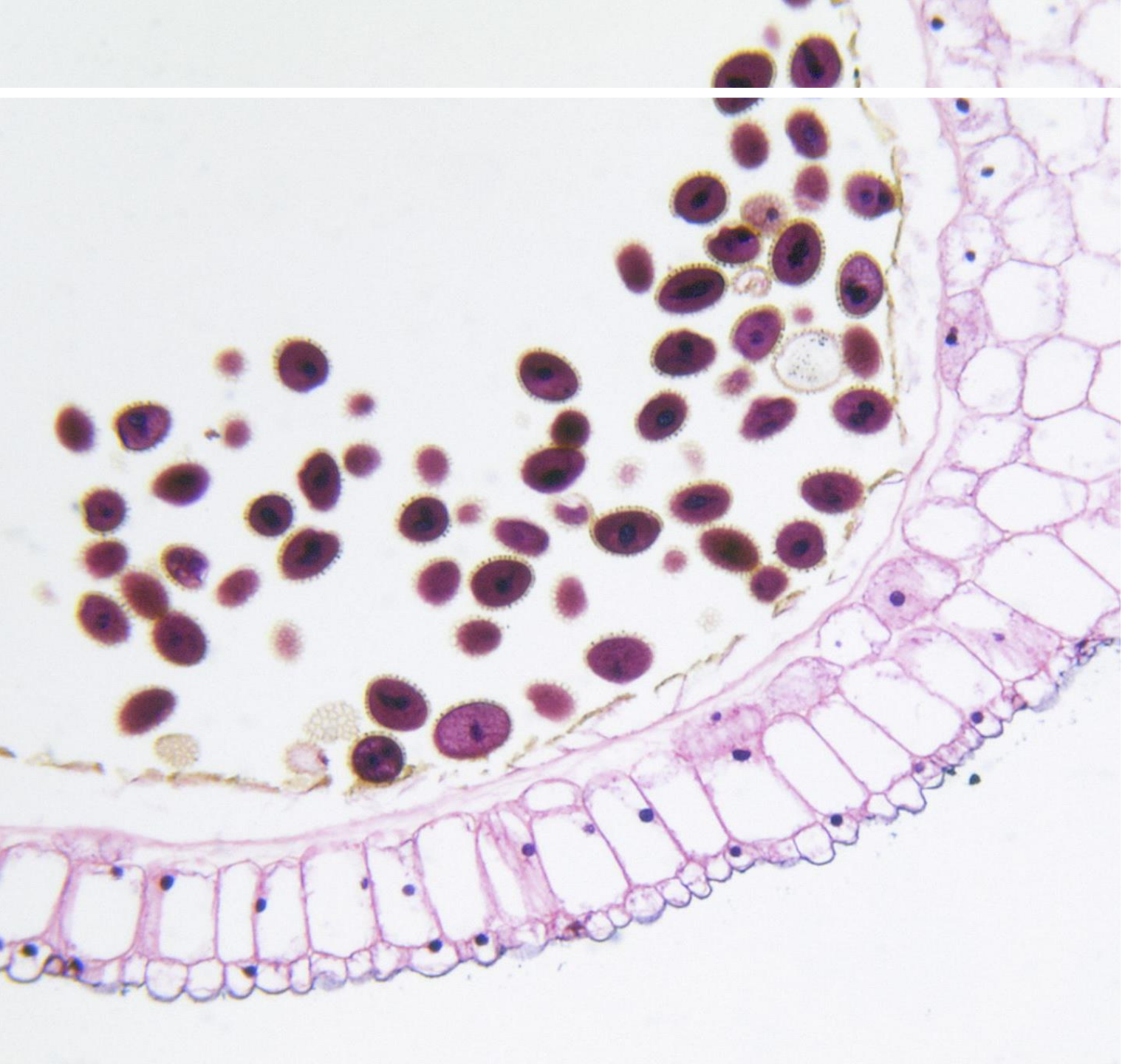


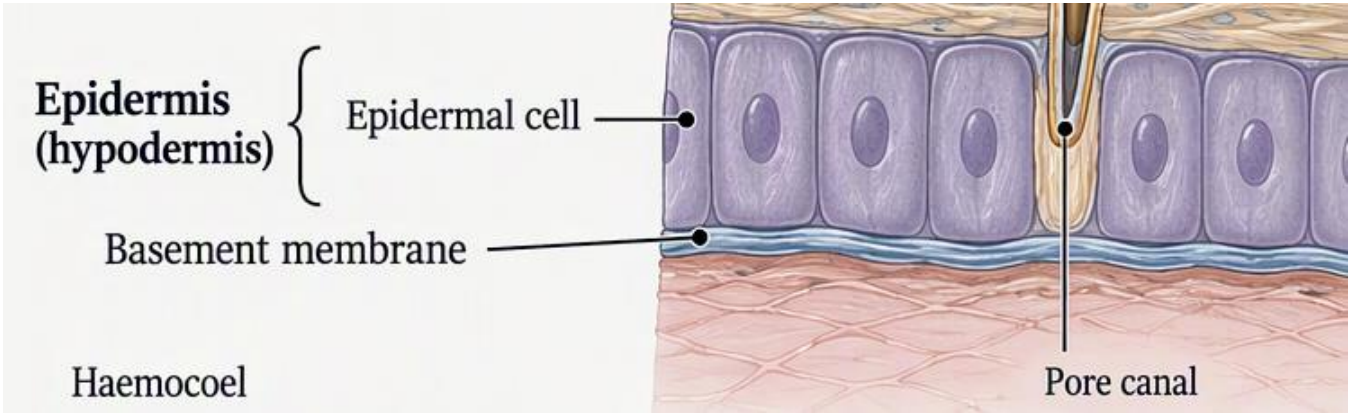
FORMATION OF THE CUTICLE

and its invaginations

1 The epidermis begins a new cuticle

Apolysis creates space for a replacement

The epidermis separates from the old cuticle. Its cells release moulting fluid into the gap and begin secreting the new covering.



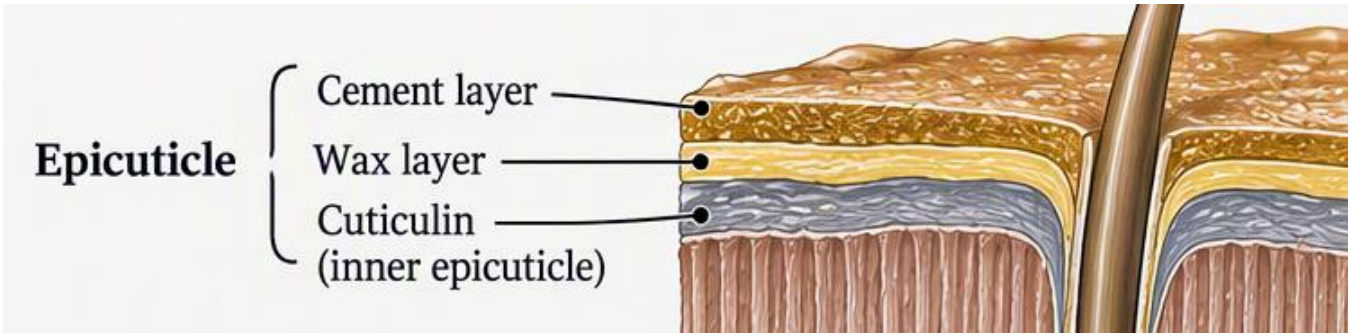
Epidermis and basement membrane

Mature anatomy shown for reference

2 The new epicuticle forms first

A protective layer appears before digestion

The epidermis secretes a cuticulin layer. This early part of the epicuticle protects the new surface from the digestive action of the moulting fluid.



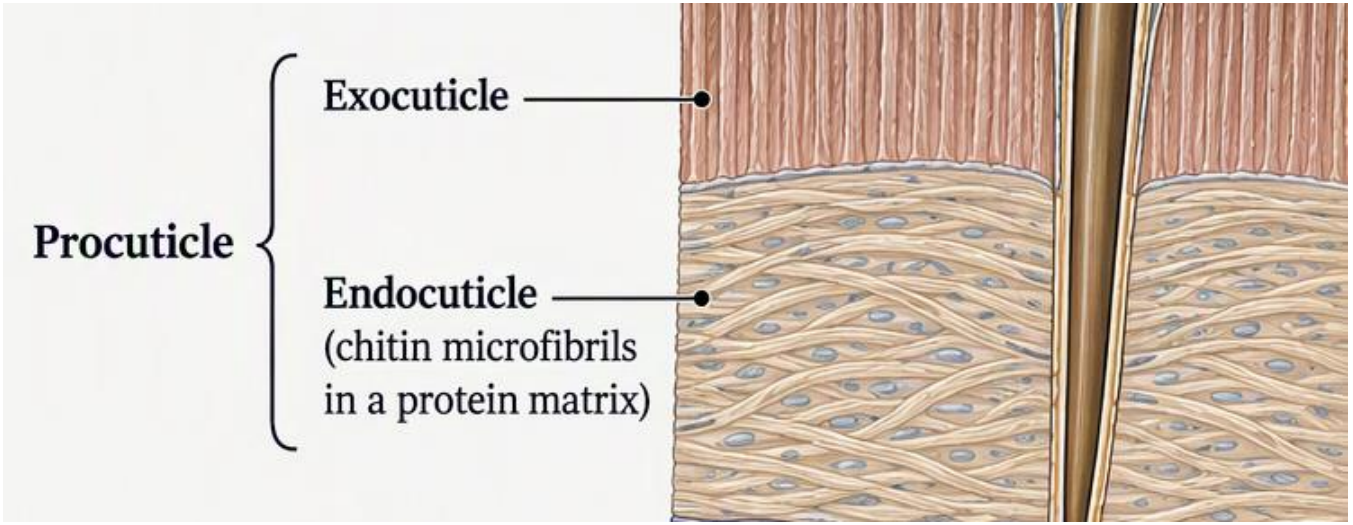
Outer layers of the mature cuticle

Mature anatomy shown for reference

3 The procuticle develops underneath

Chitin and protein build the main thickness

The epidermis deposits new procuticle beneath the epicuticle. Moulting fluid digests the old endocuticle, allowing the insect to reuse material.



