Università degli Studi di Bari Aldo Moro
DiSSPA Sec. Entomologia e Zoologia

Module: **Applied Entomology (6 ECTS),**

(6 TU: 4 TU Frontal + 2 TU Labs)

Part of **"I.C. Applied entomology and Agricultural zoology"**

Scienze e Tecnologie Agrarie (D.M.270/04)

Course given by
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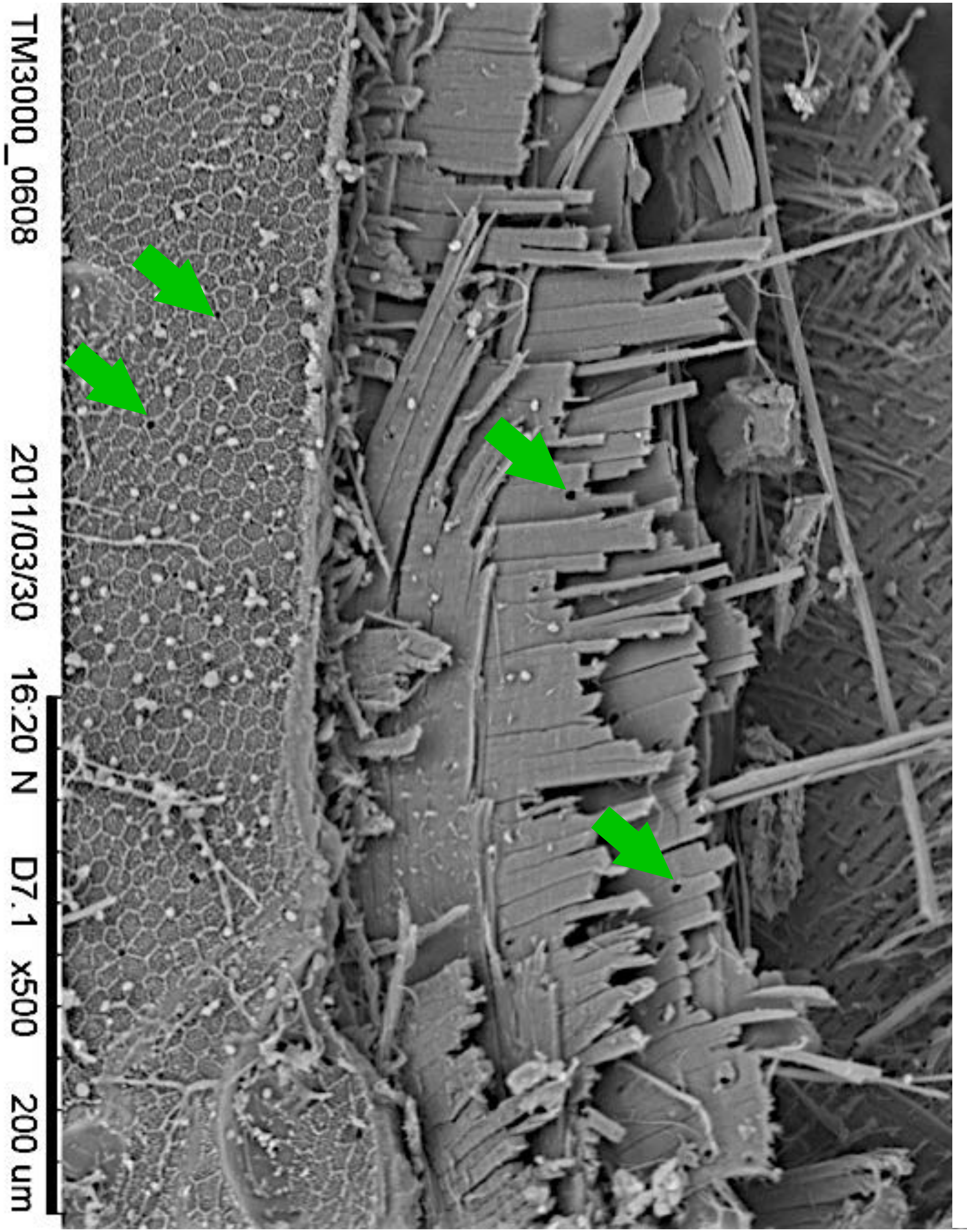
Tel. 0039 080 544 2880 Mobile 0039 329 8112593

01 Gross Morphology, Cuticle and its specialization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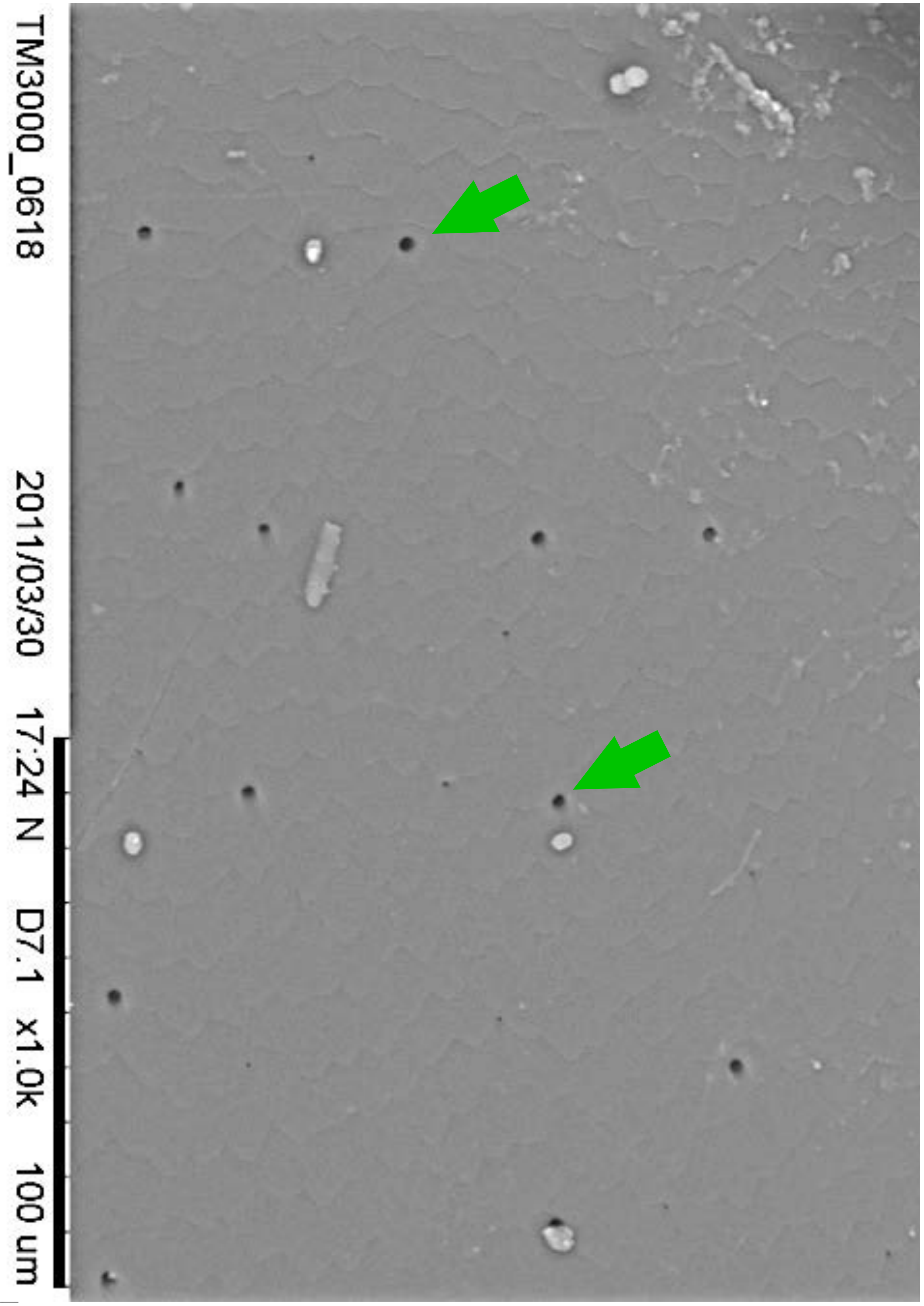
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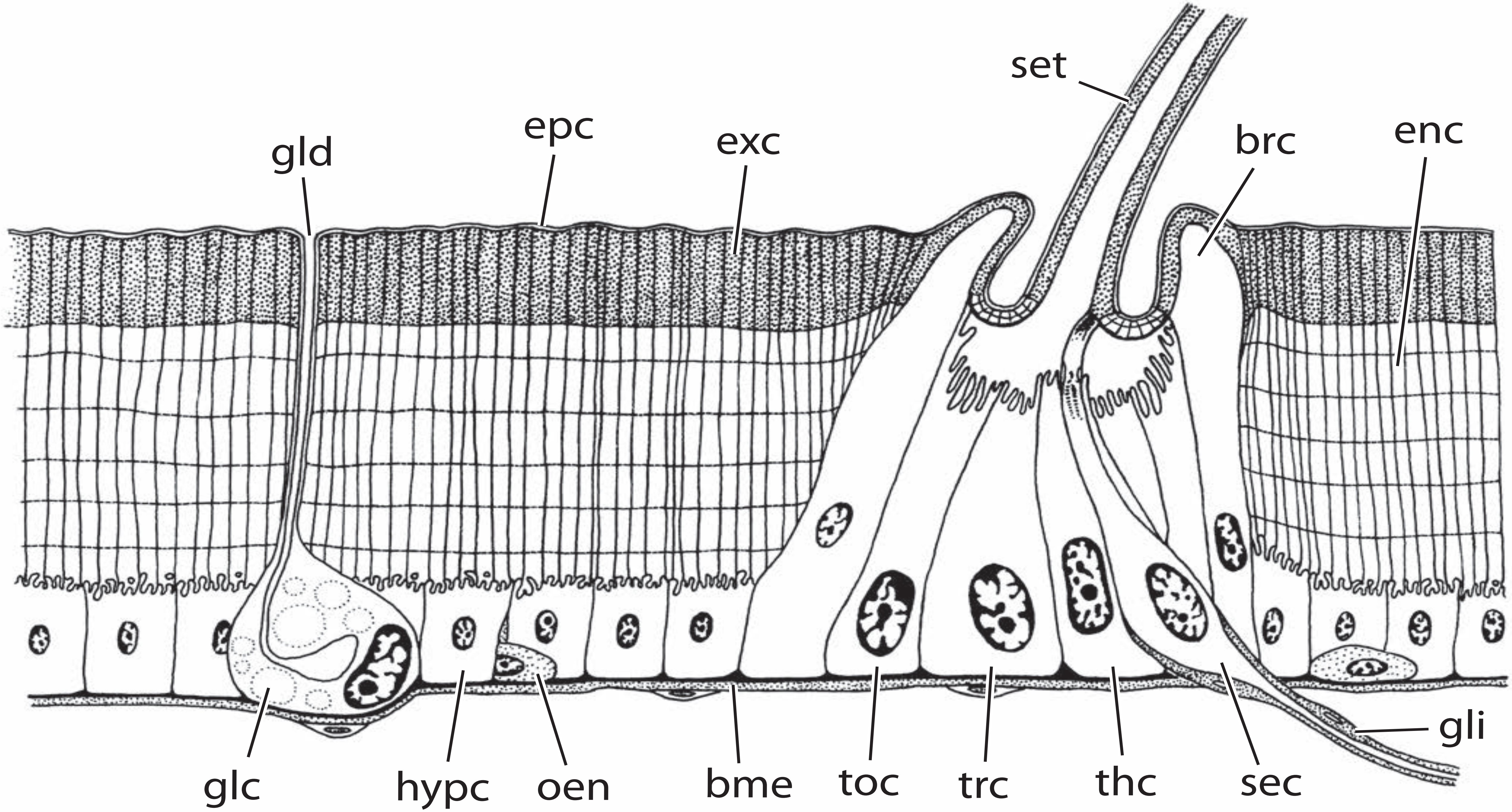
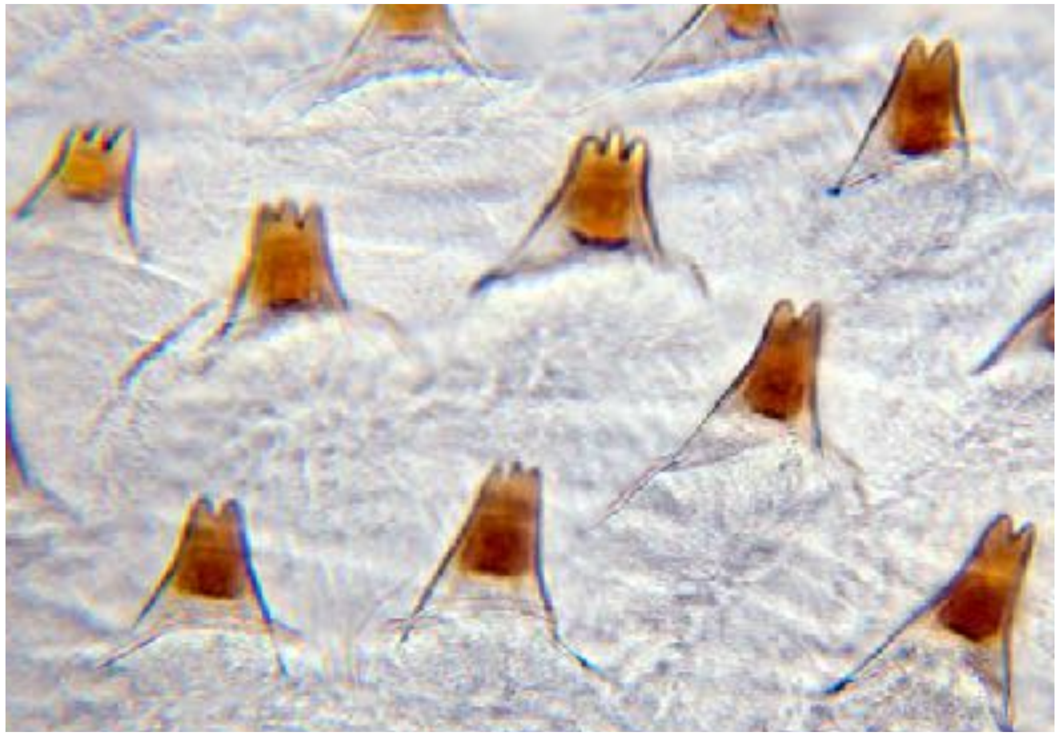
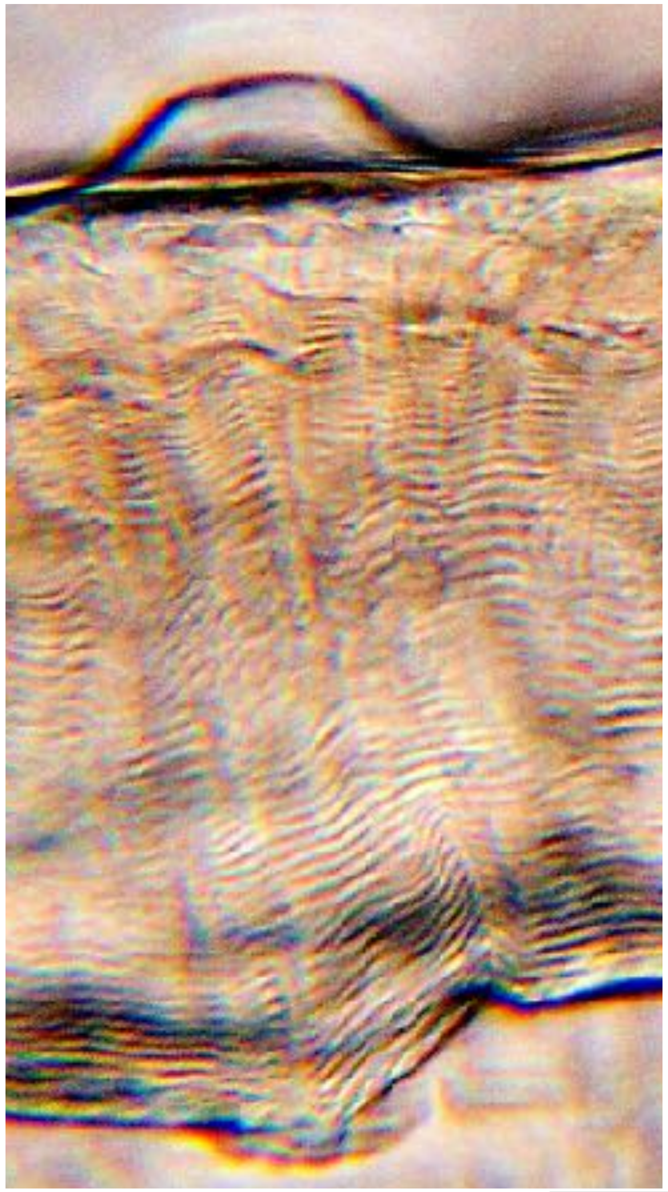


Integument. **bme:** basement membrane, **brc:** basal ring cell, **enc:** endocuticle, **epc:** epicuticle, **exc:** exocuticle, **glc:** gland cell, **gli:** glia cell, **hypc:** hypodermal cell, **oen:** oenocyte, **set:** seta, **sec:** sensory cell, **thc:** thecogen cell, **toc:** tormogen cell, **trc:** trichogen cell.