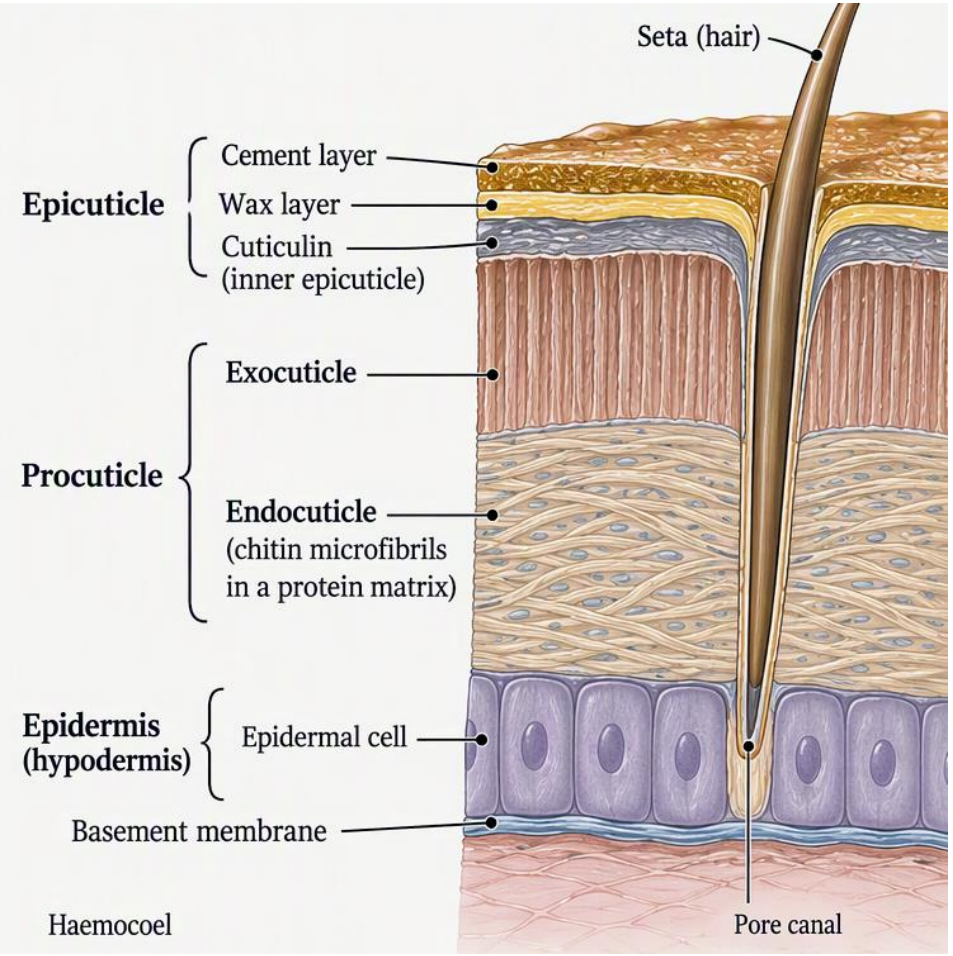
Exocuticle and endocuticle

Mature anatomy shown for reference

4 Shedding and hardening complete the moult

The new covering expands and strengthens

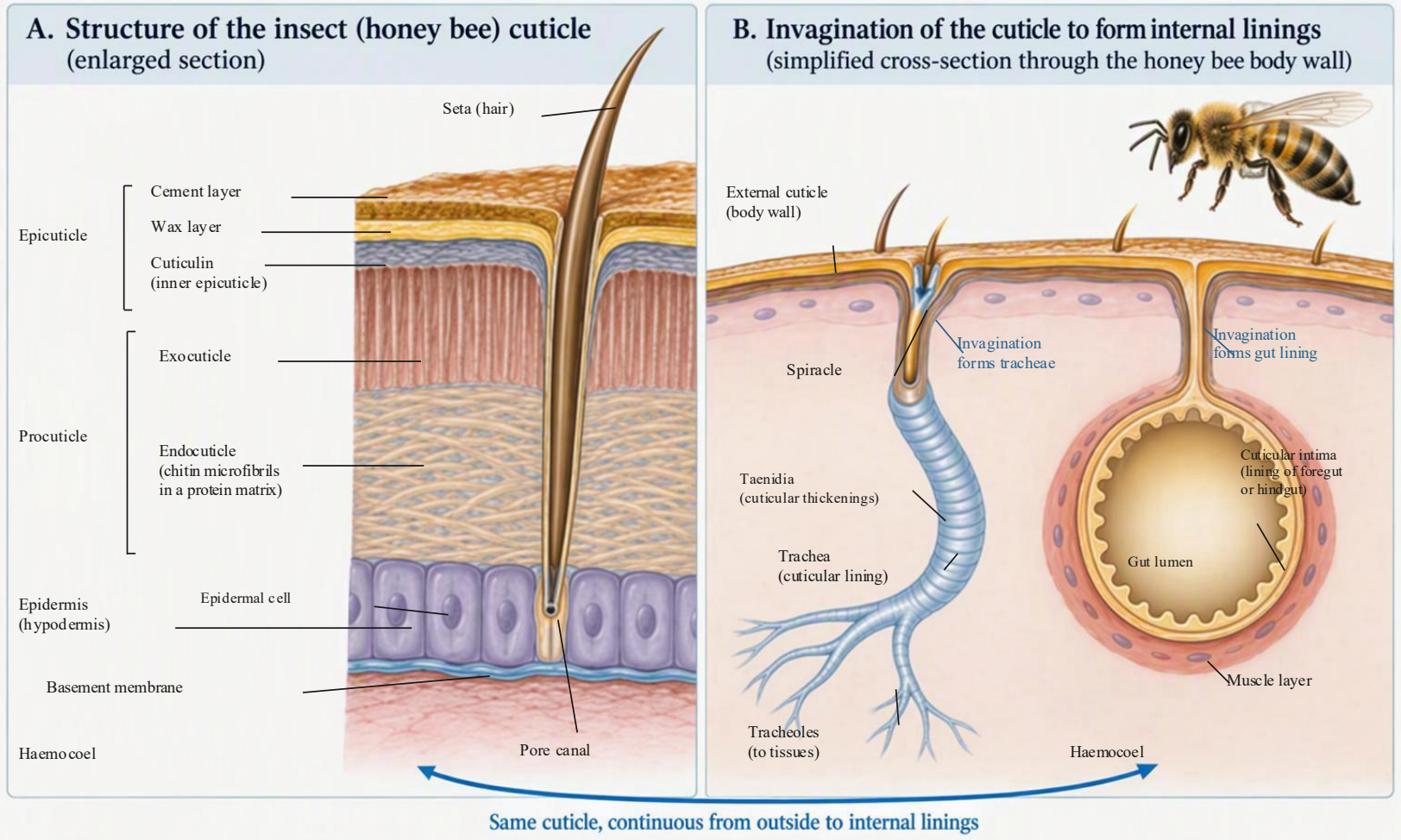
The insect sheds the old covering during ecdysis. The new cuticle then hardens by sclerotisation. The outer procuticle forms a hardened exocuticle above the softer endocuticle.



The mature, layered cuticle

Mature anatomy shown for reference

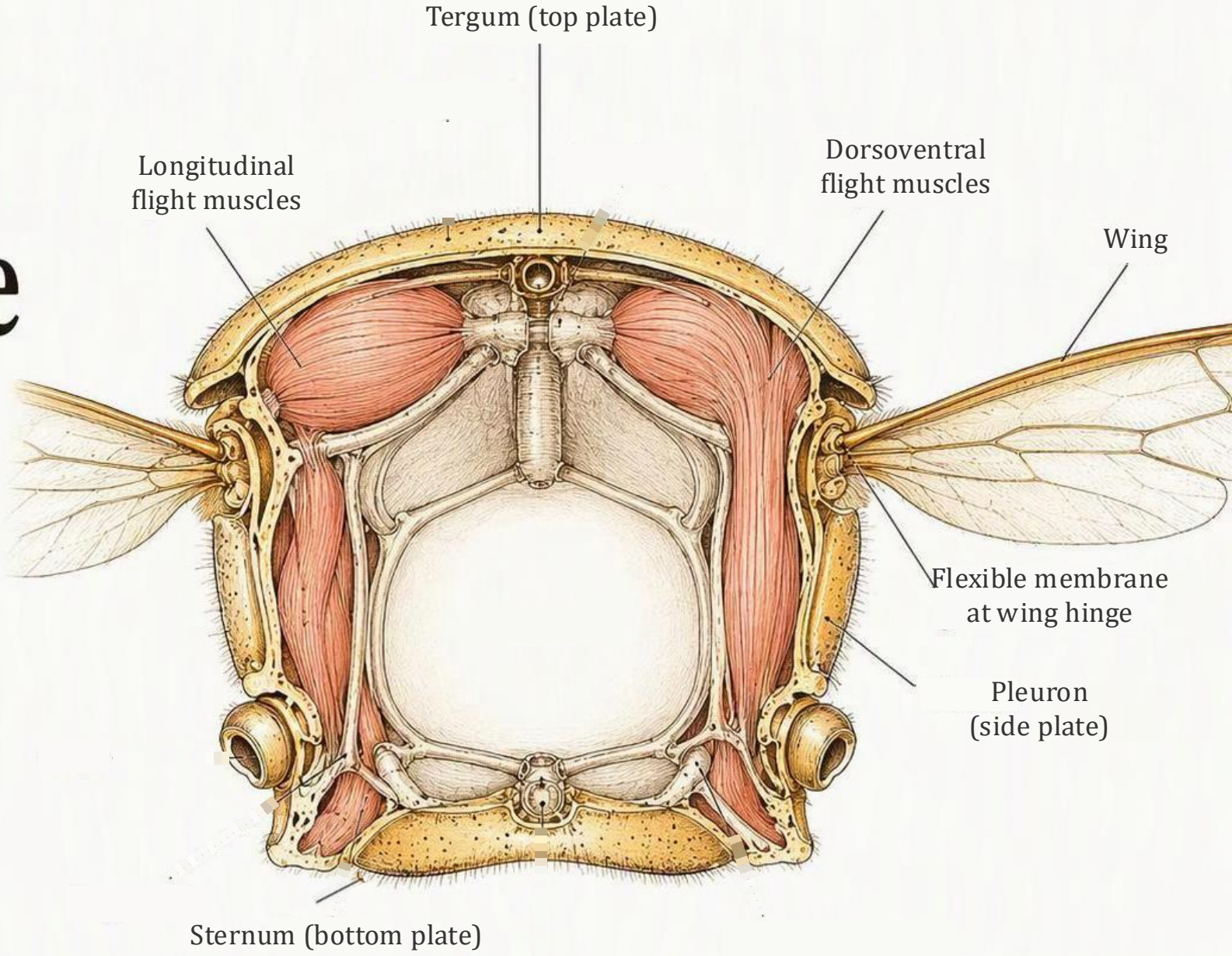
Insect Cuticle: Structure and Internal Invaginations



The Honey Bee Exoskeleton

Structure and function of the bee's external skeleton

Alan Baxter, Education Officer, FDBKA



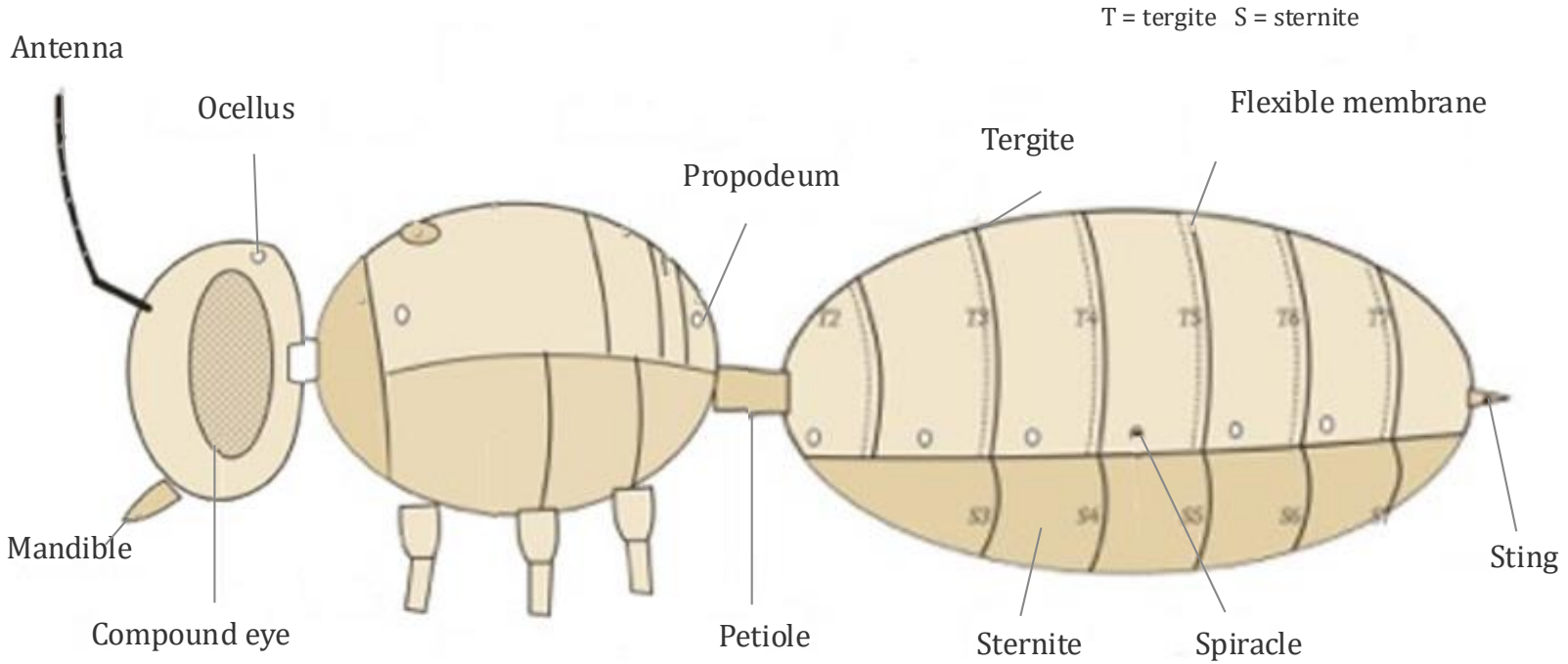
The honey bee’s exoskeleton

- A tough outer covering made of **chitin and protein**.
- Hard plates and flexible membranes form the **head, thorax and abdomen**.
- The worker’s visible abdomen has 6 tergites (upper plates) and 6 sternites (lower plates).
- It supports and protects the body, while its waxy surface reduces water loss.
- Muscles attach inside it, allowing the bee to walk, fly and move its abdomen.
- Today we will identify the main parts and explore how their structure supports their function.

A skeleton on the outside

	Our skeleton (endoskeleton)	Bee's exoskeleton
Position	Inside, surrounded by muscle	Outside, surrounding the muscles and organs
Made of	Living bone (calcium phosphate)	Non-living cuticle (chitin and protein) secreted by the epidermis
Muscles attach	To the outside of bones by tendons	To the inside of the plates and to internal ingrowths
Growth	Grows with the body	Cannot grow: must be shed and replaced (moulting)
Also gives	Support	Support, armour, waterproofing and a surface for sense organs

Honey bee body plan



Worker, side view. Schematic; wings and most of the legs omitted.

Head

Eyes, antennae and mouthparts sit on a rigid head capsule.

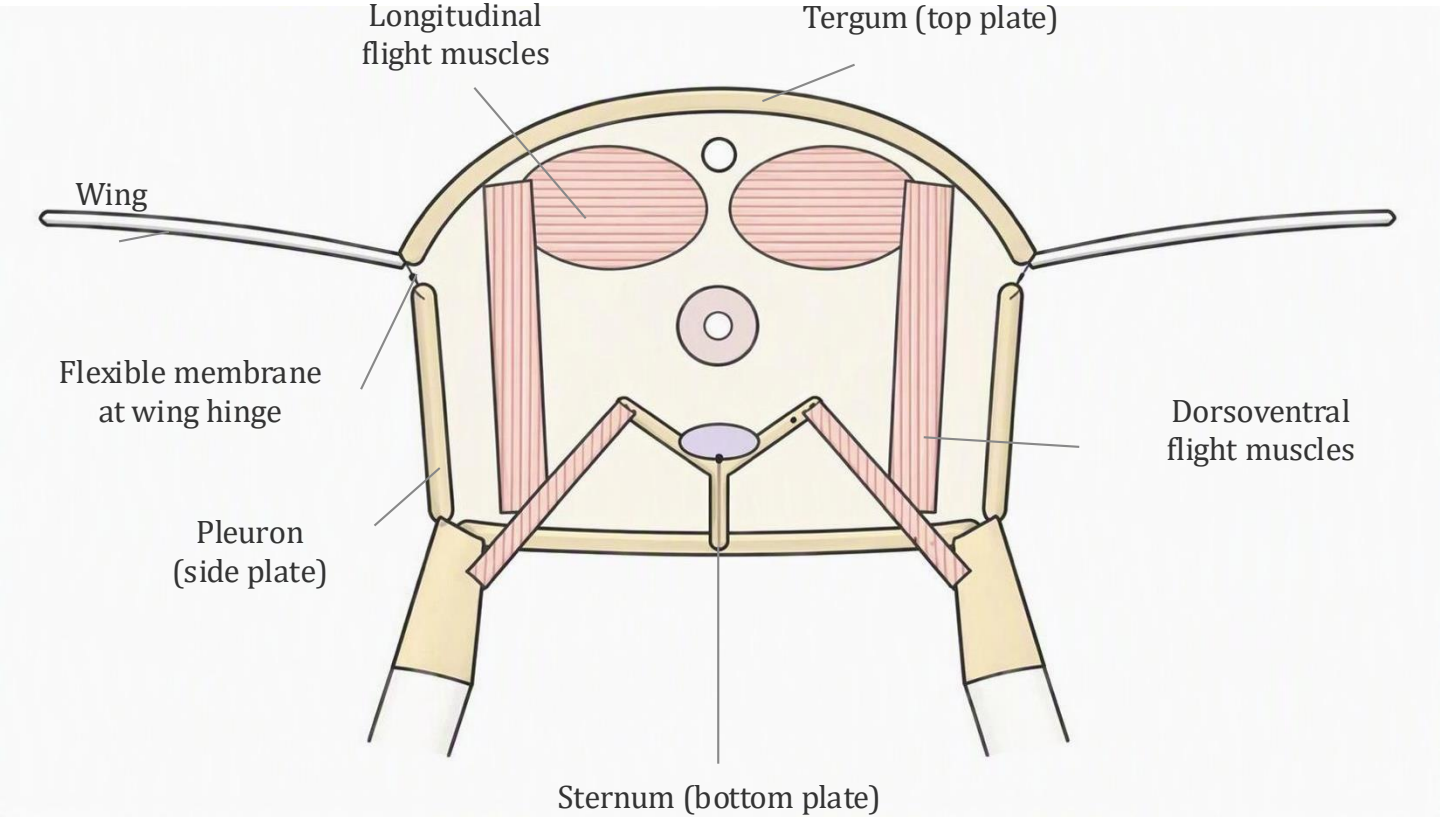
Thorax

Three thoracic segments carry the legs and wings. The propodeum is the first abdominal segment, fused to the thorax.

Abdomen

The petiole forms the narrow waist. Tergites above and sternites below overlap, with flexible membranes between them.

The thorax: plates, membranes and muscles



Transverse section through a wing-bearing segment of the thorax. Schematic.

Sclerites

Hard plates form the outer support: tergum above, pleuron on each side and sternum below.

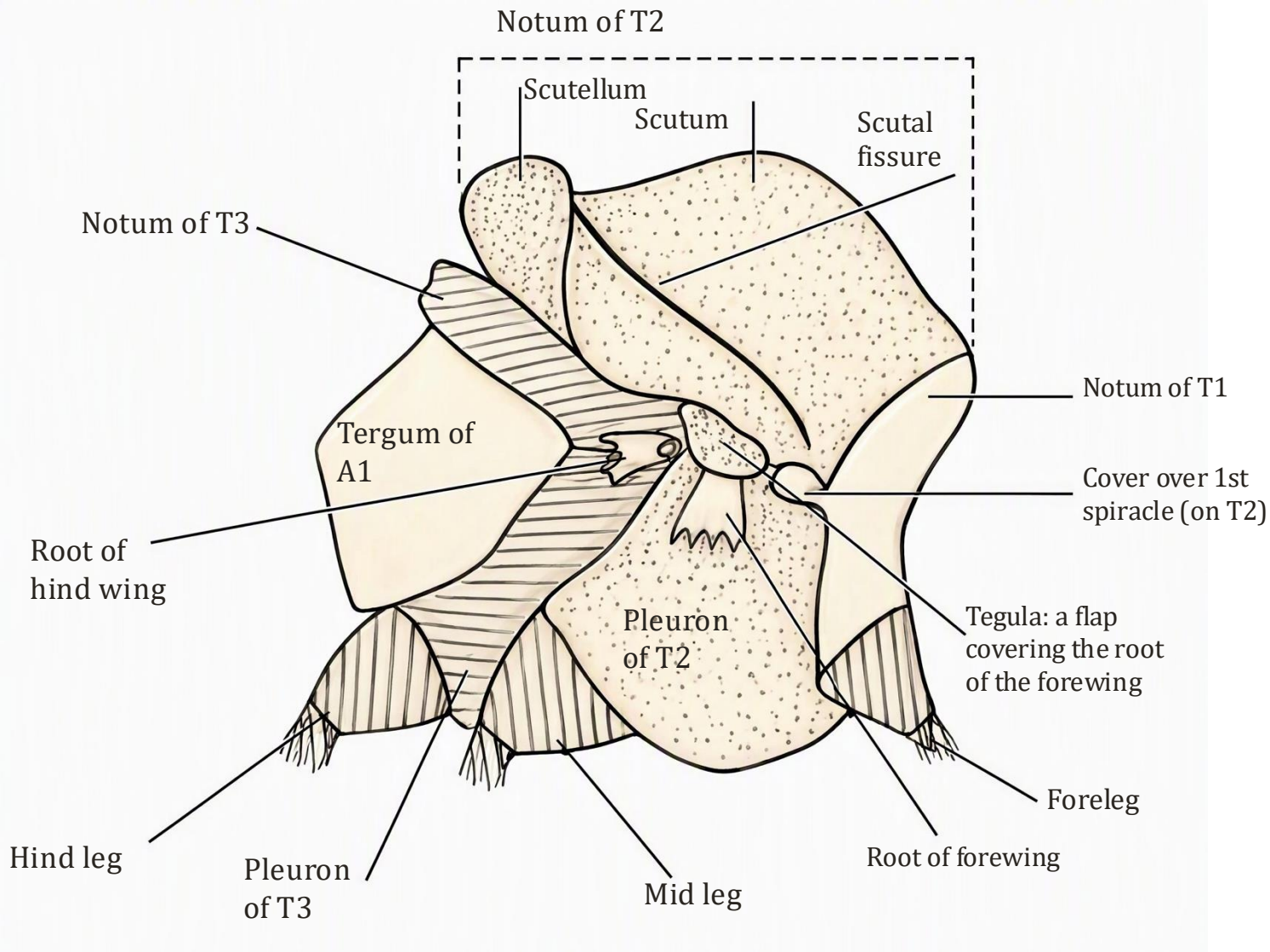
Membranes

Flexible cuticle joins the plates and allows movement at the wing hinge.

Flight muscles

Longitudinal and dorsoventral muscles change the shape of the thorax to move the wings.

The thorax



Prothorax (T1)

The first segment behind the head carries one pair of legs.

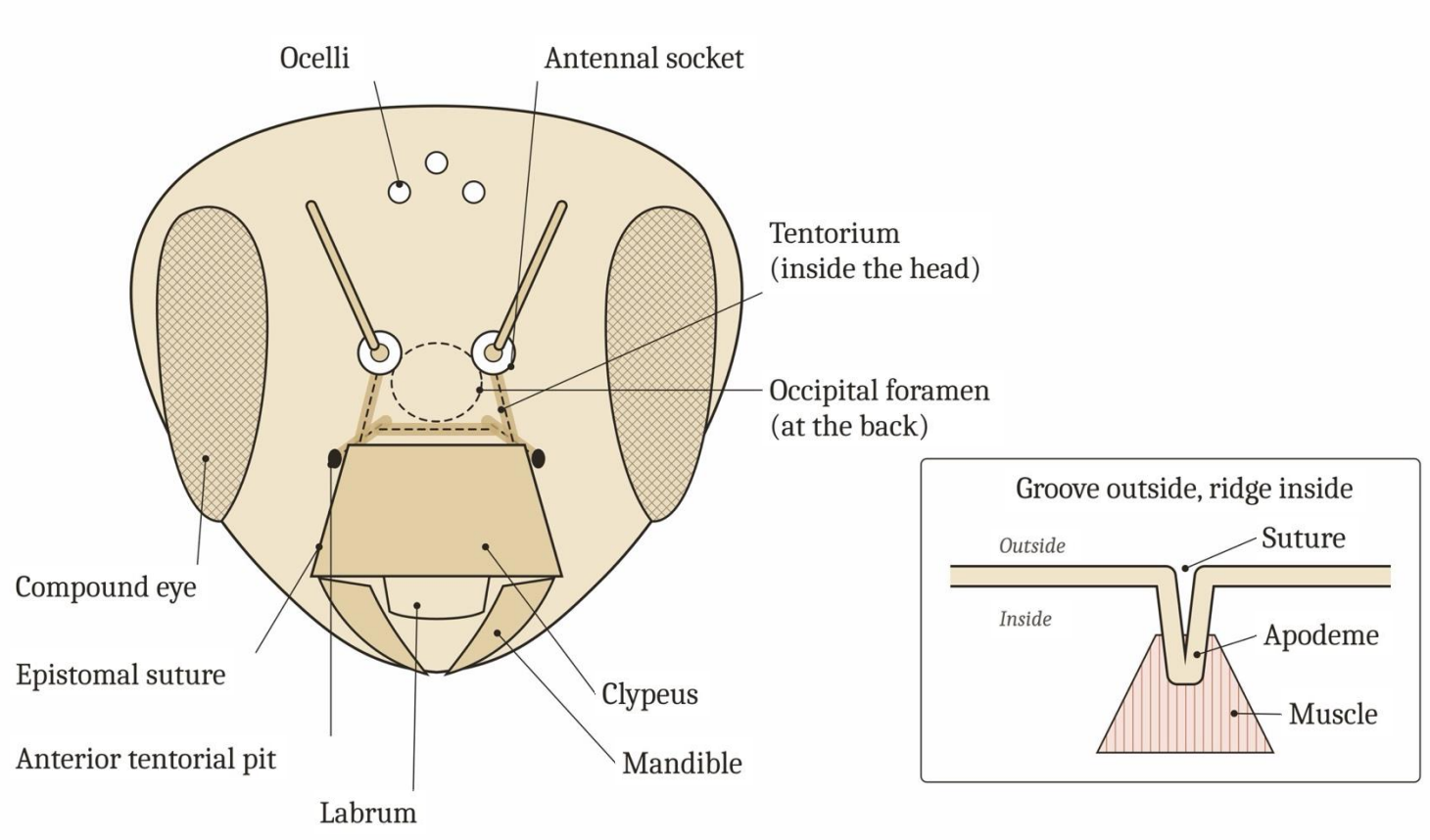
Mesothorax (T2)

The middle segment carries one pair of legs, one pair of wings and one pair of spiracles.

Metathorax (T3)

The rear segment carries one pair of legs, one pair of wings and one pair of spiracles.

The skeleton also grows inwards



Worker head, front view; the tentorium lies inside the head (dashed). Inset: a suture in section.

Apodemes

Infoldings of cuticle. Each external groove (suture) marks an internal ridge.