The cuticle is a secretion of the epidermis and covers the whole of the outside of the body as well as lining ectodermal invaginations such as the stomodeum and proctodeum and the tracheae. It is differentiated into two major regions: an inner region, up to 200 µm thick, characterized by the presence of chitin and forming the bulk of the cuticle, and the thin outer epicuticle, 1–4 µm thick, which contains no chitin. The cuticle varies in nature in different parts of the body and between insects with different life forms. The most obvious difference is between the rigid cuticle of the sclerites and the flexible cuticle of the membranes between them.





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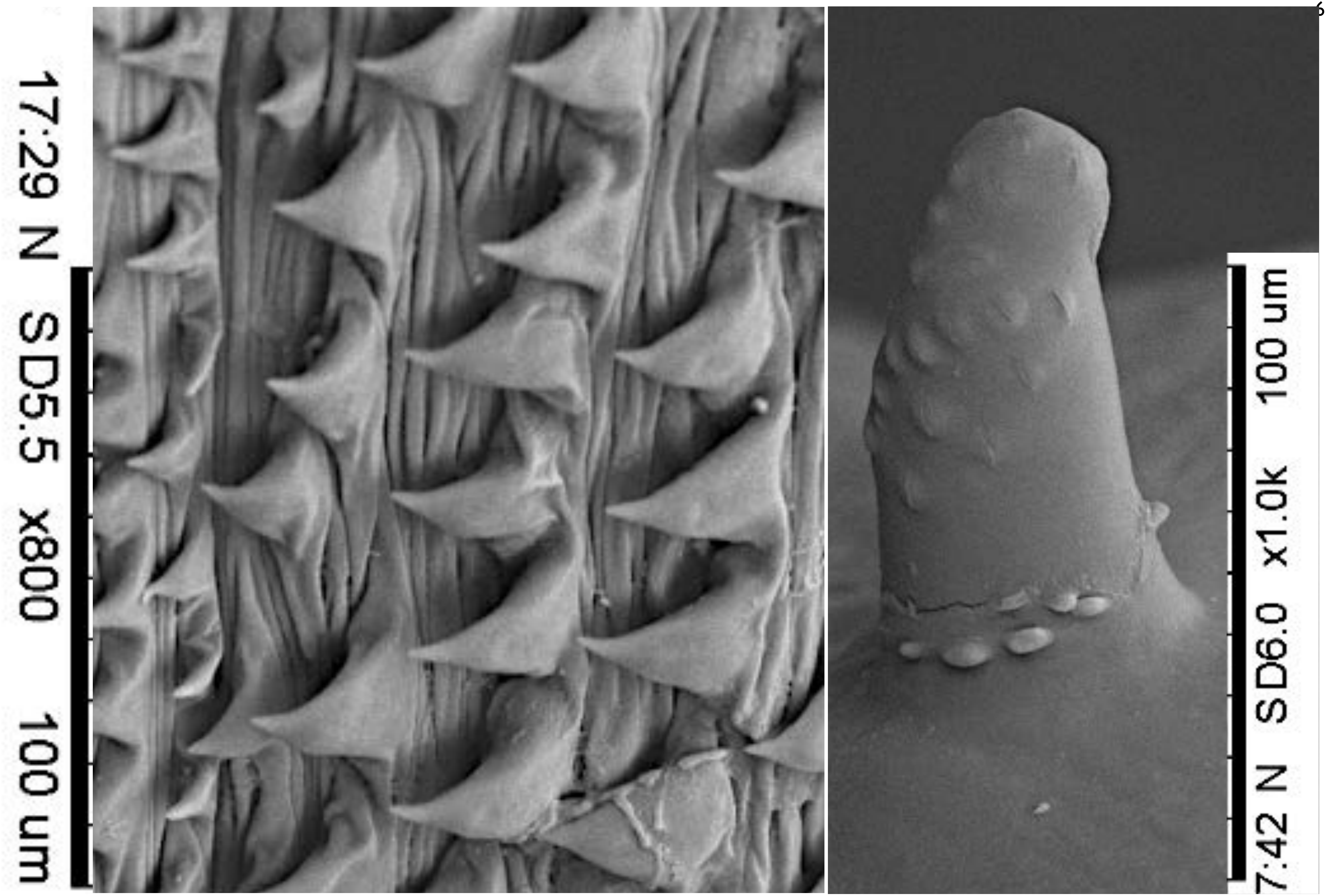
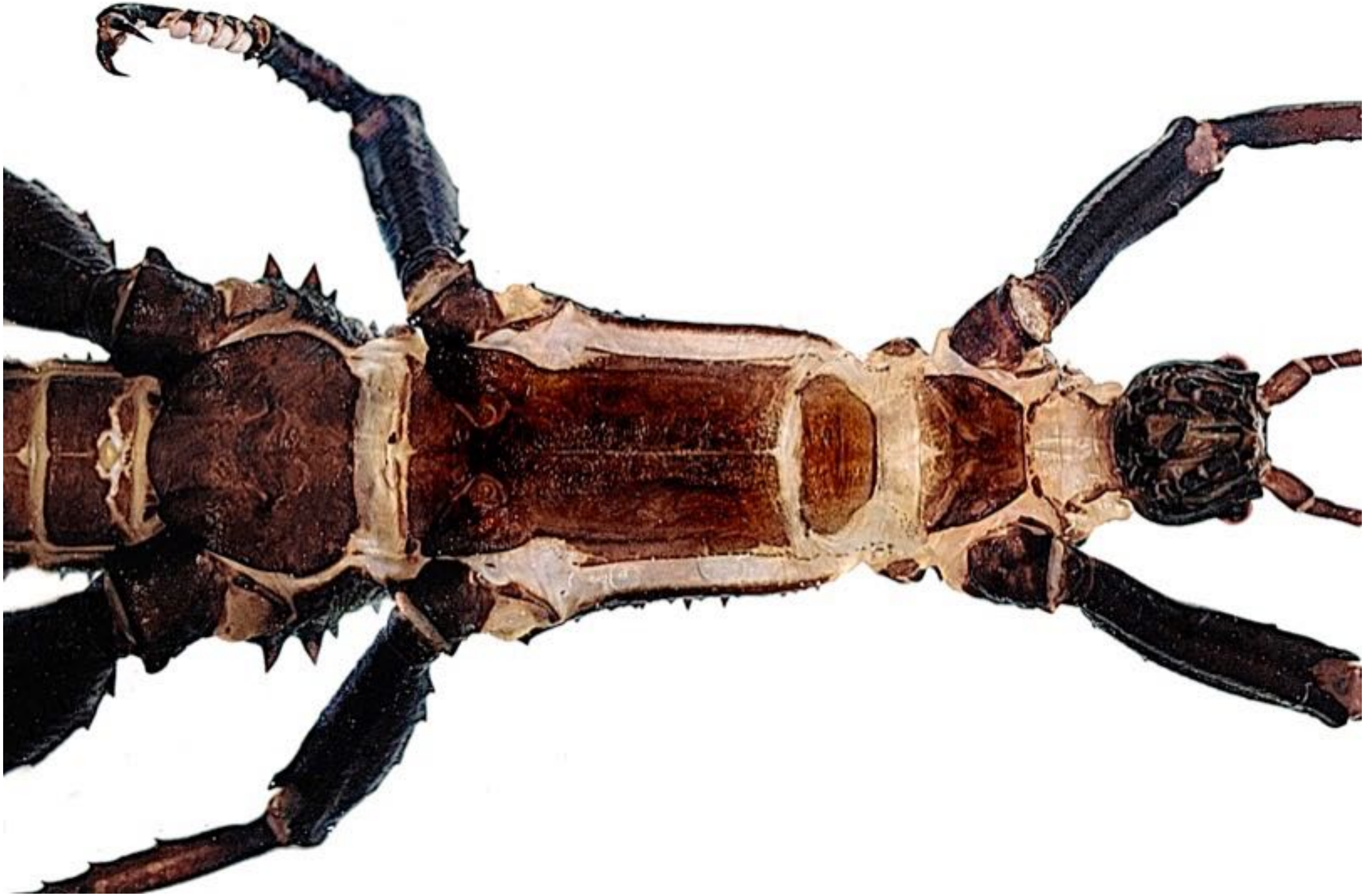


Spines (left) or processes (right) look like outgrowths that are integral parts of the substance of the Cuticle. They are rigidly connected with the Cuticle and lack a membranous articulation. Because of this they are distinct from cuticular appendages.



A Sclerite is any hard portion of the insect Integument separated from similar areas by membrane, apodeme, suture or sulcus. It is described also as an hardened areas of an insect's body wall that are consequences of the process of sclerotization. Sclerites (also called 'plates') are variable in size and shape. Sclerites do not define anatomical areas and do not reflect a common plan of segmentation. Sclerites develop in several ways. including as de novo hardening of membranous areas of the body wall and as de novo separations from larger sclerotized areas of the body. Sclerites receive different names. depending upon the region of the body in which they are located. Tergites are sclerites that form a subdivision of the dorsal part of the body wall (Tergum). Laerotergites are sclerites that form as a subdivision of the lateral portion of the Tergum. Sternites are sclerites that form as a subdivision of the ventral part of the body wall (Sternum). or any of the sclerotic components of the definitive Sternum. Pleurites are sclerites in the pleural region of the body wall that are derived from limb bases.

Exuviae is a plural noun describing in general the portion of the Integument of a larva, nymph or naiad that is shed from the body during the process of moulting. Errouneusly in Diaspididae the term refers to a nymphal integument that is shed from the body and incorporated into the scale cover.

Ecdysis

The ecdysis, i.e. the molting, shedding and replacement of the cuticle, was traditionally considered as an autapomorphy of Arthropoda in the widest sense, i.e. also including Onychophora and Tardigrada (“Panarthropoda”). This interpretation was based on the Articulata-concept, with Annelida (“ringed worms”) and arthropods as sistergroups. It is assumed today that it evolved earlier, as a derived groundplan feature of a clade Ecdysozoa, which includes Arthropoda and the Cycloneuralia (Nematoda, Nematomorpha, Priapulida, Kinorhyncha, Loricifera).

Due to mechanical properties of the cuticle the extensibility of the integument is very limited. Therefore, before reaching their maximum size and maturity, hexapods and other arthropods molt several times. During these intervals the integument, i.e. the hypodermis (=epidermis) + cuticle, undergoes a period of expansion, and this allows an increase in size of the body. However, ecdysis affects not only the body surface, but also endoskeletal elements (tentorium, furcae, pleural ridges etc.) and other chitinized internal invaginations such as the tracheae and also the ectodermal fore-and hindgut. The cuticle of these structures is also replaced during molts.

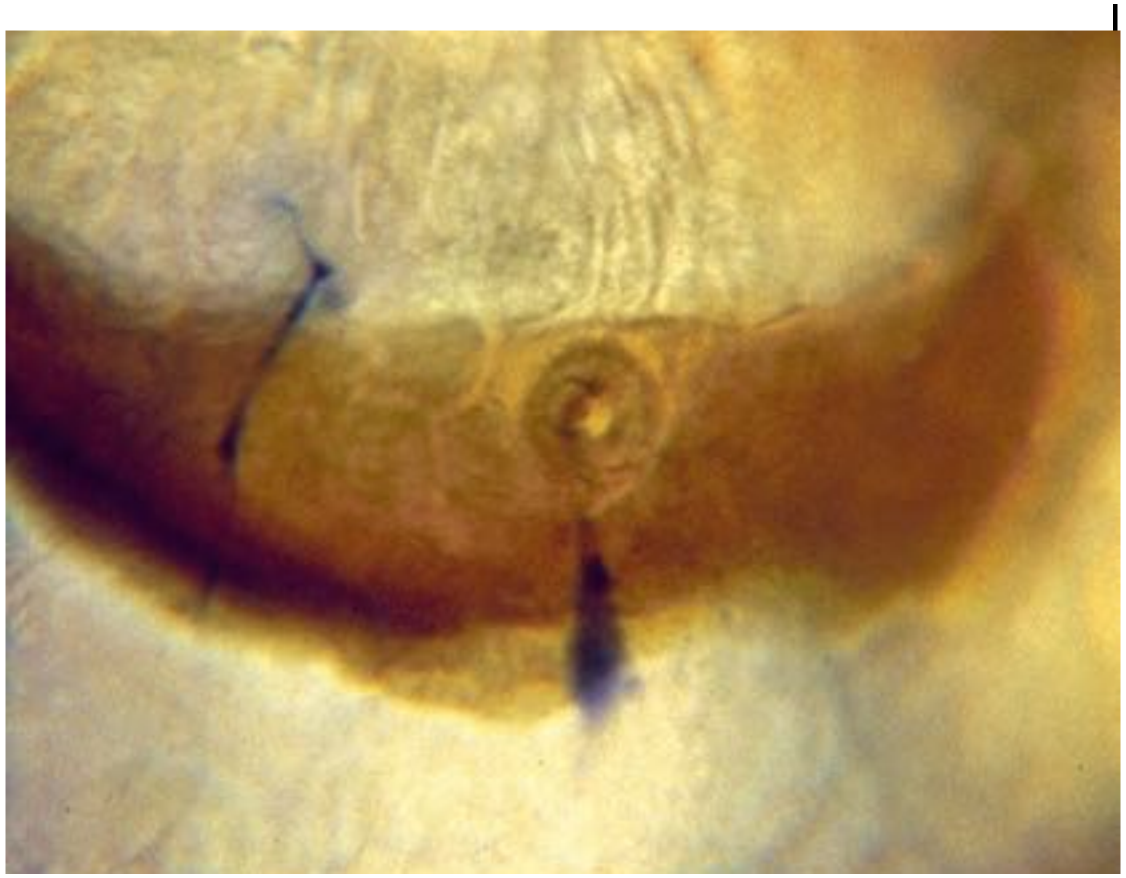
The succession of ecdyses divides the life cycle of hexapods and other arthropods into a series of stages or instars. The number of stages in the postembryonic development differs strongly between groups and depends on different factors, such as for instance, availability of food, temperature, or humidity. It is mainly taxon-specific and usually relatively constant but may even vary between individuals of the same species in some groups. Molting stops after maturity is reached in most groups of hexapods. However, this is not the case in the basal apterygote lineages, which are characterized by a large number of molts (e.g., up to 50 in Collembola). The number of ecdyses is still relatively high in basal pterygote orders (e.g., Ephemeroptera, Odonata, Plecoptera) but most insects molt only 4–6 times before reaching the adult stage. Ephemeroptera are the only insects molting as an immature winged instar, the subimago.

Molting comes at an evolutionary cost corresponding to the various benefits of a solid integument. Ecdyses are always critical intervals in the life cycle: hexapods and other arthropods lack their mechanical protection during this process and their mobility is strongly restricted. The condition of hexapods just after ecdysis is called teneral.