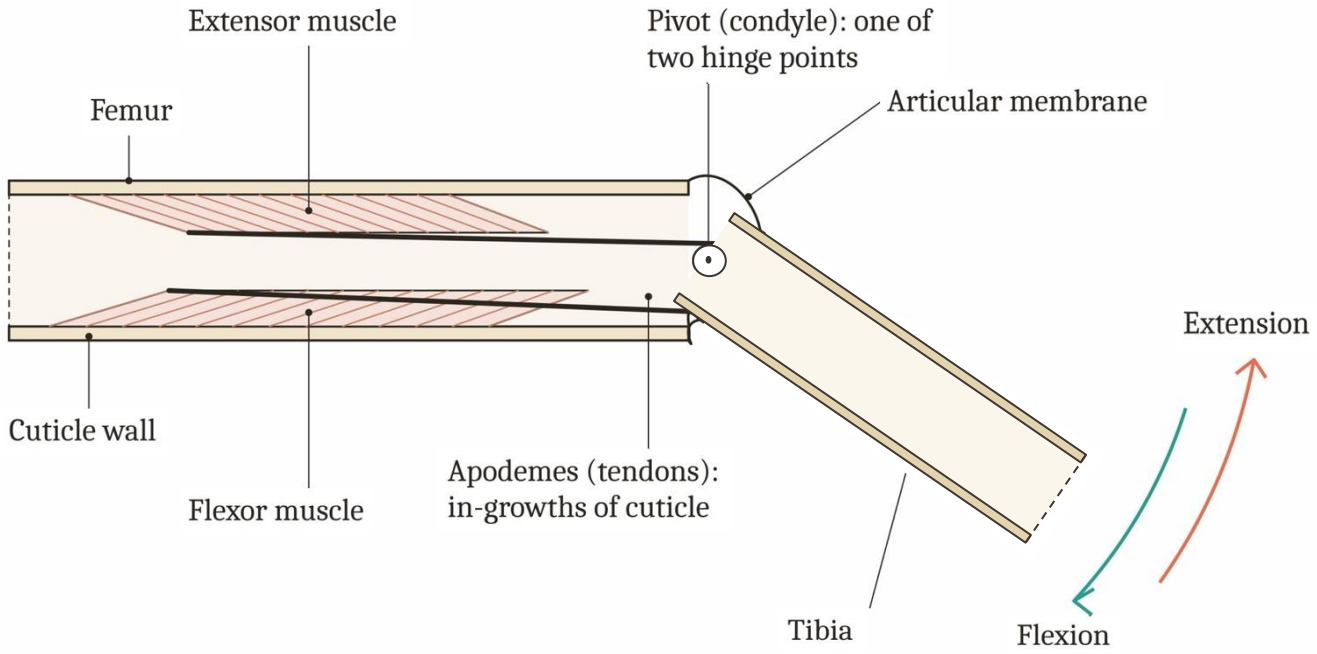
Tentorium

Internal struts that brace the head and anchor the muscles of the mandibles and antennae.

Phragmata and furcae

Plates in the thorax for the flight muscles, and forked struts for the leg muscles.

Joints: hard tubes, soft hinges



Femur–tibia joint in section. Schematic.

Hinge joints

Two pivots allow movement in one plane, as in most leg joints and the mandibles.

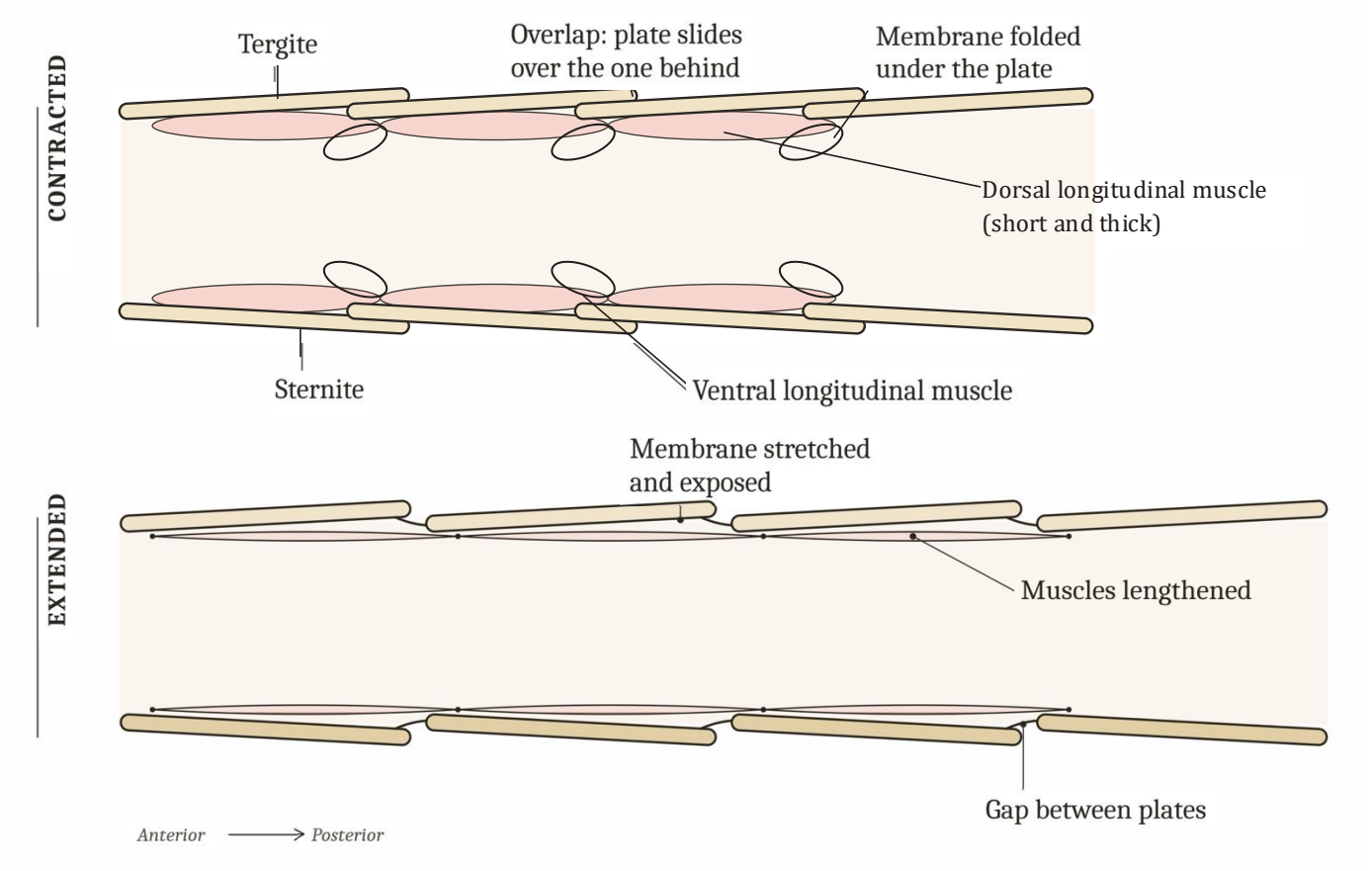
Ball-and-socket

A single pivot allows wide movement, as at the base of the antenna.

Muscles only pull

So they work in opposing pairs: a flexor bends the joint, an extensor straightens it.

The abdomen telescopes



Longitudinal section through four abdominal segments. Schematic.

Filling the crop

A forager carrying a full honey stomach extends her abdomen to make room.

Breathing

Pumping movements of the abdomen push air through the tracheal system.

The queen

Membranes stretch greatly as her ovaries fill with eggs.

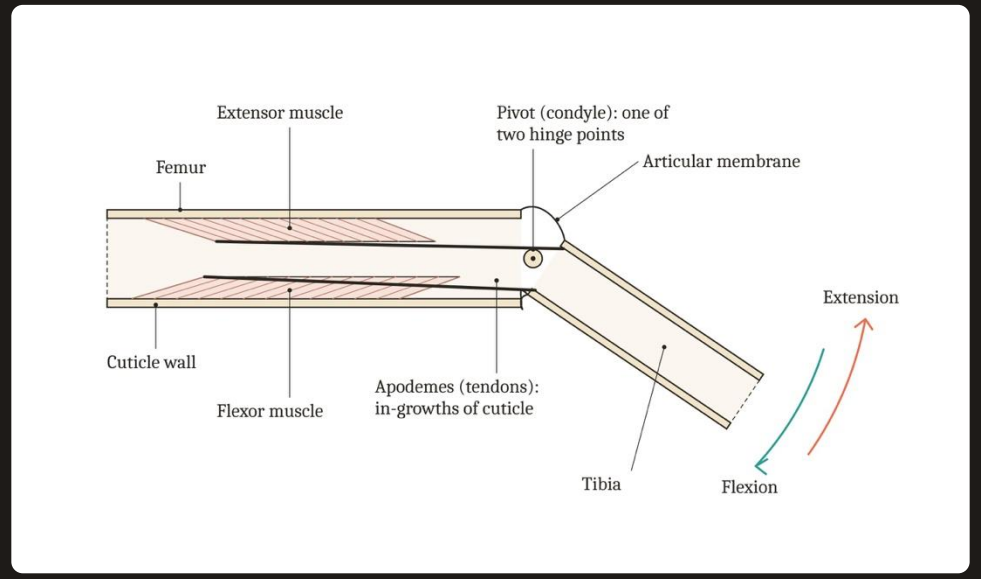
Wax glands

On sternites 4–7, under the overlap of the plate in front.

PART 2

What the exoskeleton does

Six jobs, and the price the bee pays for them.



Six jobs for one skeleton

Support and shape

Holds the body's shape without any internal bones.

Muscle attachment

Plates, apodemes and joints act as levers for movement and flight.

Protection

Armour against knocks, abrasion, predators and pathogens.

Waterproofing

The waxy epicuticle cuts water loss from a small body.

Sensing

Hairs, pits and pore plates turn the surface into a sense organ.

Specialised tools

Pollen baskets, antenna cleaners, wax mirrors and the sting are all exoskeleton.

The price of an exoskeleton



It cannot grow

Growth happens only in the larva, which sheds its cuticle at each moult. The adult bee never moults, so her size is fixed when she emerges.



It limits size

A shell heavy enough for a large animal would be too heavy to move, one reason insects stay small.



Its joints are weak points

Varroa feeds through the soft membranes between abdominal plates; the tracheal mite enters through the spiracles.

SUMMARY

Key points

1. The exoskeleton is cuticle: hard plates (sclerites) joined by soft membranes.
2. The body has three regions; each segment is a ring of tergum, pleura and sternum.
3. Apodemes fold inwards to brace the body and anchor muscles: tentorium, phragmata, furcae.
4. Joints are hinges of membrane and pivots, moved by opposing pairs of muscles.
5. It supports, protects, waterproofs and senses, but it cannot grow and must be moulted.

Further reading

Snodgrass, R.E. (1956) Anatomy of the Honey Bee. Comstock Publishing. Chapters on the body wall, head, thorax and abdomen.

Chapman, R.F. (2013) The Insects: Structure and Function, 5th edn (eds Simpson & Douglas). Cambridge University Press.

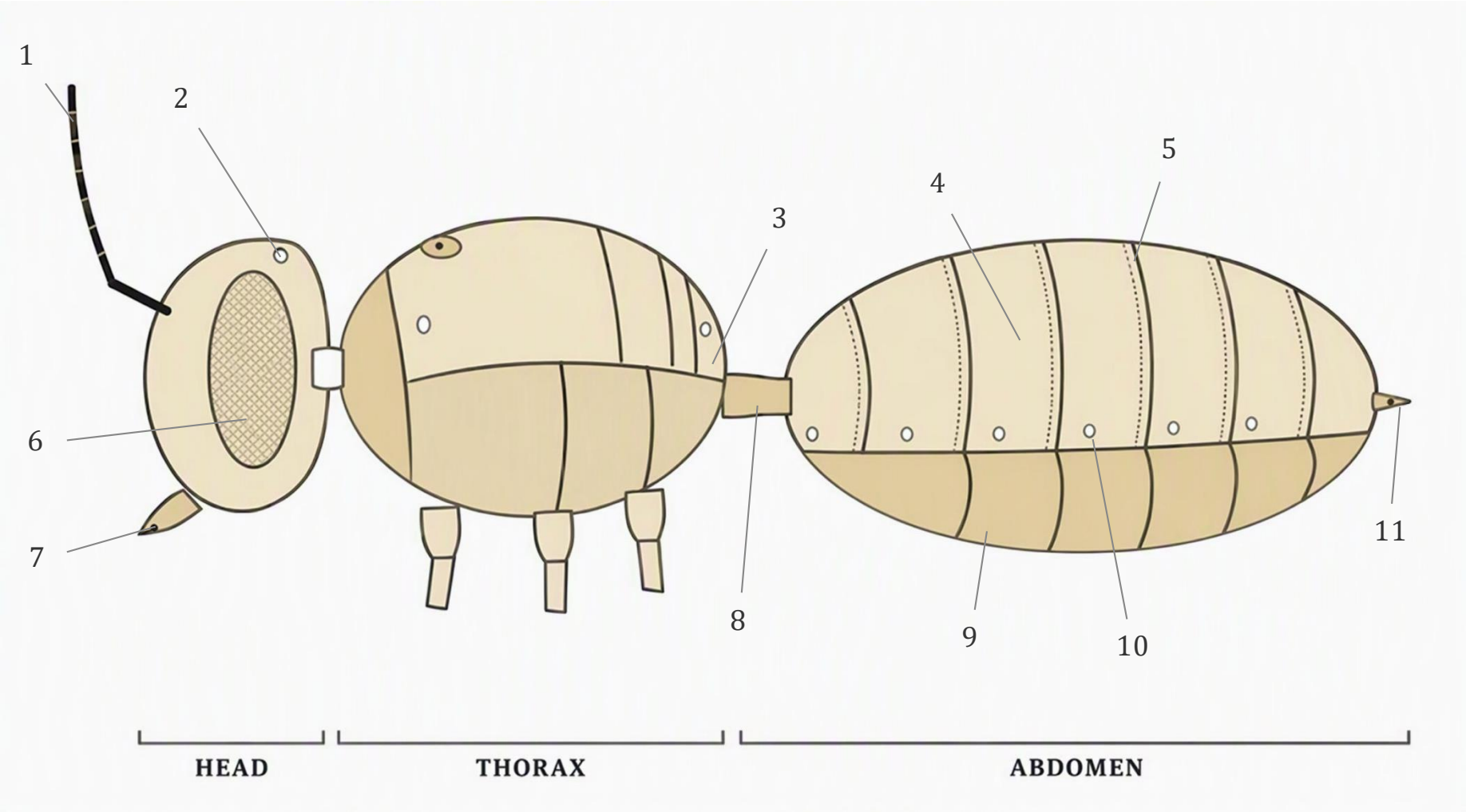
Dade, H.A. (1962) Anatomy and Dissection of the Honeybee. IBRA.