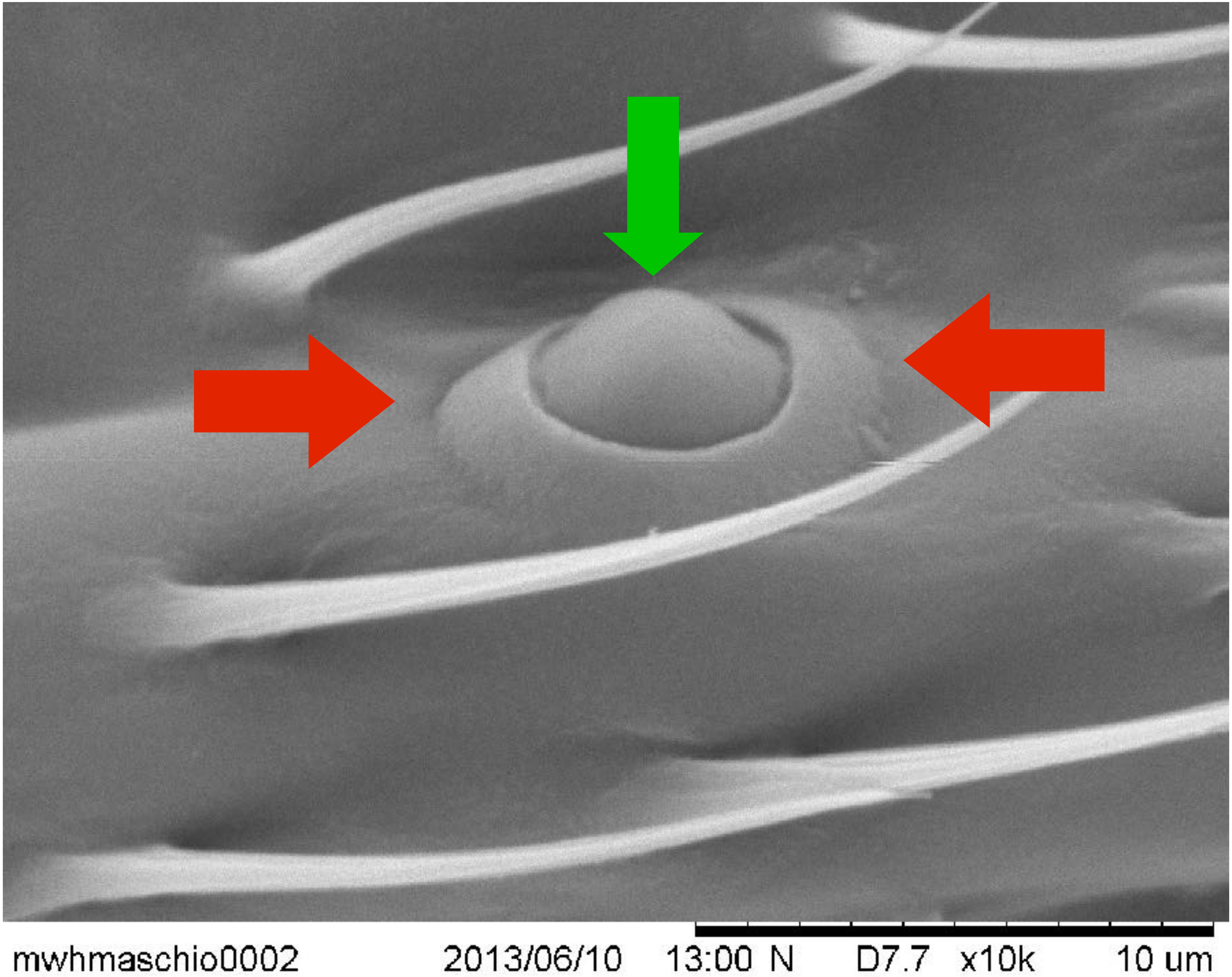
Molting starts with the apolysis, the separation of the old cuticle from the epidermis. This is induced by an increased level of ecdysteroids functioning as molting hormones. The size of the epidermal cells increases and a series of mitoses take place subsequently. Shortly before and immediately after apolysis vesicles within each epidermal cell release their electron-dense contents at the cell apex. These are principally enzymes involved in the degradation of the old cuticle or material for building the new one. The vesicles are still recognizable below the old endocuticle before they release their contents. A thin hyaline and homogenous lamina formed from the inner layers of the endocuticle is called ecdysial membrane. Due to a specific sclerotization process it is not affected by enzymes in the following stages of ecdysis. That part of the cuticle separating from the epidermis and the ecdysial membrane is referred to as the exuvia and the gradually expanding space below it as ecdysial space. The latter is filled with exuvial fluid secreted by the epidermal cells. The enzymes begin with the degradation of the old endocuticle after a short period of inactivity. The formation of the new cuticle is not affected due to the barrier provided by the ecdysial membrane. The degradation products of the old cuticle are absorbed by the epidermis and used to build the new exoskeleton in the following process.

The secretion of new cuticle starts during the degradation of the old one. This process is initiated by the formation of the epicuticular cuticulin layer on top of the projections or ridges of the apical membrane of the epidermal cells. After consolidation and hardening of this lamina the secretion of the new inner layers of the epicuticle and of the procuticle starts. The precise modalities of the hardening of the external procuticle, i.e. the formation of the exocuticle, are still disputed. Phenoloxidases (tyrosinases, laccases) apparently play a role in this process, but also in other functional contexts such as the repair of damaged cuticle or melanization. Movements of epidermal microvilli and plaques at the apices of these minute structures are probably responsible for the regular arrangement of chitin filaments.

The final stage of molting is the ecdysis in the narrow sense, the shedding of the old epi- and exocuticle. In most groups it splits open at the epicranial sutures (frontal- and coronal sutures) and the dorsomedian ecdysial line of the postcephalic tergites. Muscle contractions usually increase the haemolymph pressure in the anterior body, which results in the rupture of the old exoskeleton at the dorsal preformed zones of weakness. The teneral exoskeleton is soft, unpigmented and wrinkled. During this stage, the expansion of the body takes place involving locally increased haemolymph pressure (e.g., in the limbs) and often also air uptake, especially in larger hexapods. In the typical case the tanning process in the exocuticle results in the re-formation of a hardened and pigmented exoskeleton within a few hours after eclosion, but this process can also take days or even weeks in the members of some groups. After the normal mechanical properties of the cuticle are restored, the animal has regained its full mobility and mechanical protection.



The sensillum (pl. sensilla) is the basic unit of sensory ability in insect. It appears as a simple sense organ or sensory receptor that occurs on various appendages and sclerite of the insect body. Traditional classification of Sensilla was based on the anatomy that was studied imperfectly with light microscopy. Consequently, many names were provided for Sensilla that were unnecessary. Presently, entomologists are confronted with many different and complex names applied to Sensilla. A perfected anatomical classification of Sensilla requires time and careful systematic study with SEM and TEM. A functional classification of Sensilla is not coincident with an anatomical classification of the receptors. Functionally, Sensilla of various anatomical types respond to different categories of stimuli and have been broadly classed as mechanoreceptors and chemoreceptors. Additional categories that have been recognized more recently include thermoreceptors and adhesive structures.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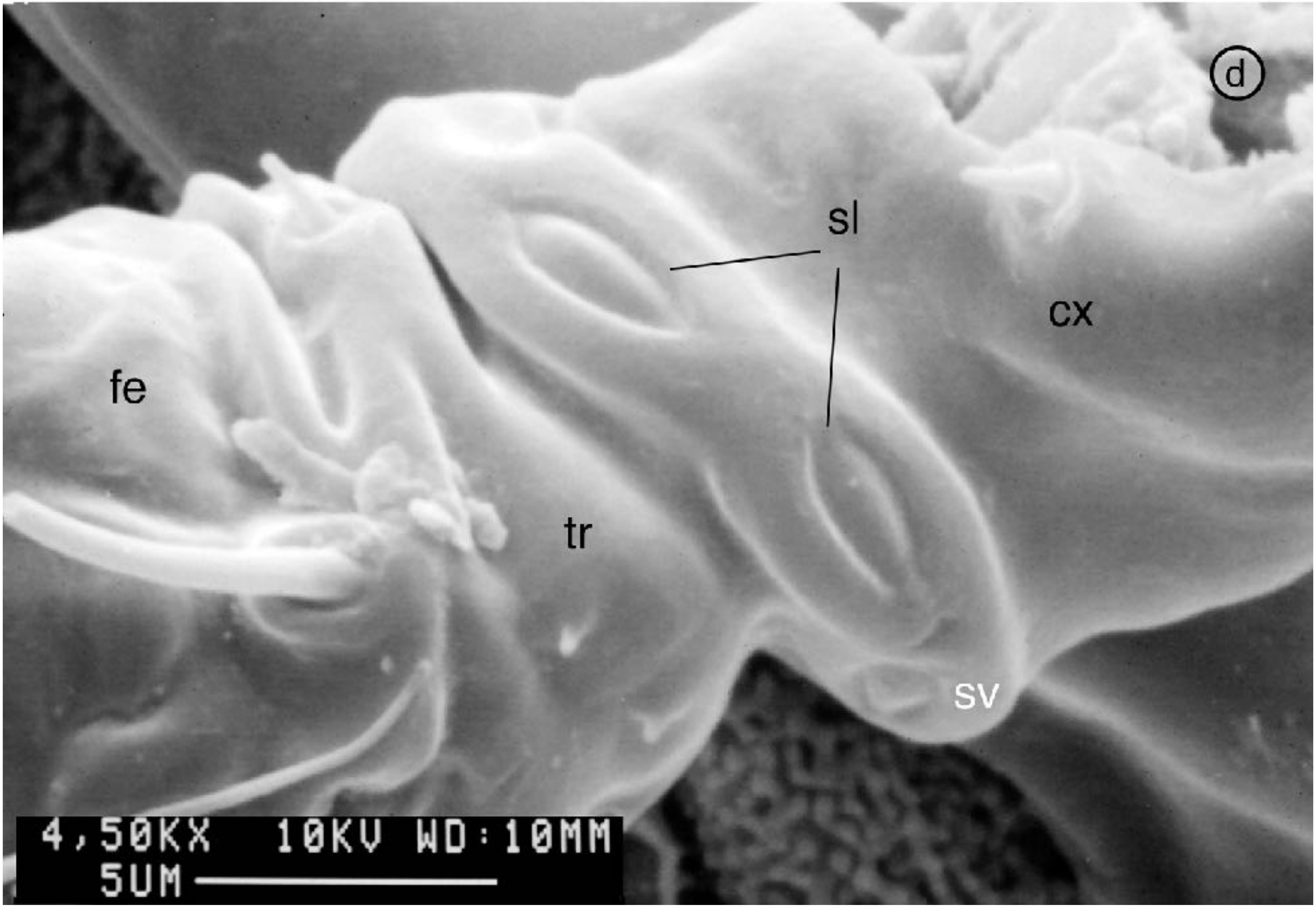
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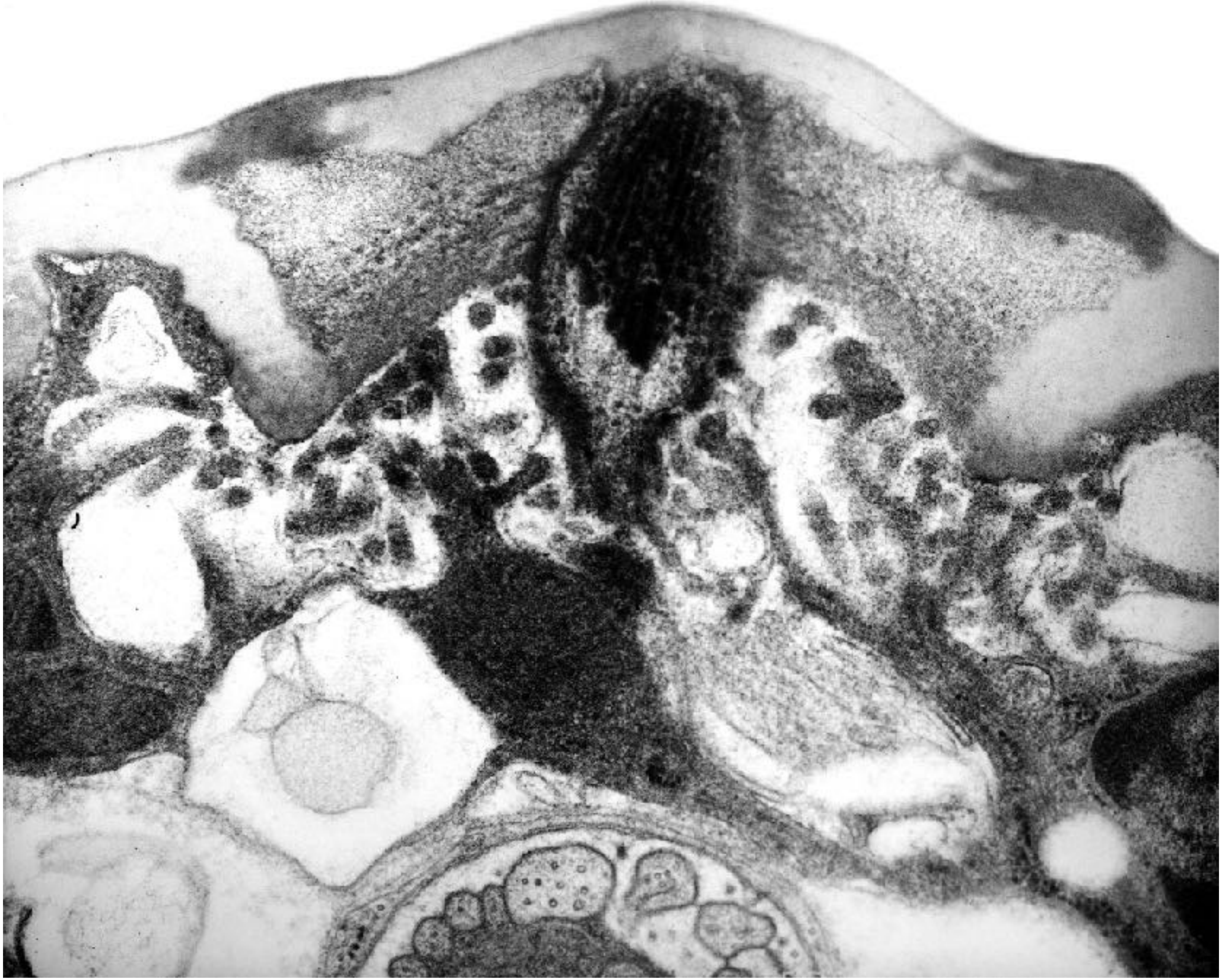