Goodman, L. (2003) Form and Function in the Honey Bee. IBRA.

BBKA Module 5 syllabus: Honey bee biology.

Diagrams: schematic line drawings made for this lesson, after the style of Snodgrass.

Label the worker



Word bank

Antenna

Compound eye

Intersegmental membrane

Mandible

Ocellus

Petiole

Propodeum

Spiracle

Sternite

Sting

Tergite

Quick quiz: test your knowledge

1 **What is the plate on the underside of an abdominal segment called?**

A Tergite
B Sternite
C Pleuron
D Scutellum

2 **What is the tentorium?**

A A suture on the thorax
B The internal skeleton of the head
C A leg joint
D A wax gland

3 **Why do muscles at a joint work in pairs?**

A Muscles can only pull
B To save energy
C The cuticle is too weak
D To move in two planes at once

4 **What lets the abdomen lengthen?**

A Resilin in the tergites
B Folded intersegmental membranes
C Moulting
D The petiole



Form & Function of Honey Bee Legs

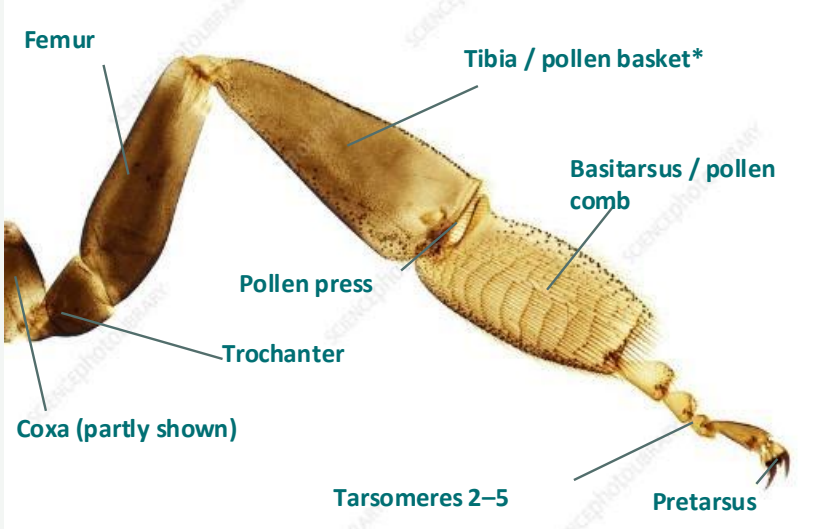
Six legs, one ground plan — cleaning, carrying, gripping and building

Alan Baxter

THE GROUND PLAN

One basic leg — six segments

Worker hindleg



Foreleg — cleaning | Midleg — support & transfer | Hindleg — pollen basket

*Pollen basket: opposite (outer) face of tibia

- **Six segments:** coxa, trochanter, femur, tibia, tarsus (5 tarsomeres) and pretarsus. The coxa articulates with the thorax; the first tarsomere (basitarsus) is enlarged in bees.
- **Three pairs, three jobs:** forelegs are smallest and specialise in cleaning; midlegs are the generalists; hindlegs are largest and carry the pollen baskets.
- **Hinge-like joints:** most leg joints have two points of articulation, so they swing mainly in one plane — good leverage for walking, packing pollen and handling wax.

PROTHORACIC LEGS (T1)

Forelegs — the antenna cleaners



Close-up of a worker's foreleg. The antenna is pulled through the notch and comb from base to tip, like drawing a thread through a comb.

1. **Strigilis:** a semicircular notch at the base of the basitarsus, lined with fine comb-like hairs, closed by a spur from the tibia (the velum) to form a ring.

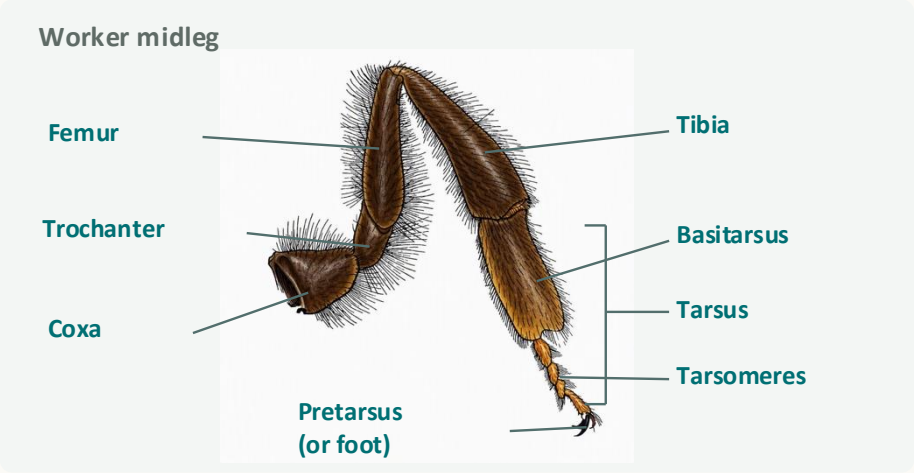
2. **How it works:** the bee lifts the foreleg, threads the antenna into the notch, closes the joint and draws the antenna through — removing pollen, dust and spores.

3. **Brushes on the foreleg** sweep the compound eyes, mouthparts and head.

4. **Why it matters:** the antennae carry the smell and touch receptors used to find flowers, read pheromones and recognise nestmates.

MESOTHORACIC LEGS (T2)

Midlegs — support and pollen transfer



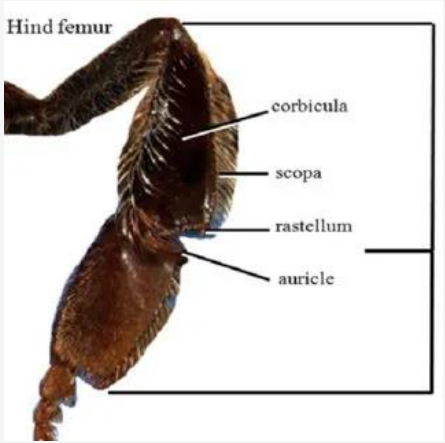
The pollen-handling chain

Forelegs → Body hairs → **Midleg brush** → Hind combs → Corbicula

- **Support:** the midlegs brace the bee on the flower while she probes for nectar, and steady her during wax work.
- **Pollen brush:** dense stiff hairs on the underside of the basitarsus sweep loose pollen off the thorax and pass it back to the hindlegs.
- **Tibial spur:** used to prise pollen pellets and propolis out of the pollen baskets when unloading, and to clean the wings.
- **Walking:** in the tripod gait each midleg moves with the fore and hind legs of the opposite side.

METATHORACIC LEGS (T3)

Hindlegs — pollen baskets and pollen press



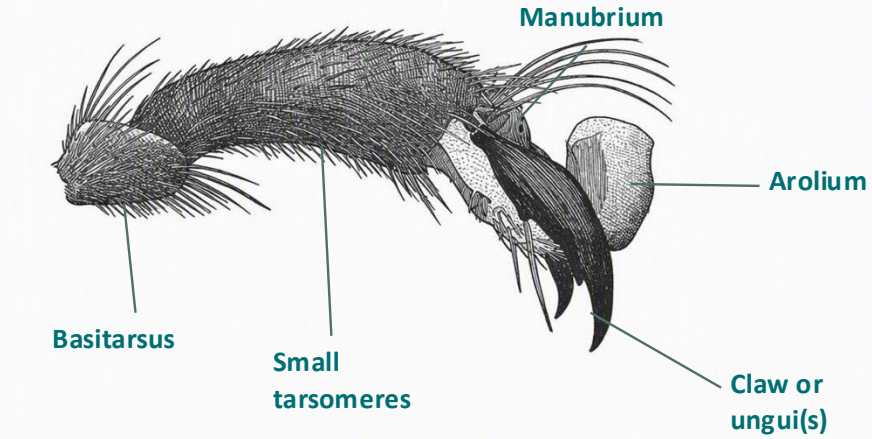


- **Corbicula (pollen basket):** the smooth, slightly concave outer face of the hind tibia, fringed by long curved hairs. Carries pollen or propolis — commonly 10–30 mg for the pair, against a body mass of c. 100 mg.
- **Pollen combs:** about nine to ten transverse rows of stiff bristles on the inner basitarsus gather pollen from the midlegs and abdomen.
- **Pollen press:** the rastellum (a comb of spines at the tip of the tibia) scrapes pollen from the opposite leg's combs onto the auricle; flexing the basitarsus then pushes it up into the basket.
- **Wax handling:** the hindlegs spear wax scales from the wax mirrors on sternites 4–7 and pass them forward to the mandibles.

THE PRETARSUS

How bees walk on almost anything

Two attachment systems on every foot



- **Dual grip:** Claws hook into rough petals, wax and bark while the arolium stays folded. On smooth surfaces, the soft pad unfolds between the claws.
- **Wet adhesion:** A thin fluid film beneath the arolium creates capillary and molecular forces that let a bee walk upside down on glass or a waxy leaf.
- **Automatic switching:** When the claws slip, the claw-flexor tendon unfolds the arolium automatically, without a conscious decision.
- **Load carrying:** The feet must hold on while nectar and pollen loads can reach a third or more of the bee's body mass.

Footprint pheromone. Glands in the tarsi leave an oily scent wherever bees walk — it helps guide bees to the hive entrance and marks flowers recently visited.

BEHAVIOUR

Grooming — more than keeping clean

Self-grooming sweeps from front to back



Dust, spores and mites are moved backwards to the hindlegs, then packed with pollen or dropped.

Varroa dislodged | **Spores removed** | **Allogrooming** | **Mite-biting lines**

Not the same as VSH. Varroa Sensitive Hygiene is about uncapping and removing mite-infested brood. Grooming of adult bees is a separate trait, selected in its own breeding lines.

- **Self-grooming:** leg brushes and combs work from head to abdomen, dislodging dust, fungal spores, mites and stray pollen.
- **Allogrooming:** nestmates groom one another, mainly with their mandibles, and can dislodge or bite Varroa on the body.
- **One-way bristles:** hairs angled backwards move debris towards the hindleg combs for packing or discarding.
- **Colony defence:** grooming is part of social immunity — behaviour that keeps parasite and pathogen loads down before individual immune defences are needed.

SUMMARY

At a glance — specialisation by pair

Feature	Foreleg (T1)	Midleg (T2)	Hindleg (T3)
Main role	Cleaning — sensory upkeep	Support and pollen transfer	Pollen and propolis transport; wax handling
Key structures	Strigilis: basitarsal notch + velum	Basitarsal pollen brush; tibial spur	Corbicula, rastellum, auricle, pollen combs
Pollen handling	Gathers from head and mouthparts	Brushes thorax; passes pollen back	Packs moist pellet into corbicula
Grooming	Antennae, eyes, head	Thorax and wings	Abdomen; removes wax scales
Size	Smallest	Intermediate	Largest, most muscular

Same six-segment ground plan; changes in shape, cuticle and bristles divide the labour — serial homology and functional specialisation.

Why six legs matter — form follows function

Same plan, different tools

Six segments repeated on every leg, each pair modified for its job.

A multi-tool

Walking, grooming, carrying and building — all done with the legs.

Pollination workhorse

The corbiculae bring home pollen and propolis — commonly 10–30 mg a trip.

A window on the colony

Pollen-load colours show what is flowering; grooming helps keep mites down.

Summary

- **Overview:** six legs share one ground plan, used for cleaning, carrying, gripping and building.
- **Ground plan:** six segments from coxa to pretarsus, hinge-like joints and an enlarged basitarsus.
- **Forelegs:** the strigilis cleans the antennae, which carry the smell and touch receptors.
- **Midlegs:** brace the bee on flowers, brush pollen back to the hindlegs and unload the baskets.
- **Hindlegs:** the corbicula carries 10–30 mg of pollen, packed by the combs and pollen press.
- **Feet:** claws grip rough surfaces, the arolium pad grips smooth ones, switching automatically.
- **Grooming:** self-grooming and allogrooming dislodge Varroa and spores; a separate trait from VSH.
- **Specialisation:** the same plan, modified pair by pair, divides the labour.
- **Why it matters:** legs drive pollination and show what is flowering and how the colony is doing.