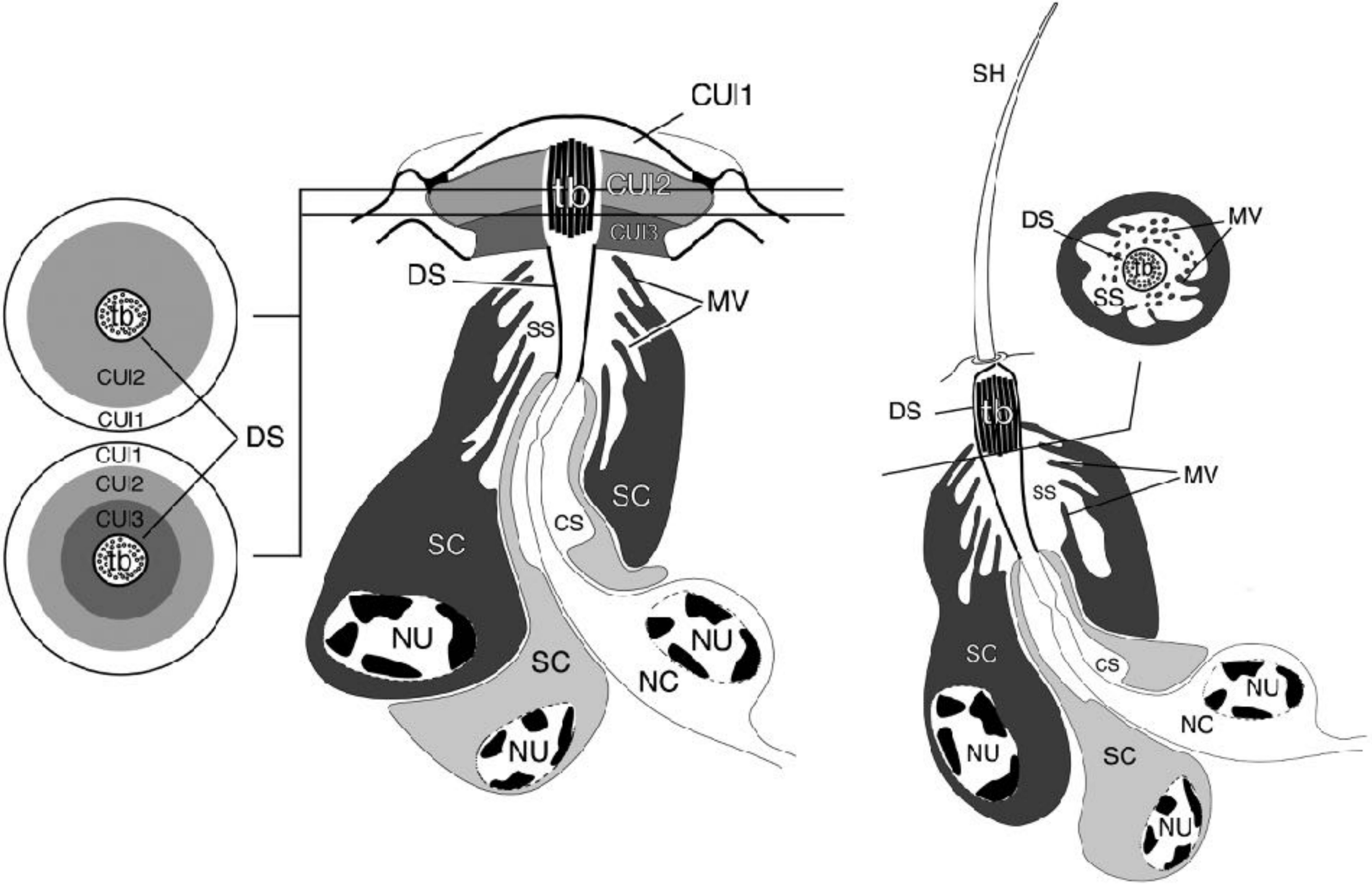
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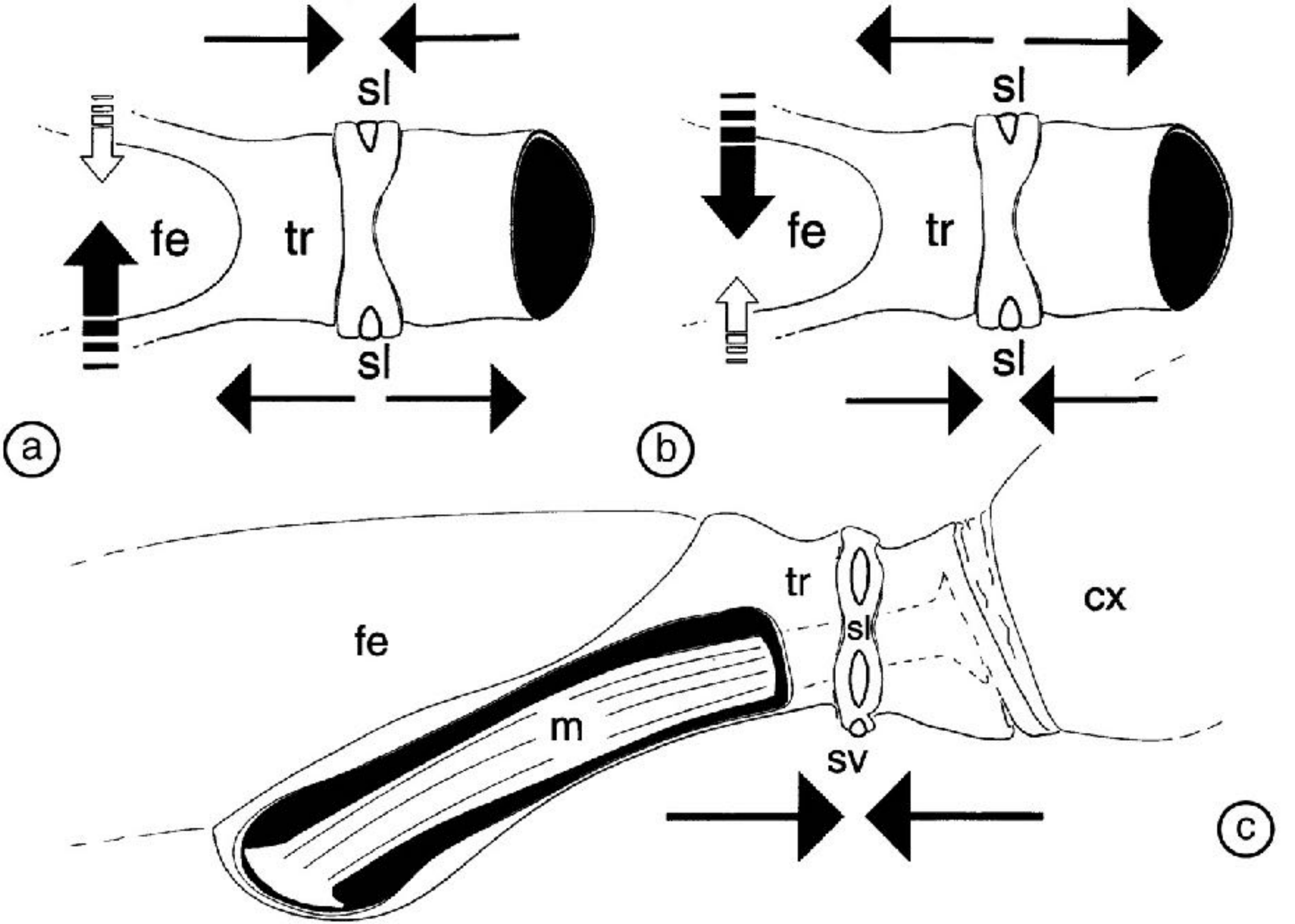
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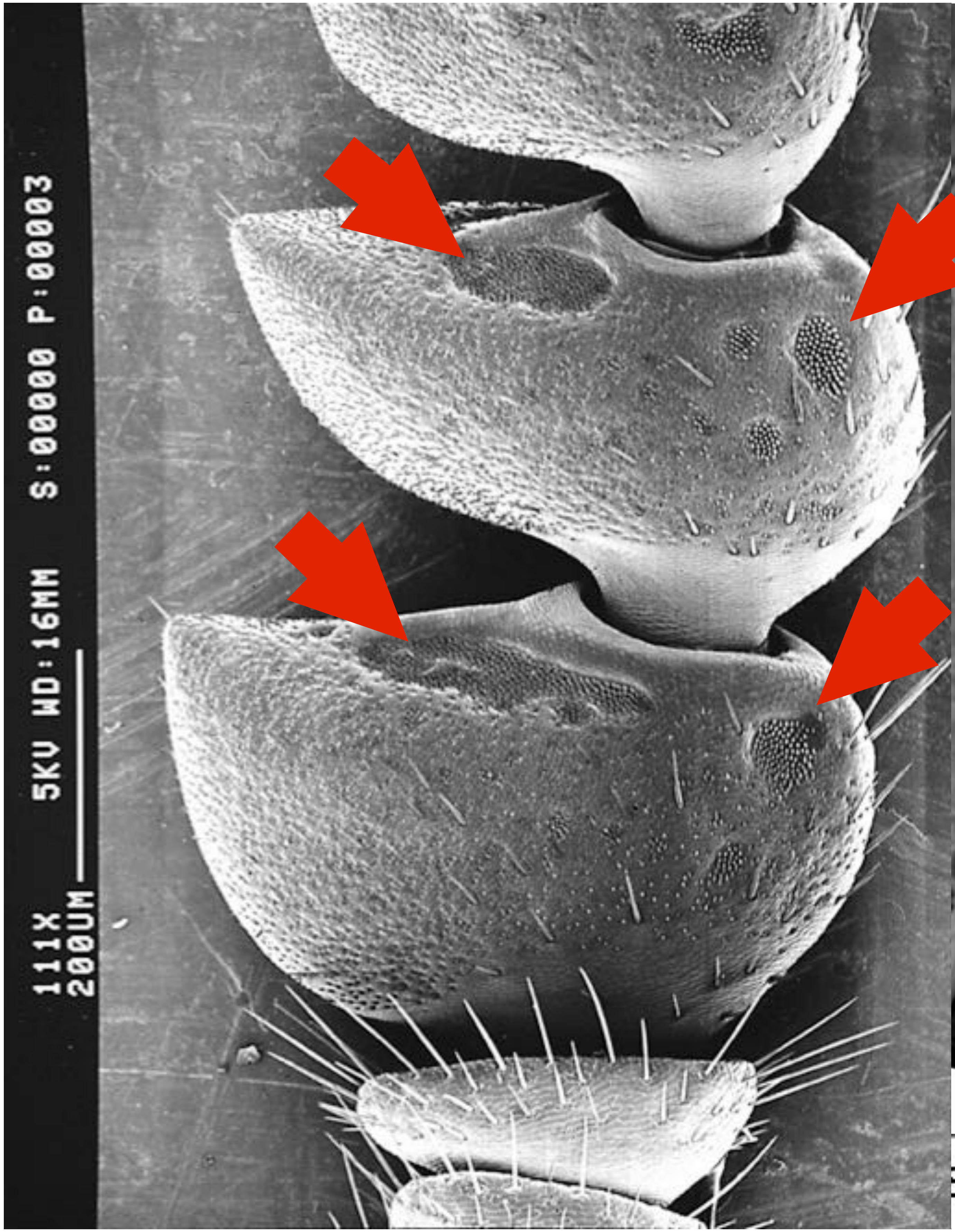
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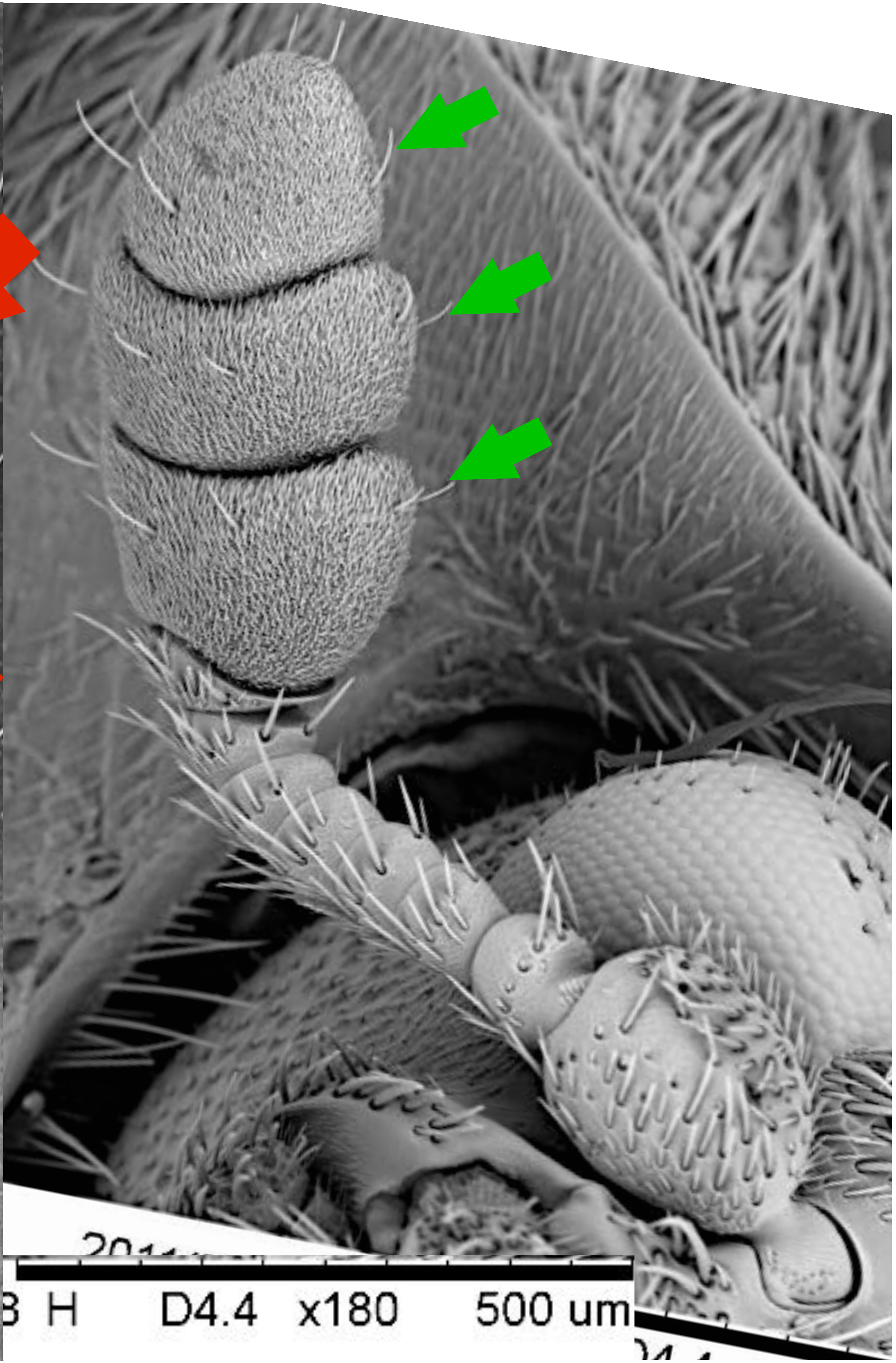
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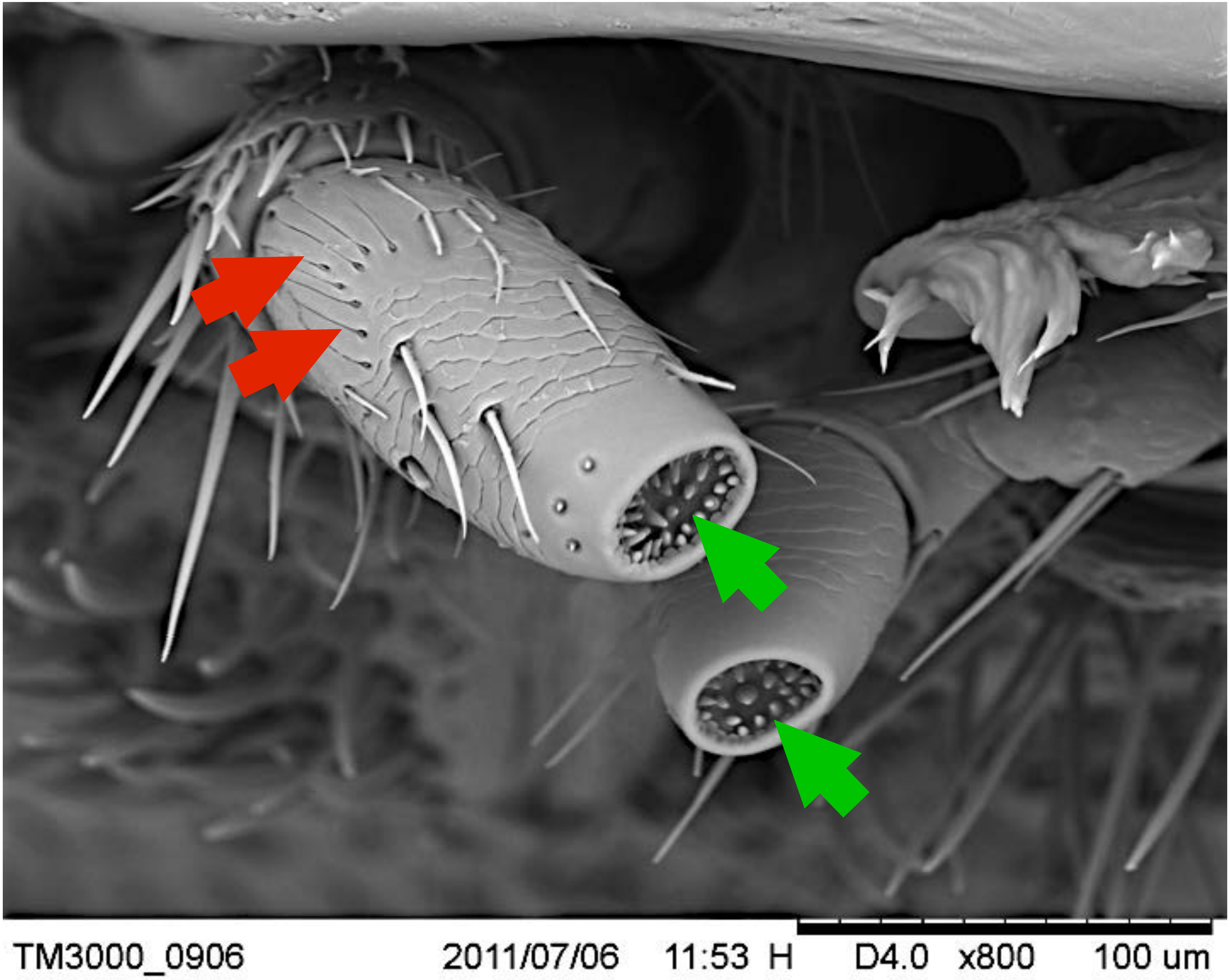
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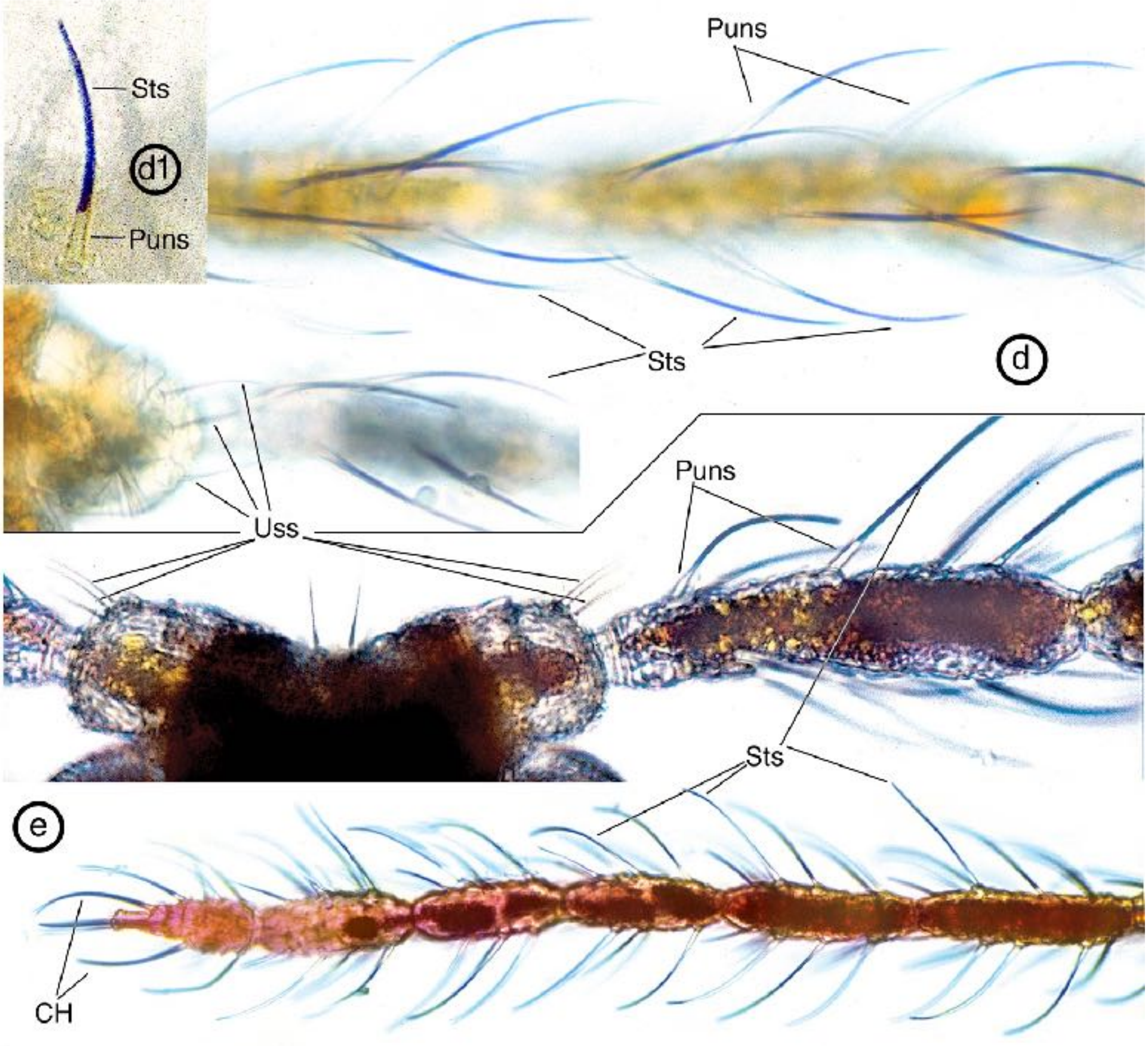