Choose the best answer — answers in the speaker notes

Quick quiz — test your knowledge

01 **Where is the strigilis (antenna cleaner)?**

- **A** Hind tibia — smooth corbicula surface
- **B** Foreleg basitarsus notch + tibial spur (velum)
- **C** Midleg pretarsus, between claws and arolium
- **D** Hind basitarsus — the pollen combs

02 **What is the main function of the corbicula?**

- **A** Secreting wax scales
- **B** Carrying pollen or propolis on the outer hind tibia
- **C** Gripping rough surfaces
- **D** Cleaning the compound eyes

03 **Which structures form the pollen press?**

- **A** Coxa and trochanter muscles
- **B** Rastellum (tibial spines) + auricle (basitarsal flange)
- **C** Claws and arolium
- **D** Antenna notch and basitarsal brush

04 **What is the main function of the arolium?**

- **A** Digging into wax cappings
- **B** Producing footprint pheromone only
- **C** Gripping smooth surfaces with a soft pad and fluid film
- **D** Scraping pollen off the thorax

05 **How many segments in the basic insect leg?**

- **A** 4 — coxa, femur, tibia, tarsus
- **B** 5 — coxa, trochanter, femur, tibia, tarsus
- **C** 6 — coxa, trochanter, femur, tibia, tarsus, pretarsus
- **D** 8 — counting basitarsus and auricle separately

Practical follow-up

At the hive entrance, watch returning foragers: note pollen-load colours, and try to spot a bee packing pollen in flight or grooming her antennae on the landing board.

MODULE 5 · HONEY BEE BIOLOGY

The Mouthparts of the Worker Honey Bee

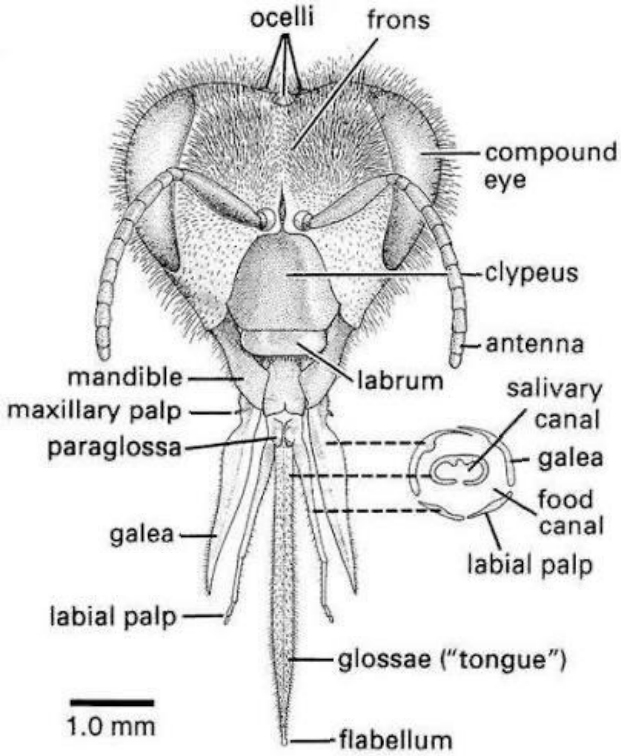


Chewing, lapping and sucking: how one set of tools feeds the colony and builds the comb

Alan Baxter, Education Officer, FDBKA

A chewing–lapping set of tools

Front view of the head, proboscis extended



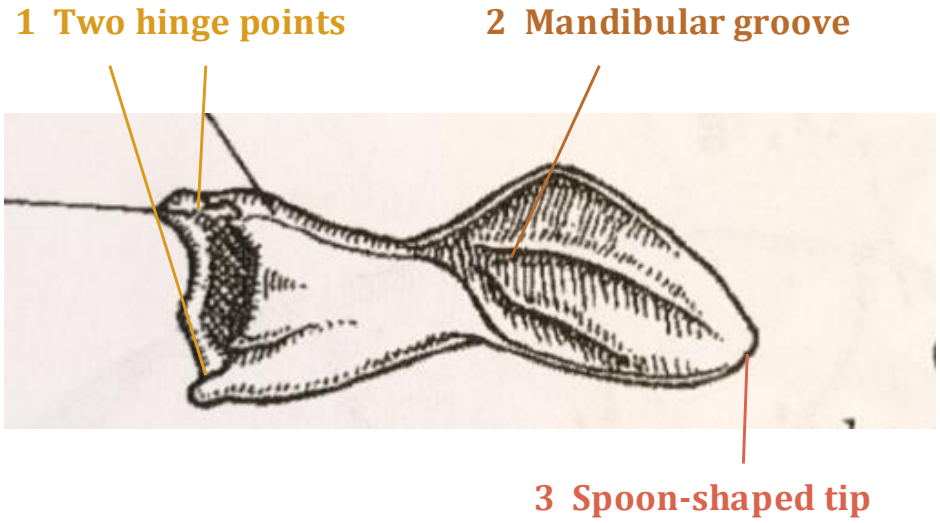
Flabellum

The small, spoon-shaped structure at the tip of the glossa, also called the labellum.

The labrum and the worker mandible

Inner face of the right worker mandible

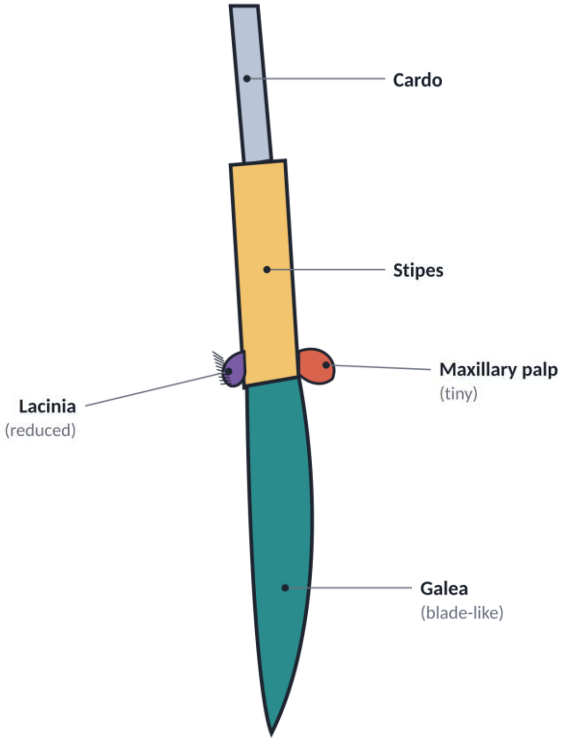
1. **Two hinge points**
   Each mandible swings sideways, powered by large adductor and smaller abductor muscles in the head.
2. **Mandibular groove**
   The groove carries mandibular gland secretion along the inner face to the cutting edge.
3. **Spoon-shaped tip**
   The broad tip has a smooth edge with no teeth.



Labrum (not shown): A movable flap below the clypeus. Its inner surface, the epipharynx, carries taste receptors.

The maxillae

One maxilla, seen from behind



Cardo
Short rod hinging the maxilla to the head; it swings the proboscis forward.

Stipes
The main plate, containing muscles that move the galea.

Galea
Long, blade-like lobe. The two galeae form the roof and sides of the food canal.

Lacinia and palp
Both much reduced: a small hairy lobe and a tiny maxillary palp.

The labium and the tongue

The labium spread out, seen from below

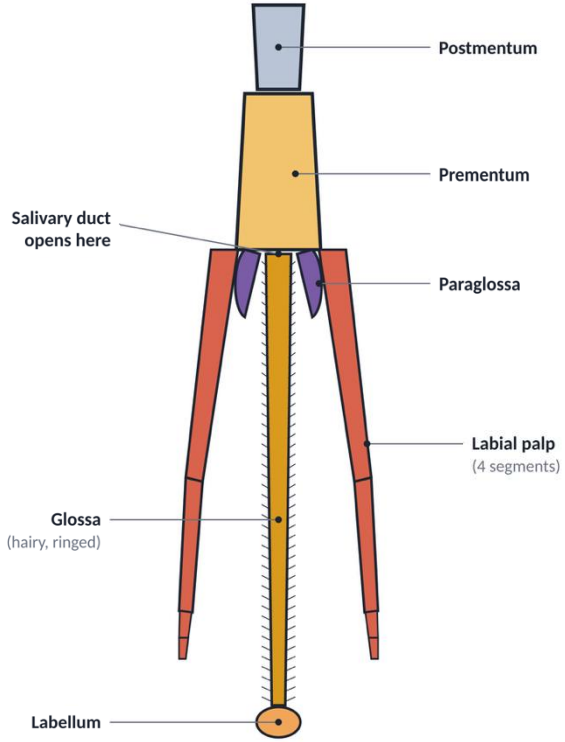
Prementum
Box-like base. The salivary duct opens on it, at the base of the glossa.

Glossa
The true tongue: long, hairy and ringed, with a channel underneath and a stiffening rod.

Labellum
Small spoon-shaped tip of the glossa.

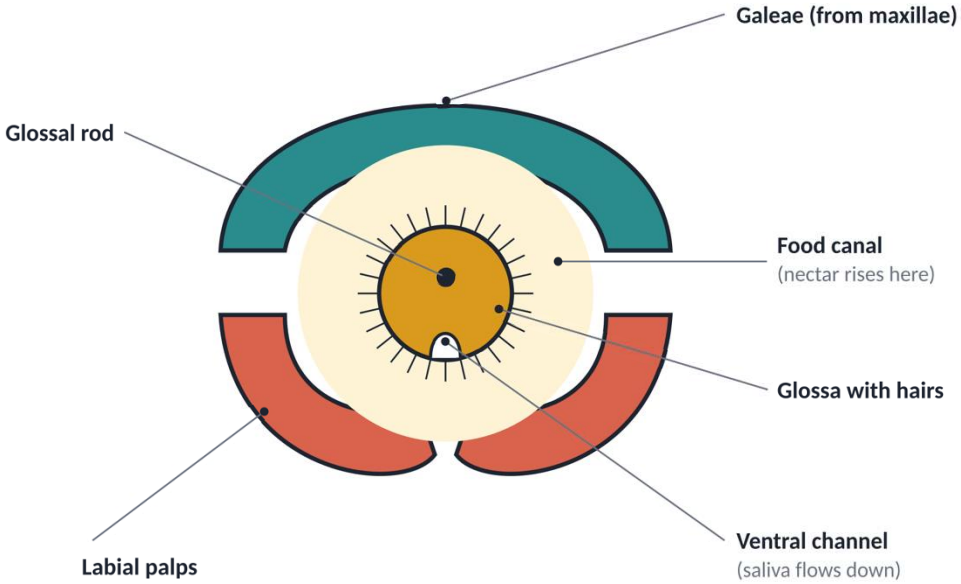
Paraglossae
Two lobes that wrap the base of the glossa and guide saliva on to it.

Labial palps
Four segments; the first two are long and flat and form the floor of the food canal.



Building the proboscis

Cross-section through the extended proboscis



6–7 mm

typical worker proboscis length; varies between subspecies

A tube within a tube

Galeae and labial palps fit together around the glossa.

The glossal rod supports and helps operate the hairy tongue. Nectar travels through the food canal alongside it.

Folded away at rest

The proboscis folds back into a groove under the head.

How a worker takes up liquid

A repeated cycle, several times a second

1

Extend

The proboscis unfolds and the glossa is pushed out; its hairs stand erect.

2

Load

Dipped into nectar, the hairy glossa holds liquid by capillary action.

3

Retract

The glossa is drawn back into the food canal, leaving the liquid behind.

4

Pump

The cibarial pump in the head sucks the liquid up into the pharynx.

Saliva: runs down the underside of the glossa to dilute thick syrup or dissolve crystallised sugar.

Many jobs, one set of mouthparts

What workers use their mouthparts for during their working life

Feeding

Nectar, honey, water and syrup taken up through the proboscis.

Sharing food

Food passed mouth to mouth between bees (trophallaxis).

Feeding brood

Nurses place gland secretions (brood food) in cells.

Building comb

Mandibles chew and mould wax scales into cells.

Cleaning

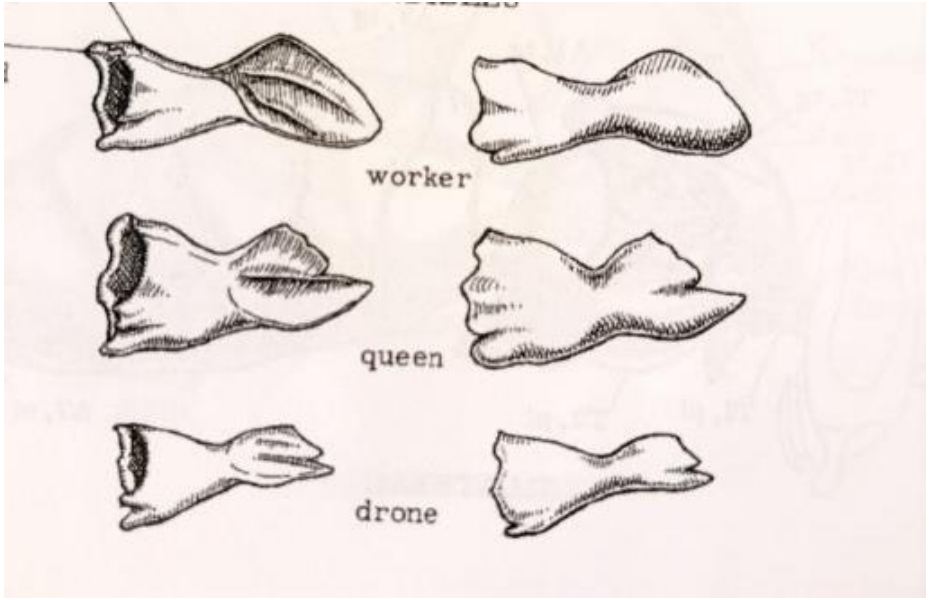
Uncapping, removing debris and dead brood, grooming.

Propolis and defence

Handling propolis, biting intruders and mites.

Mandibles of worker, queen and drone

Compare the shapes and edges in the paired drawings



Worker

Smooth, spoon-shaped tip with a groove. Large mandibular glands supply brood food and alarm signals. Used for wax work, cleaning and uncapping.

Queen

Large, pointed mandible with a deep notch near the tip. Very large mandibular glands produce queen pheromone. Used to cut out of the queen cell.

Drone

Small, pointed mandible with a small notch near the tip. Small mandibular glands. Little used, as workers feed drones.

The mandibular glands

Paired head glands with different roles in workers, queens and drones

Location and outlet

One gland lies on each side of the head. Its duct opens at the base of the mandible, releasing secretion onto the inner surface.

Workers

Brood food

Nurse workers supply fatty acids for brood food and royal jelly.

Their secretion combines with material from the hypopharyngeal glands.

Queen

Chemical signals

The glands produce queen mandibular pheromone (QMP).

The blend attracts attendants and helps suppress worker reproduction.

Drones

Reduced glands

The mandibular glands are small and poorly developed.

Their function is not clearly established.

Key points

1. Worker mouthparts are chewing–lapping: free mandibles plus a proboscis.
2. The proboscis is a tube of galeae and labial palps around the hairy glossa.
3. Liquid is lapped by the glossa and sucked up by the cibarial pump; saliva flows down.
4. The worker mandible is smooth and spoon-shaped, ideal for moulding wax.
5. Queen and drone mandibles are notched; the queen's are the largest.

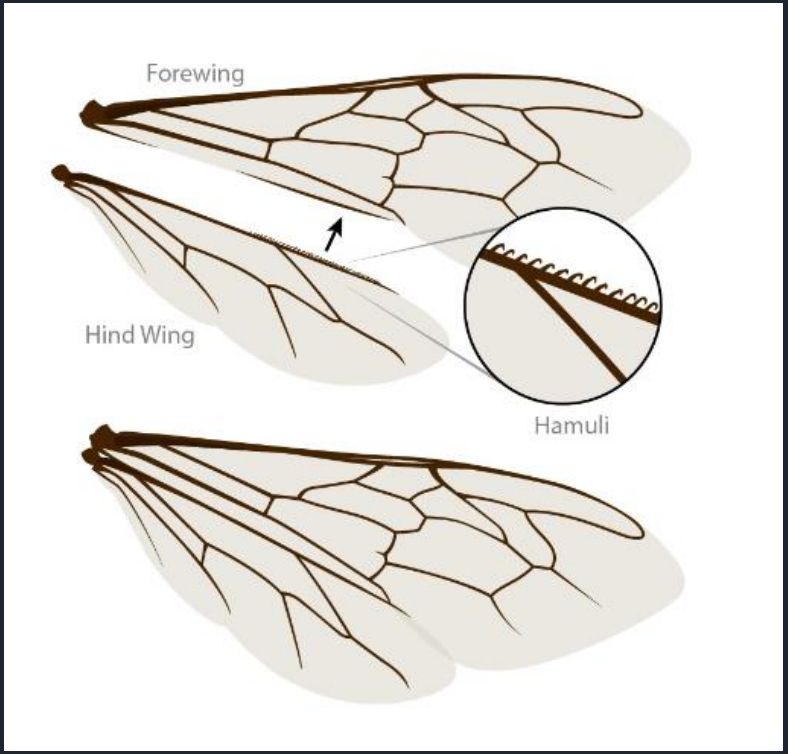
Main source: R. E. Snodgrass, Anatomy of the Honey Bee (Cornell University Press, 1956)

MODULE 5 · HONEY BEE BIOLOGY

Direct and Indirect Flight Muscles

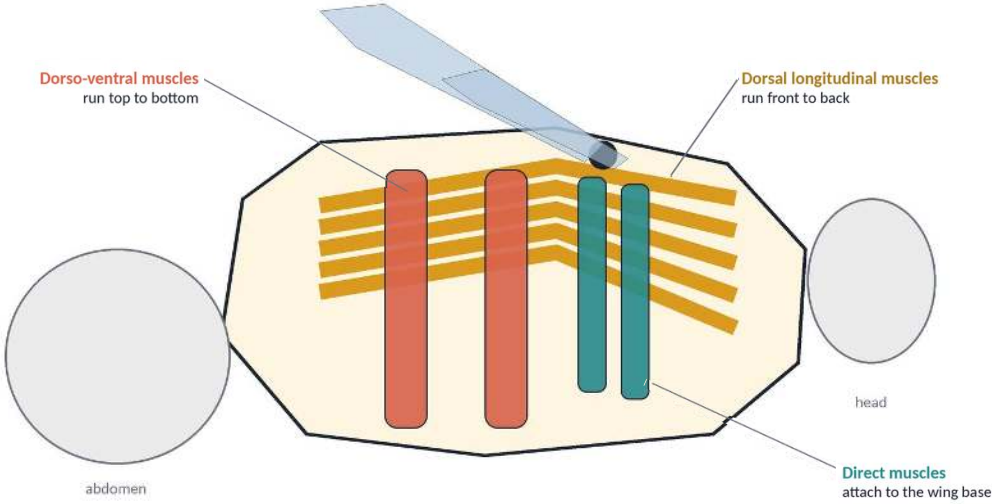
Their role in flight, and in the life of the colony

Alan Baxter, Education Officer, FDBKA



Two muscle systems, one thorax

Lateral view of the worker thorax (schematic)



Lateral view of the thorax (schematic): only the main bundles are shown

Indirect muscles

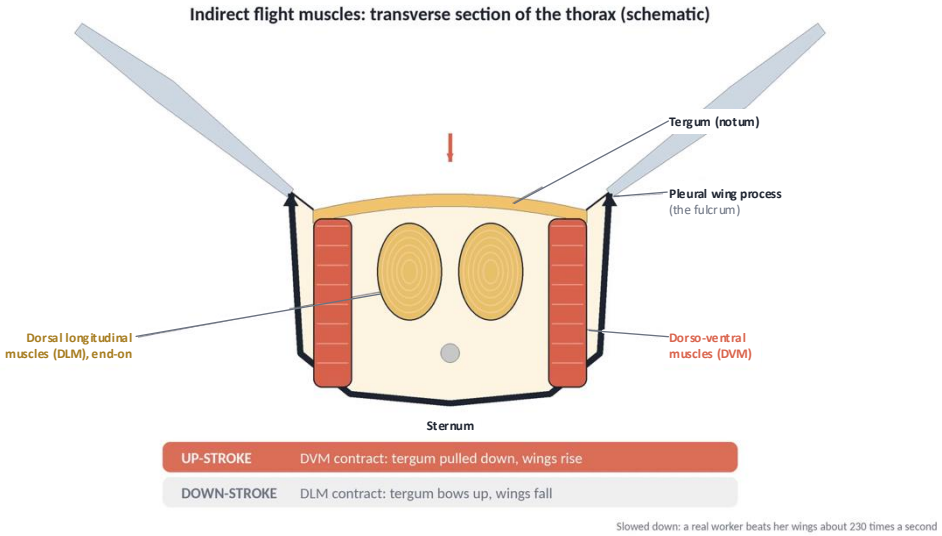
- Two huge sets: DLM and DVM
- Move the thorax wall, not the wings
- Provide the power

Direct muscles

- Small, attached to the wing base
- Twist, steer and fold the wings
- Provide the control

How the indirect muscles beat the wings

Animation: the thorax acts as a spring-loaded box





1 No direct pull

The wings move because the thorax changes shape.

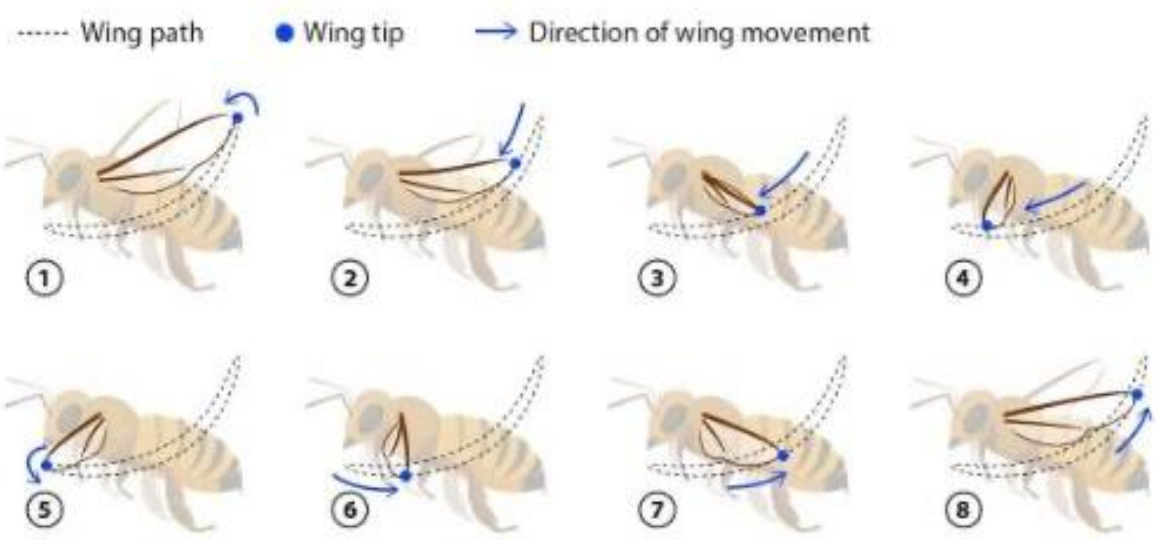
2 DVM contract

Tergum pulled down: wings levered up over the fulcrum.

3 DLM contract

Thorax shortens, tergum bows up: wings go down.

The wingbeat sequence



Asynchronous muscle: built for speed

Why a bee can beat her wings far faster than her nerves can fire

≈ 230
wingbeats per second in a worker

1 → many
one nerve impulse sets off several contractions

Stretch
each muscle is triggered by being stretched by the other

Fibrillar muscle. The indirect muscles are packed with mitochondria and fed by a dense supply of tracheae. Nerve impulses only keep them "switched on"; the beat itself comes from the resonant thorax and the alternating stretch of the two muscle sets.

Longitudinal and vertical flight muscles



Direct muscles steer, twist and fold

Small muscles inserted on the sclerites at the wing base

1. **Twist the wing**
   Change the angle of the wing on each stroke, so both up- and down-stroke produce lift.

2. **Steer**
   Adjust stroke amplitude and angle on each side to turn, hover and land.

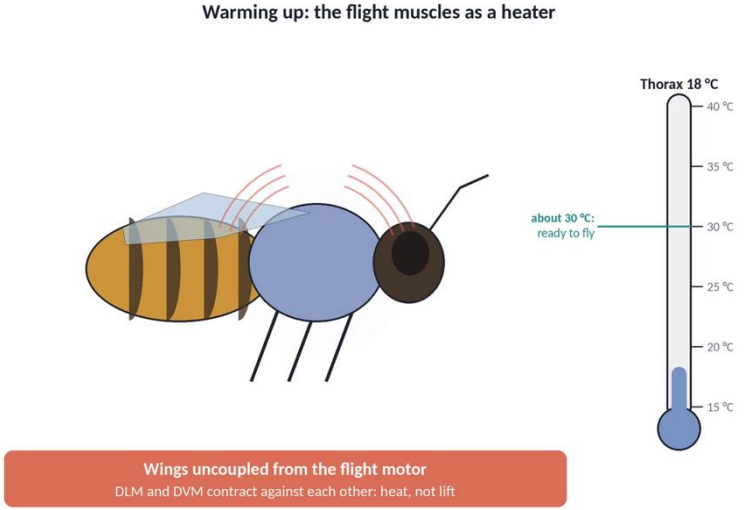
3. **Fold and unlock**
   Fold the wings over the abdomen at rest, and disengage them from the flight motor.