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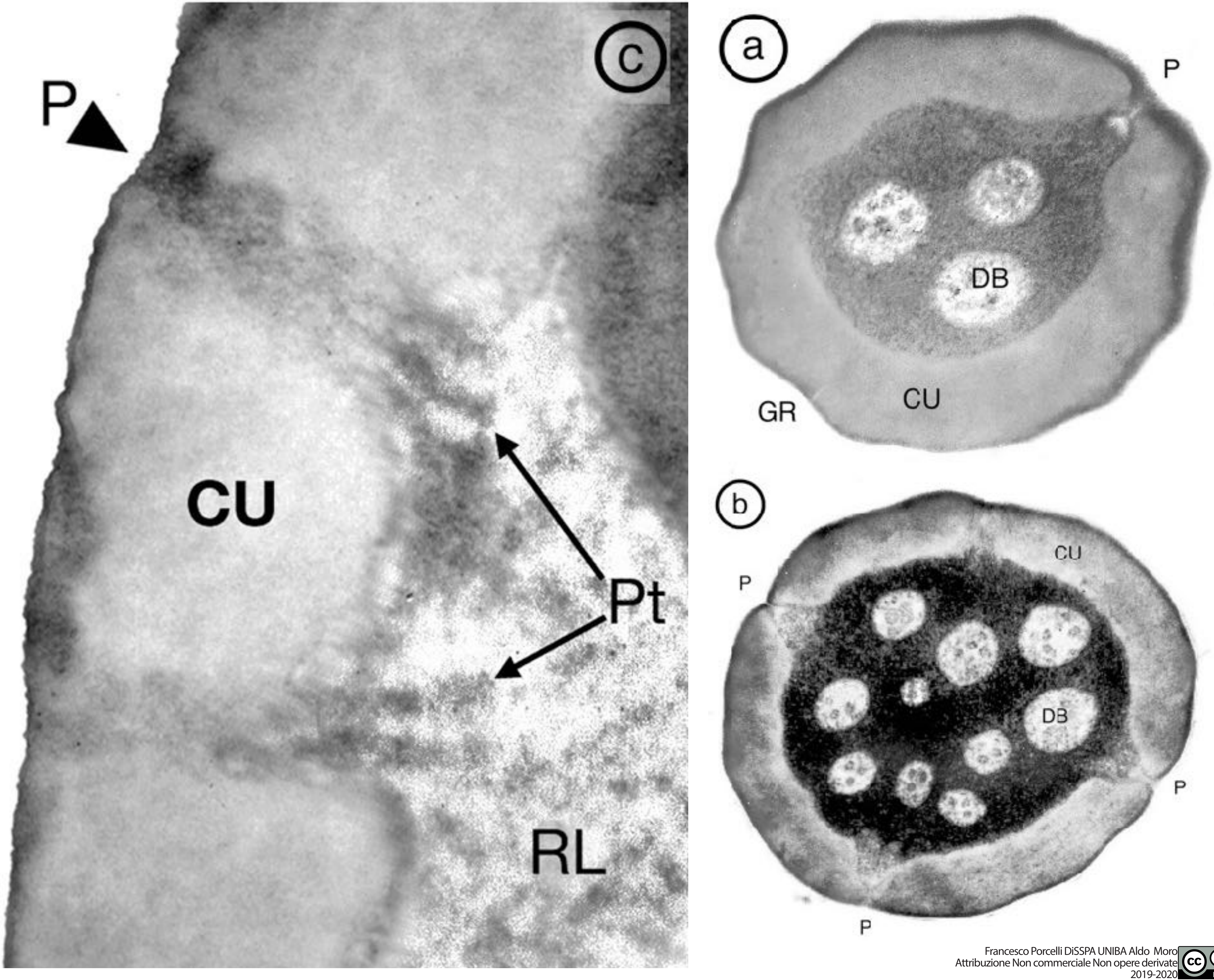
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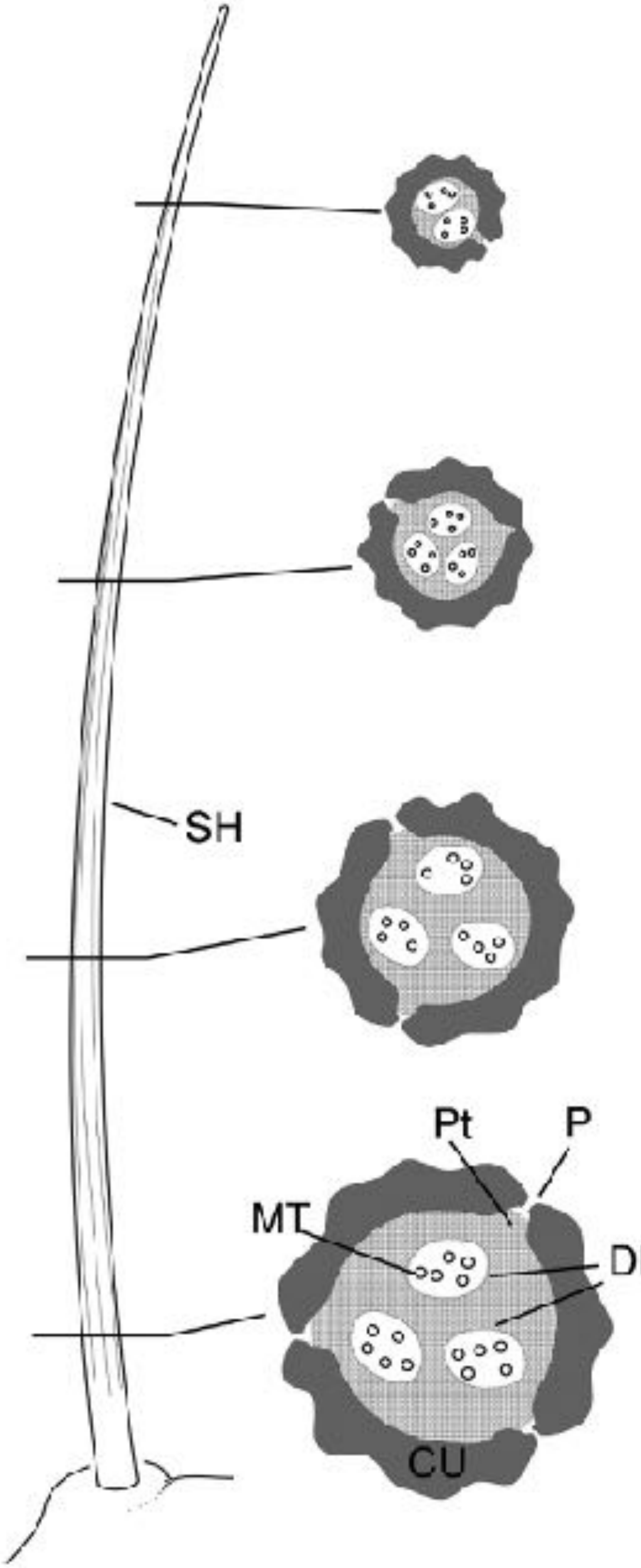
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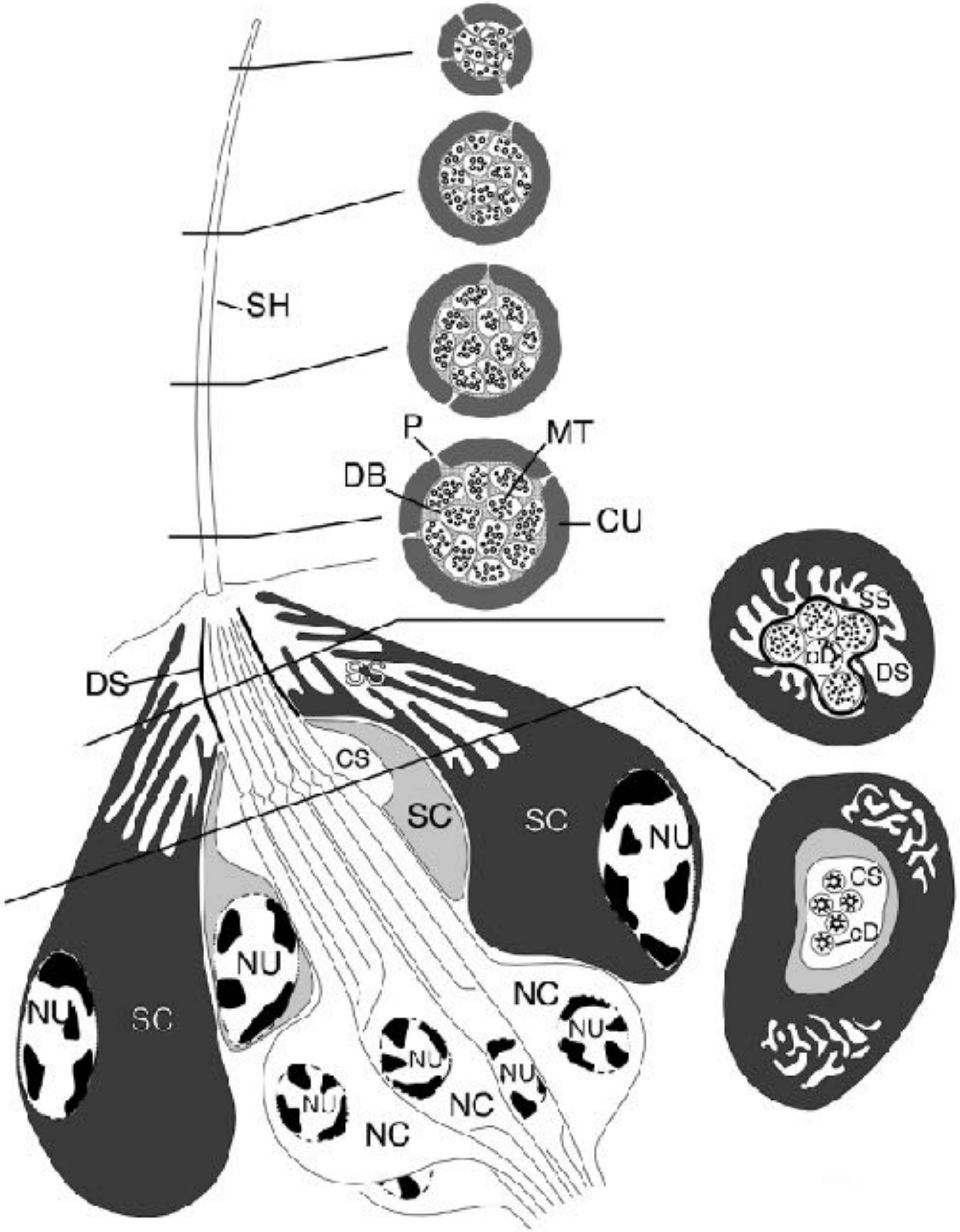
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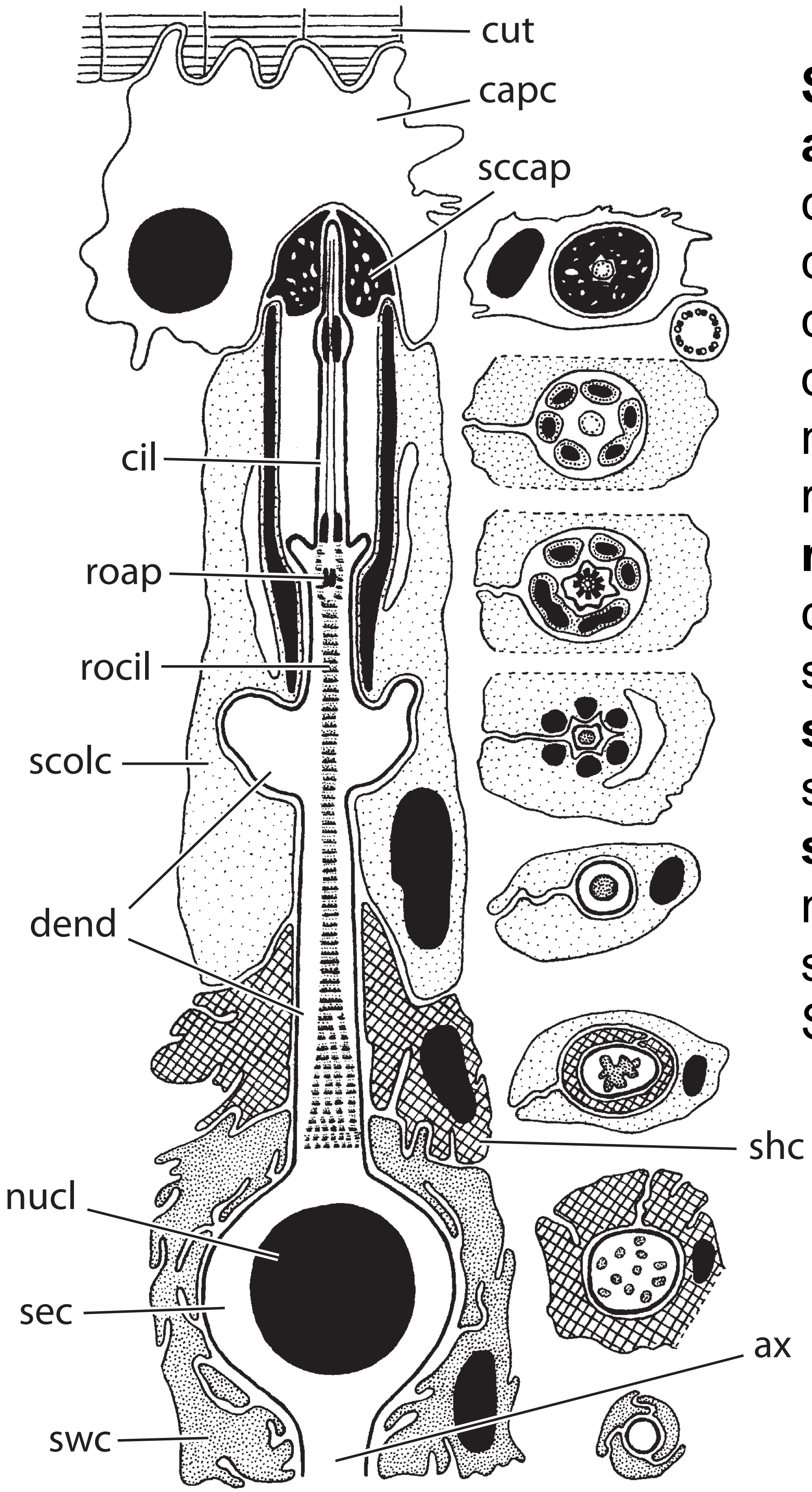
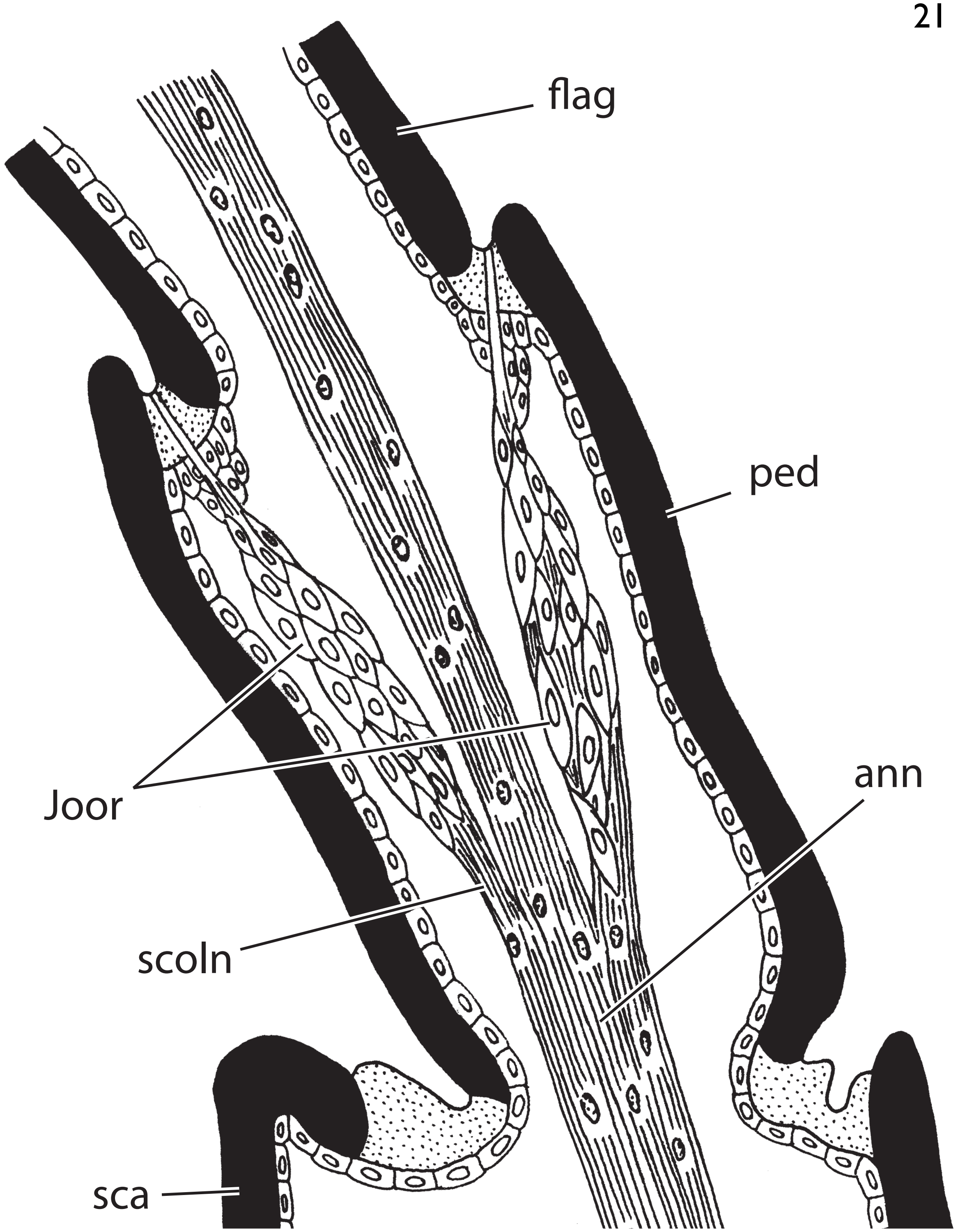
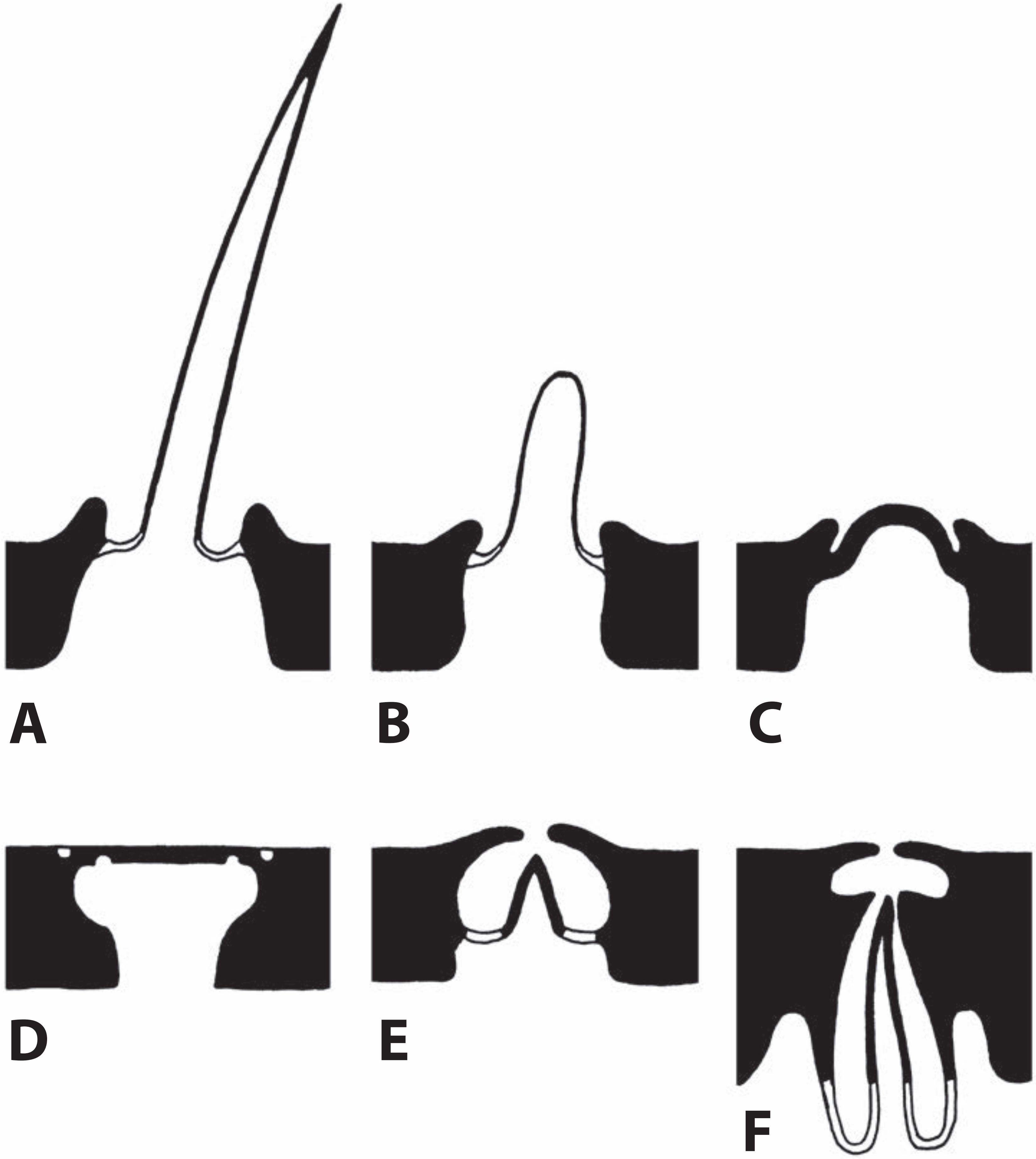