	Indirect	Direct
Attach to	Thorax wall	Wing base
Job	Power	Control
Nerve link	Asynchronous	Synchronous
Size	Very large	Small

ca

Warming up before take-off

Animation: the flight motor as a heater



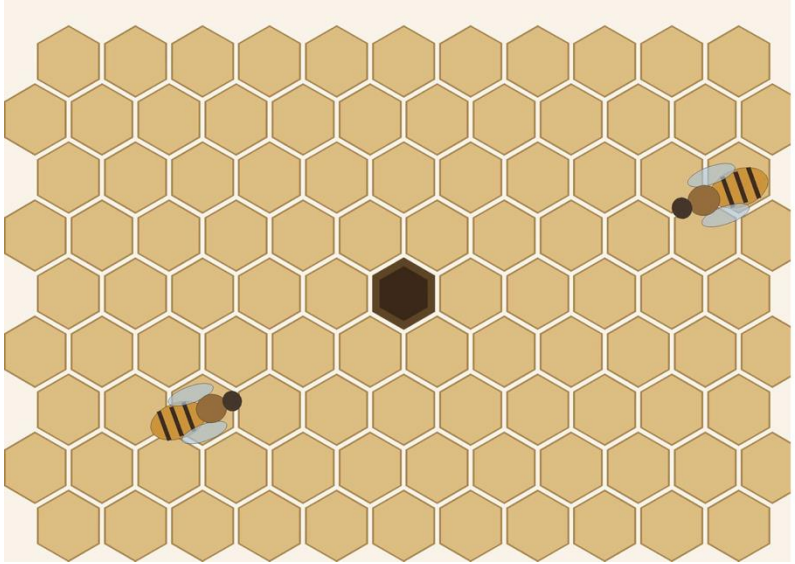


1 **Wings disengaged**
The direct muscles unlock the wings from the motor.

2 **Shivering**
DLM and DVM contract together: heat, not movement.

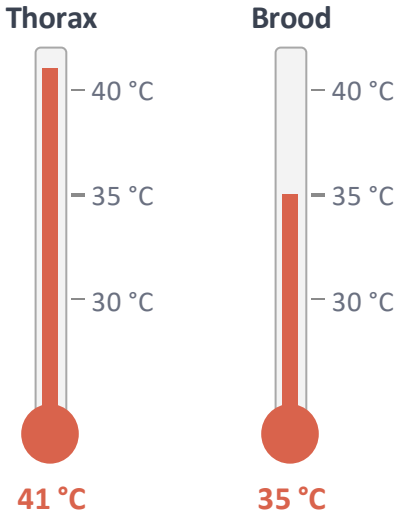
3 **About 30 °C**
Only a warm thorax can drive the wings fast enough to fly.

In the colony: heating the brood



In an empty cell
warms up to six pupae

Pressed on a cap
warms the pupa below



1 **Brood near 35 °C**
Pupae develop properly only in a narrow band of temperature.

2 **Heater bees**
Shiver in empty cells or on caps; thorax up to about 41 °C.

3 **Winter cluster**
The same shivering keeps the cluster core warm.

In the colony: moving air and making sound

The flight motor at work with the bee standing still

Fanning

Rows of bees at the entrance drive air through the hive to remove heat, CO_2 and moisture.

Drying nectar

Fanning carries away water evaporating from unripe honey.

Nasonov scenting

Fanning spreads orientation pheromone to guide bees home.

Sound signals

Dancers vibrate their wings; queens pipe with wings folded, at 200–550 Hz.

Key points

1. Indirect muscles (DLM, DVM) power flight by deforming the thorax.[1]
2. These muscles are asynchronous: about 230 beats a second from far fewer nerve impulses.[2]
3. Direct muscles at the wing base twist, steer and fold the wings.[1]
4. With the wings disengaged, the flight motor becomes a heater, warming the thorax to the 30 °C it needs for flight.
5. The same muscles heat brood and the winter cluster, and drive fanning and signals.[3,4]

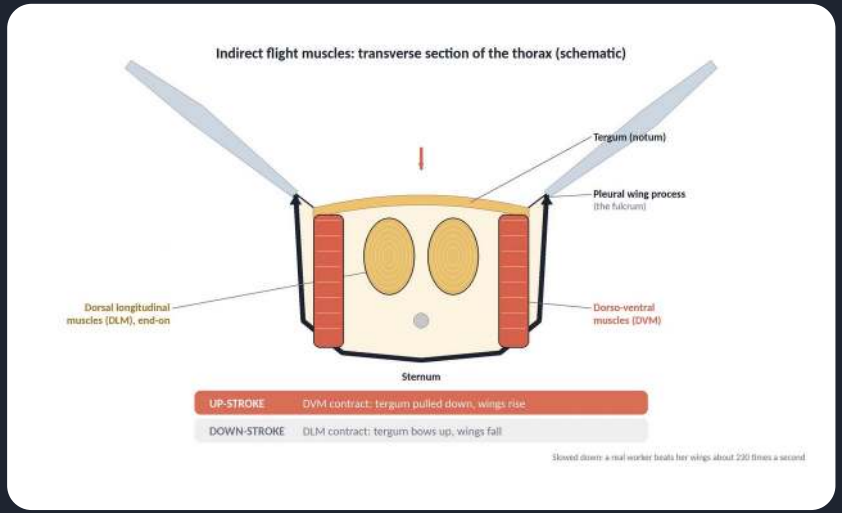
Sources: [1] Snodgrass (1956) Anatomy of the Honey Bee; [2] Altshuler et al. (2005) PNAS 102: 18213; [3] Kleinhenz et al. (2003) J Exp Biol 206: 4217; [4] Bujok et al. (2002) Naturwissenschaften 89: 299.



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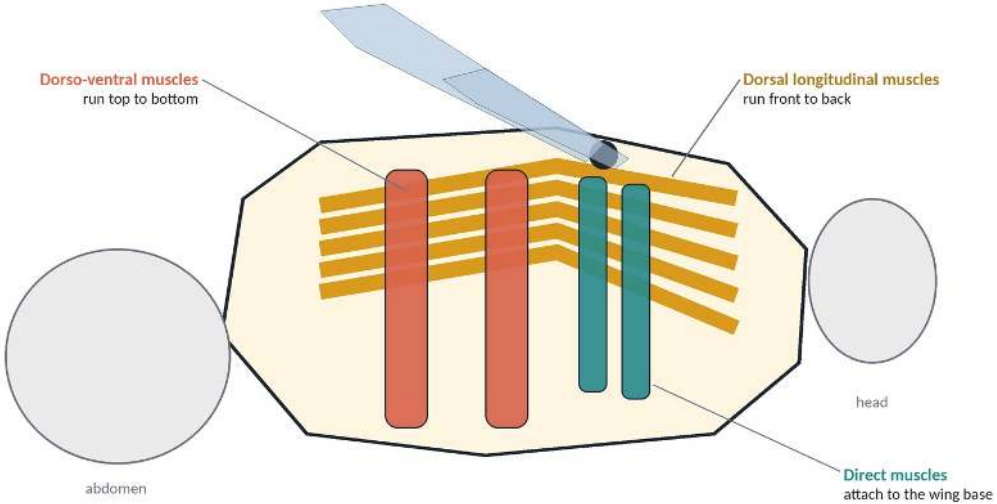
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Indirect muscles

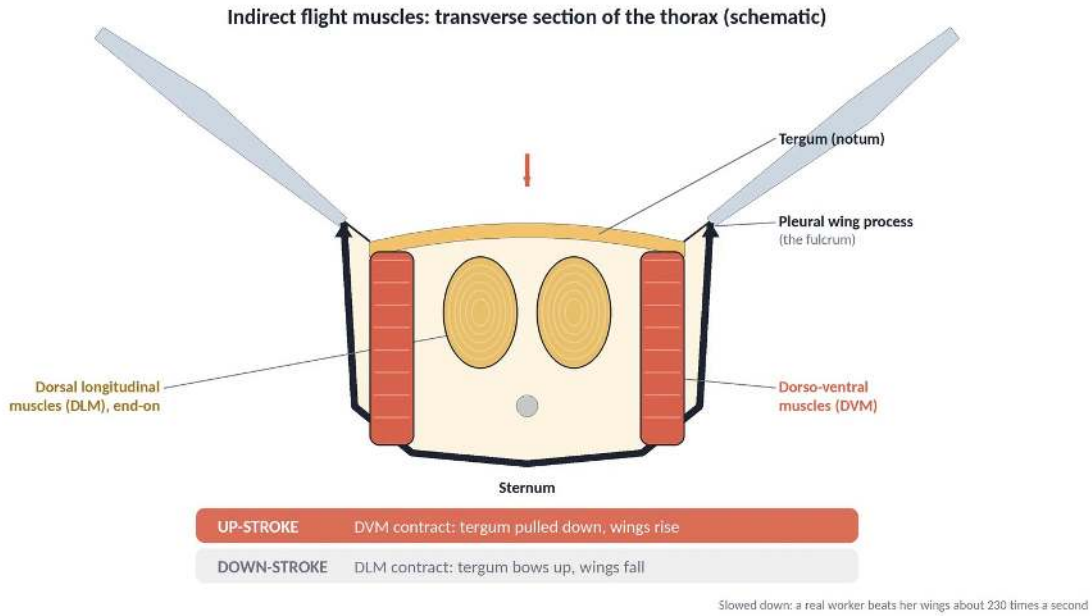
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Direct muscles

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How the indirect muscles beat the wings

Animation: the thorax acts as a spring-loaded box



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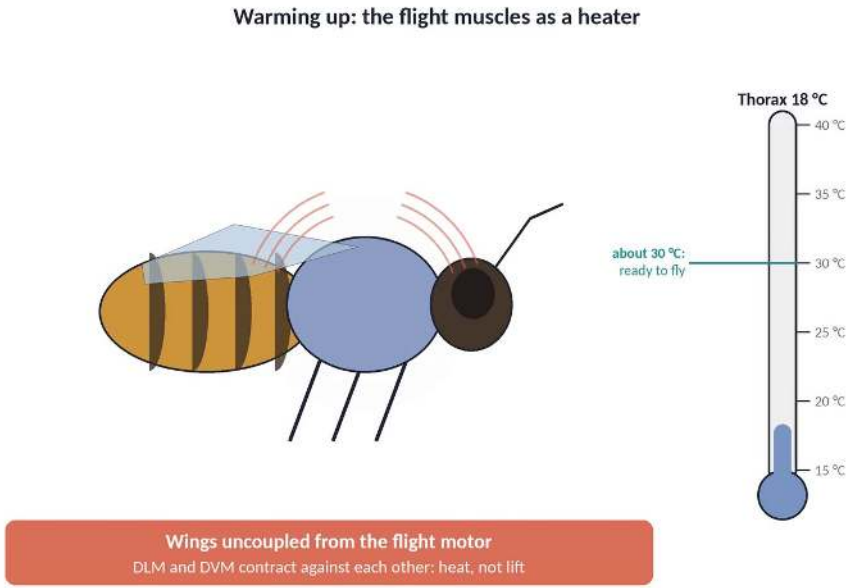
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	Indirect	Direct
Attach to	Thorax wall	Wing base
Job	Power	Control
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Warming up before take-off

Animation: the flight motor as a heater



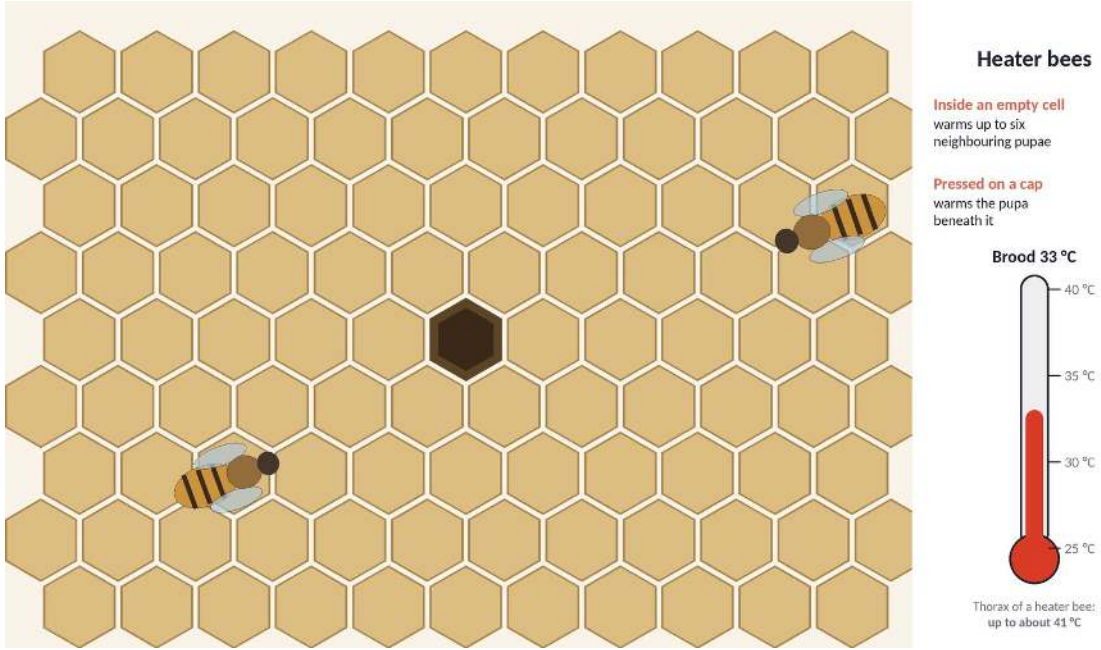
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In the colony: heating the brood

Animation: heater bees on sealed brood



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