Scolopidium
ax: axon, **capc:** cap cell, **cil:** cilium, **cut:** cuticle, **dend:** dendrite, **nucl:** nucleus, **roap:** root apparatus, **rocil:** root of cilium, **sccap:** scolopale cap, **scolc:** scolopale cell, **sec:** sensory neuron, **shc:** sheath cell, **swc:** Swann cell.



Chordotonal organ, Johnston's organ of the pedicellus. **ann:** antennal nerve, **flag:** 1st flagellomere, **Joor:** Johnston's organ, **ped:** pedicellus, **sca:** scapus, **scoln:** scolopale nerve



Different types of cuticular sensilla.

A: s. trichodeum;

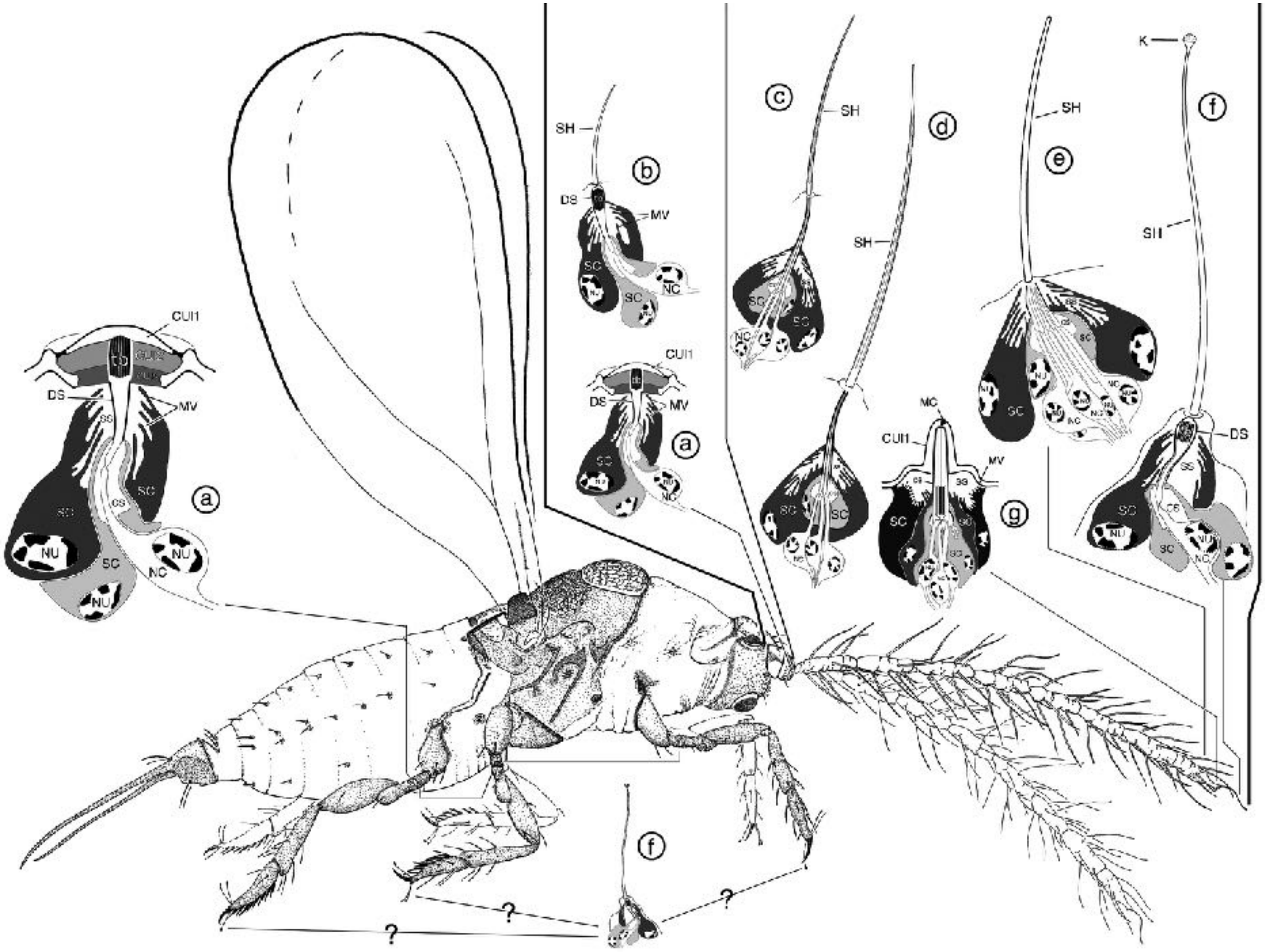
B: s. basiconicum;

C: s. campaniformium;

D: s. placodeum;

E: s. coeloconicum;

F: s. ampullaceum.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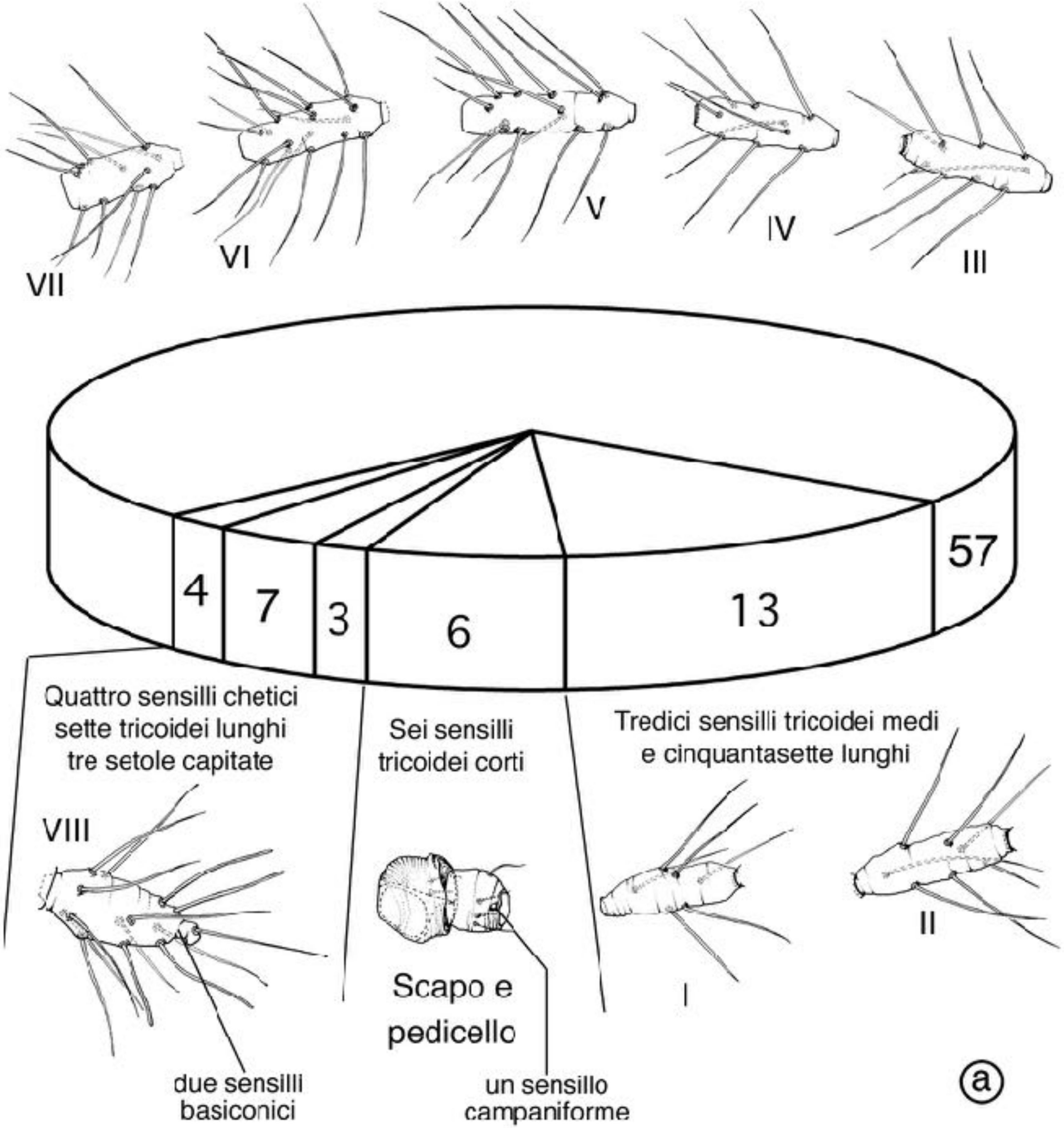
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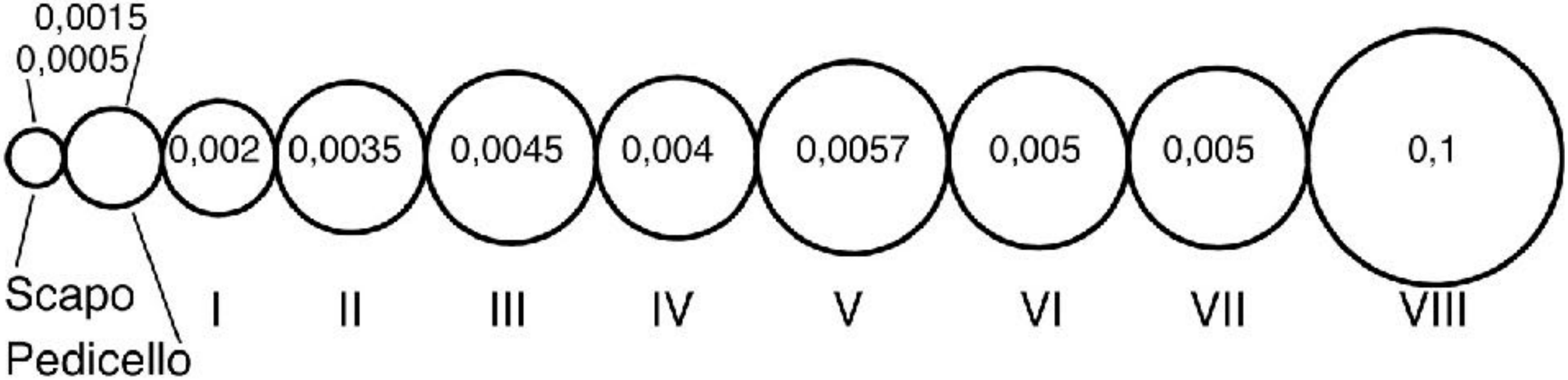
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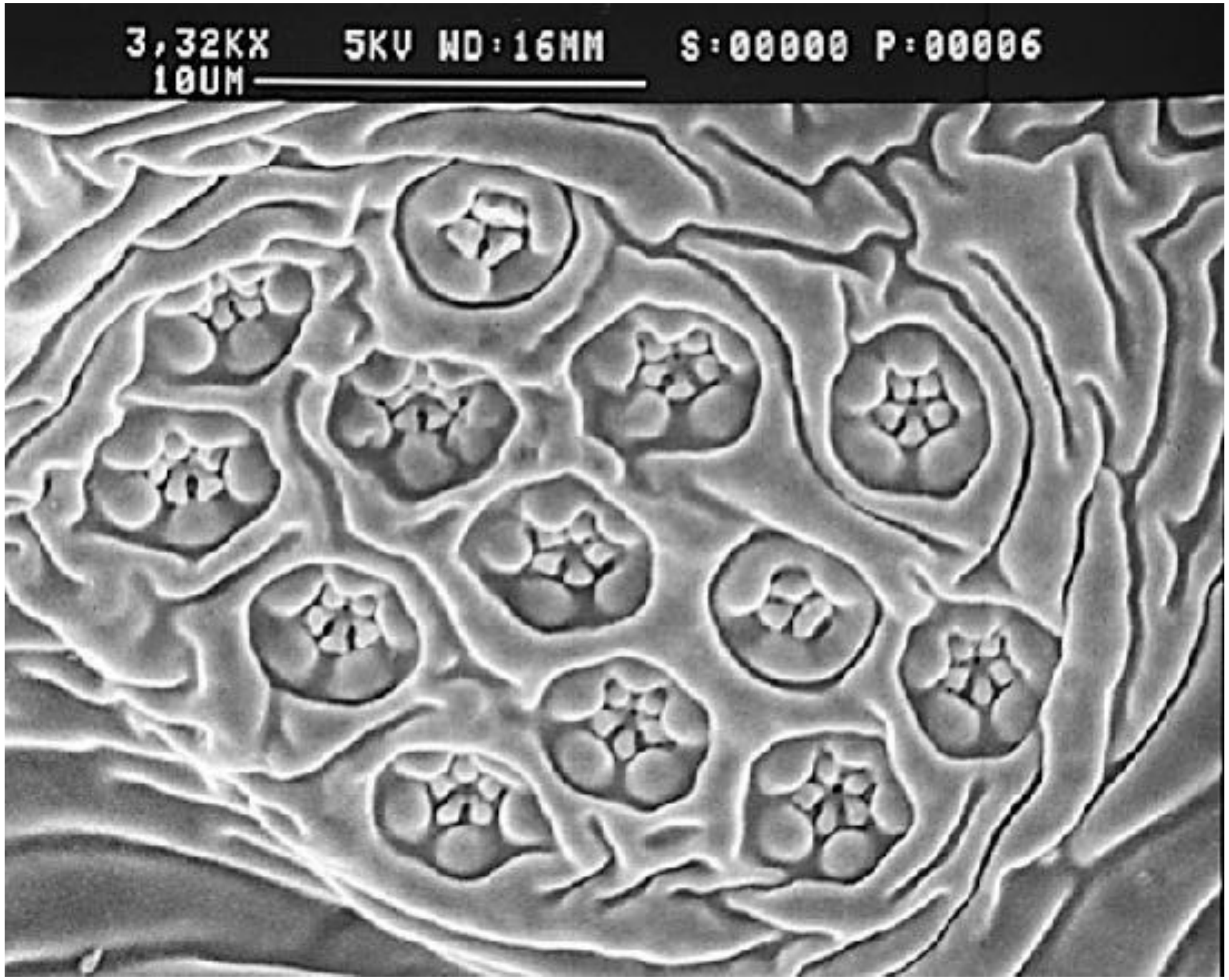
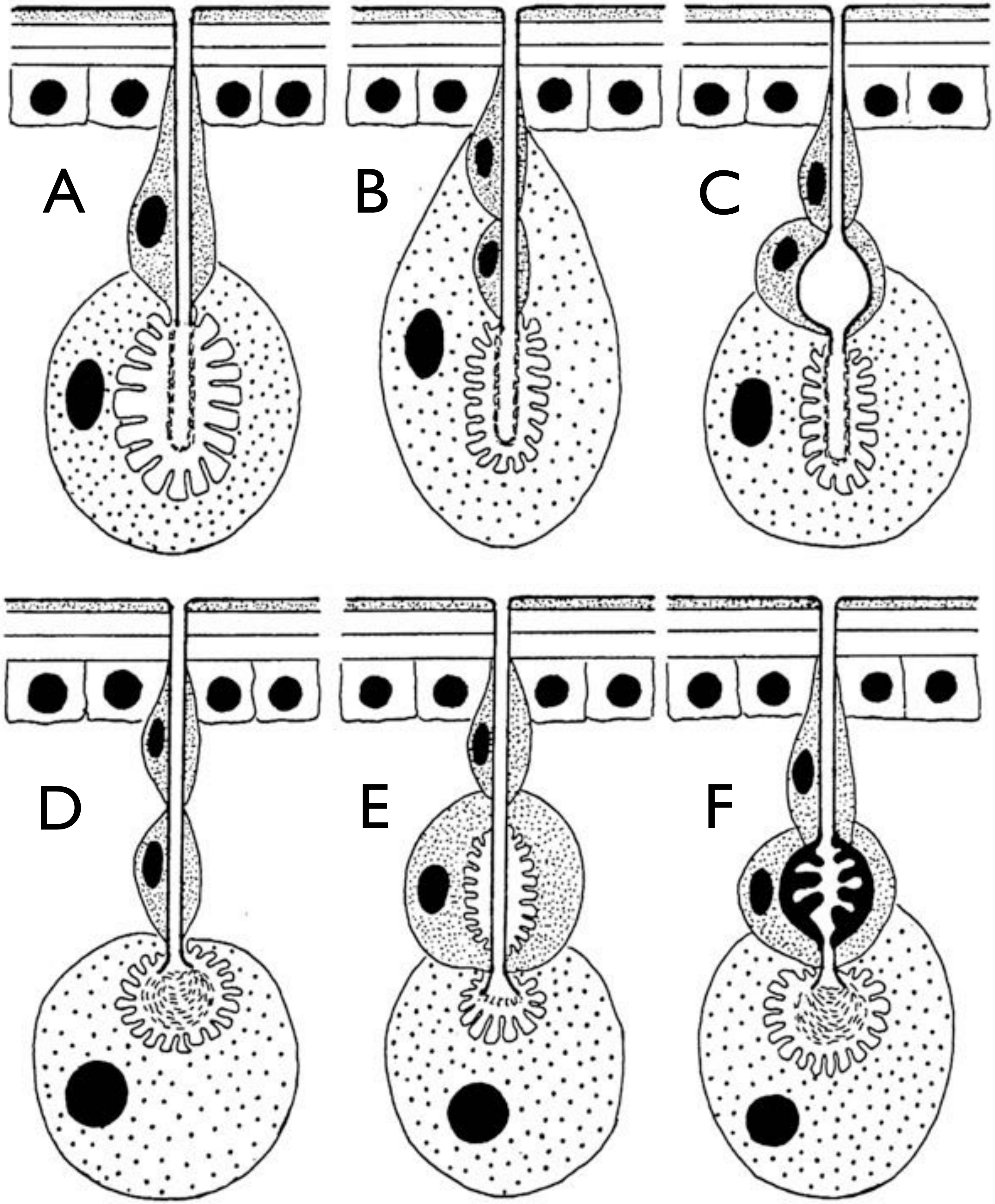
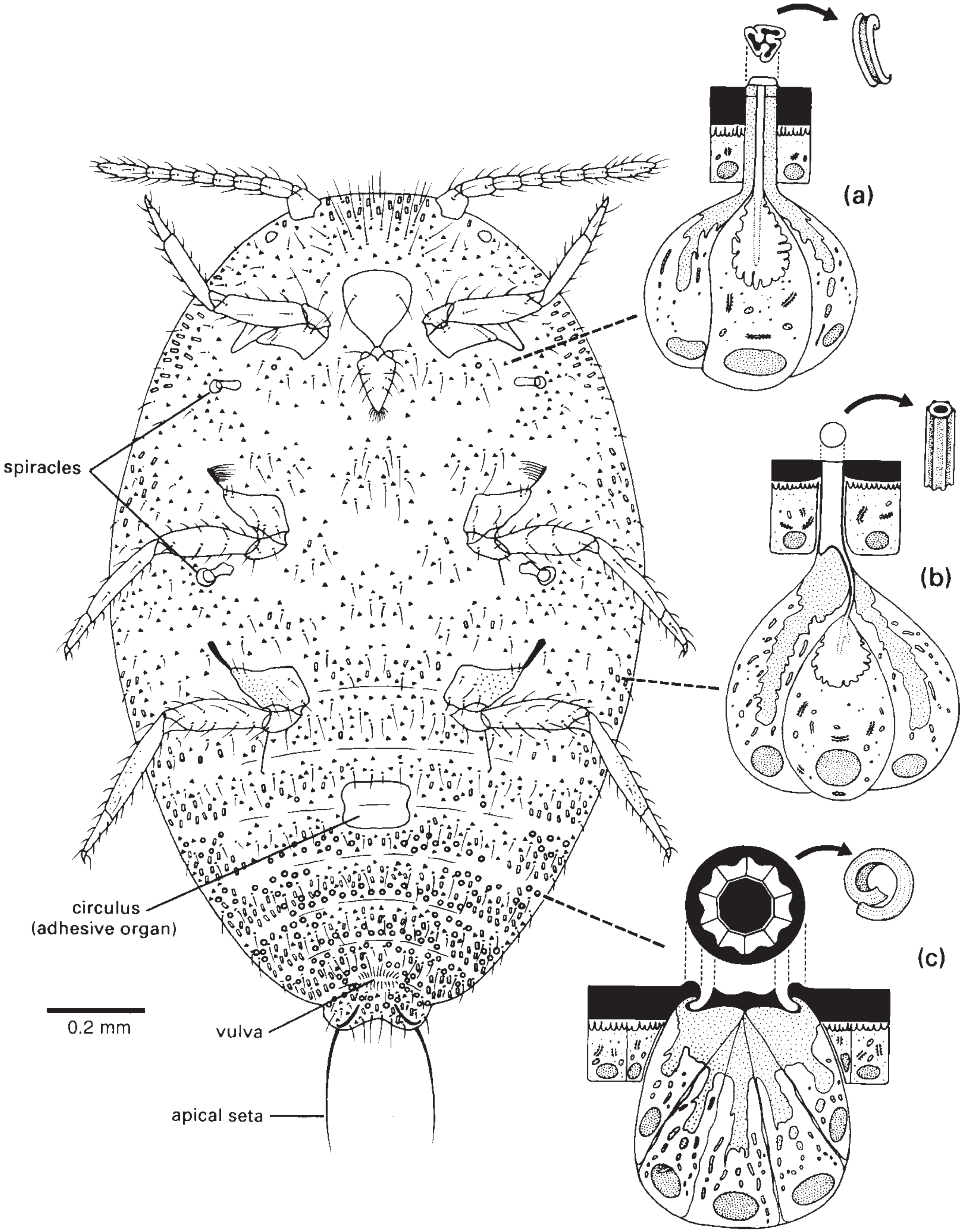


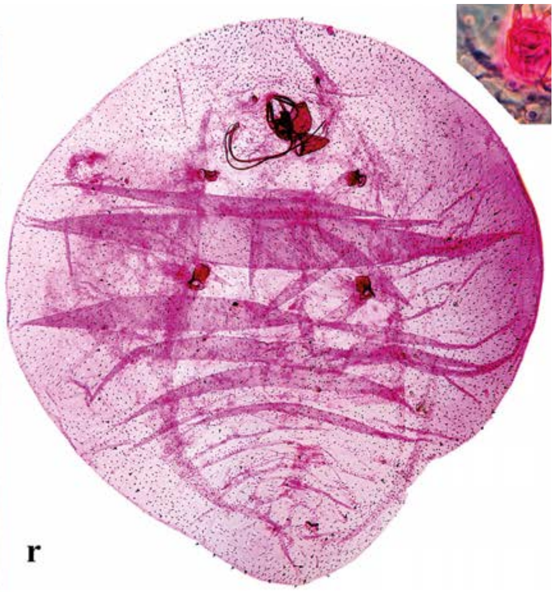
Integumental gland cells

Gland cells associated with the integument are embedded in the hypodermis (screen 4: glc, see above) and much rarer than the unmodified epidermal cells surrounding them. They usually produce secretions permanently. The shape is more rounded compared to other cells of the hypodermis and they are often extended towards the body cavity. In the typical case the nucleus appears enlarged, irregularly lobate or star-shaped. Endopolyploidy is common. Three types of cells with specialized glandular functions were distinguished. Class 1 gland cells have the apical membrane produced as microvilli or lamellae, which are in direct contact with the cuticle secreted by themselves. They are often involved in the production of pheromones. Class 2 (only present in termites) and class 3 cells have no contact with the cuticle. Microvilli are present around vesicles structurally associated with a duct forming a connection to the exterior is absent in the former but present in the latter. The duct is an invagination of the external cuticular layer. Microvilli are absent from class 2 cells.



Reported structural modifications observed for the cuticular duct of 3 cells-glands. Usually the cuticular duct is tubular, composed of an inner receiving canal surrounded by the secretory cell and a conducting canal surrounded by a canal cell (A). Two cells may be seen around the conducting canal (B-F) and a spherical part can also developed (C,F) allowing the storage of secretory material. As for the receiving canal, a tubular structure is more often seen (A -C), yet may also be strongly reduced (E) or take a spherical shape (D,F).


(a)
(b)
(c)
spiracles
circulus
(adhesive organ)
0.2 mm
vulva
apical seta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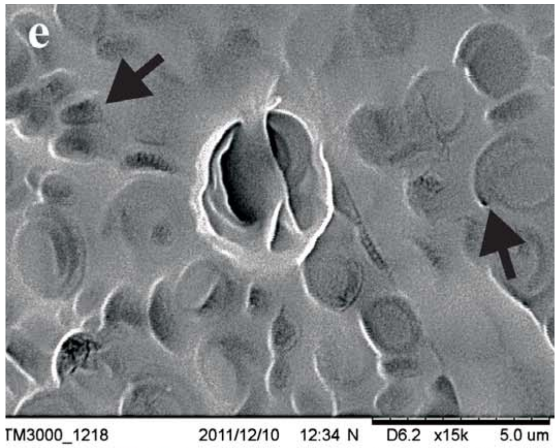
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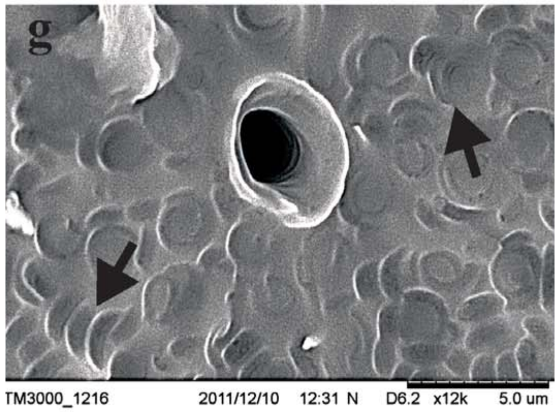
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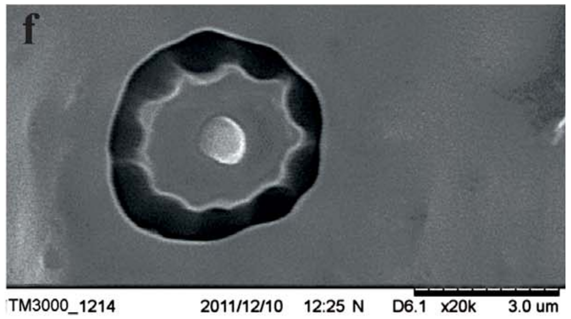
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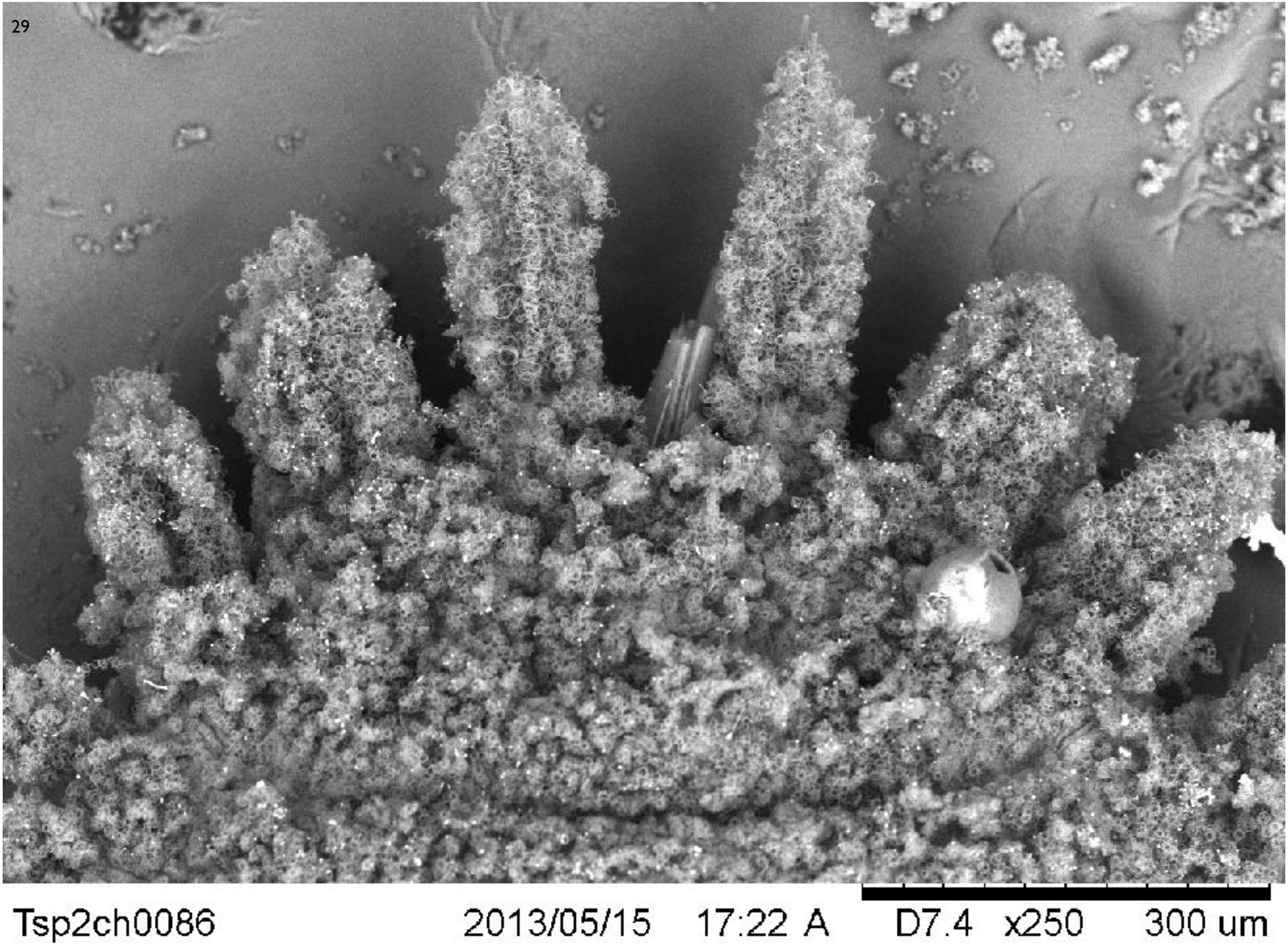
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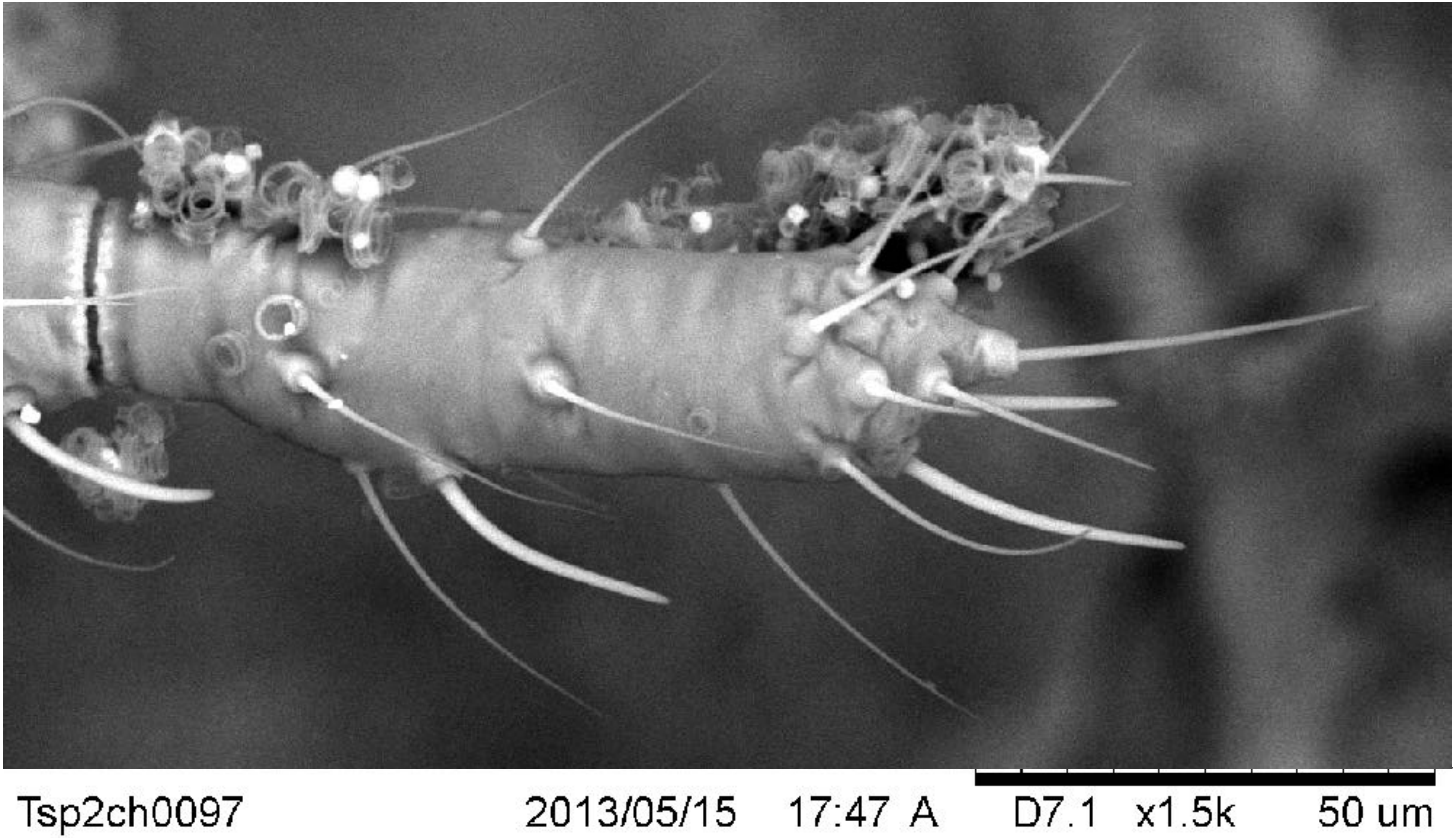
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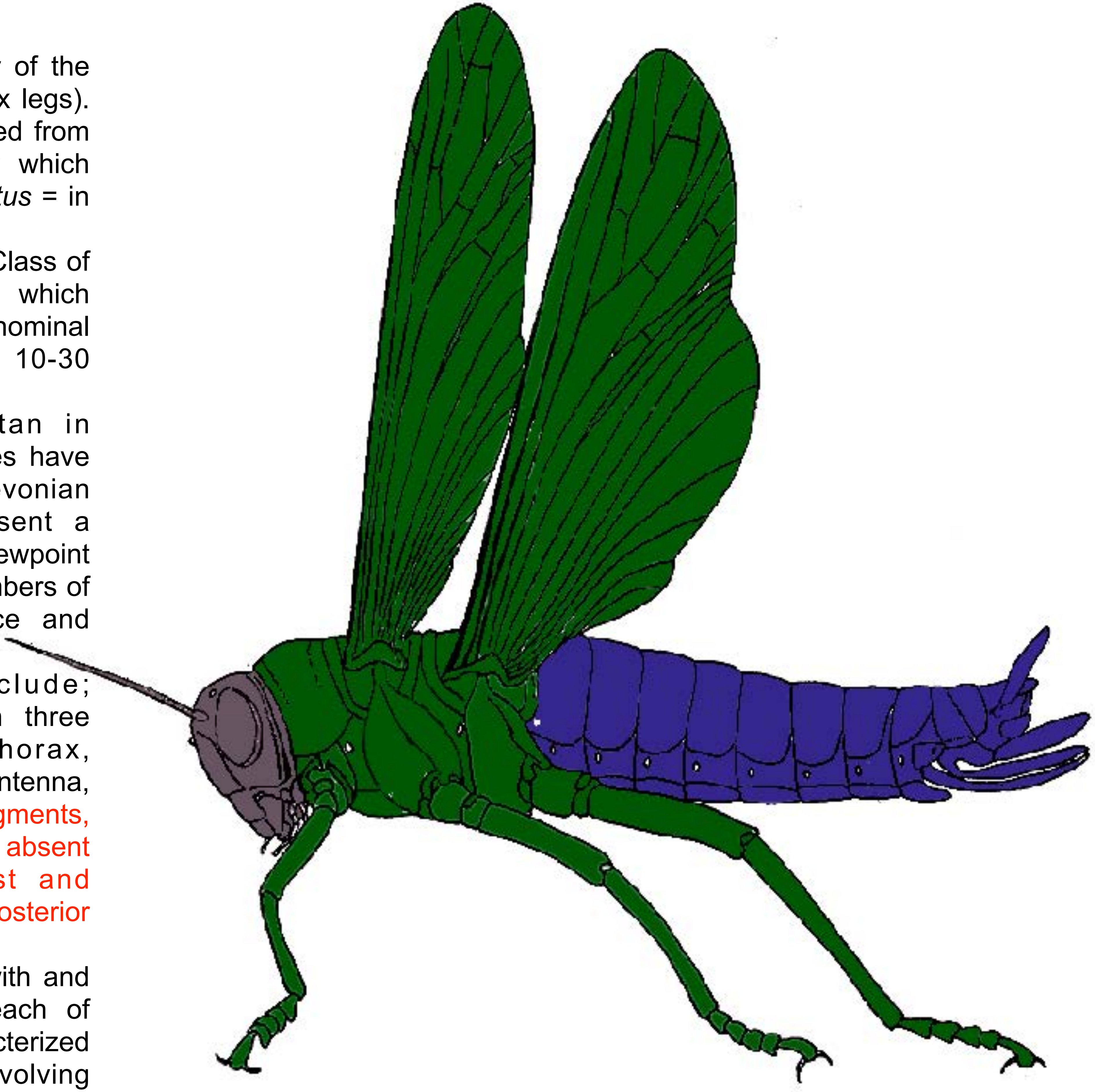
Insect definition: any member of the Class Insecta (*Hexapoda* = six legs). The name apparently is derived from the appearance of the body which appears cut or incised (*in sectus* = in part).

Insecta represent the largest Class of the Phylum Arthropoda and which contains about 1.8 million nominal Species and estimates of 10-30 million extant Species.

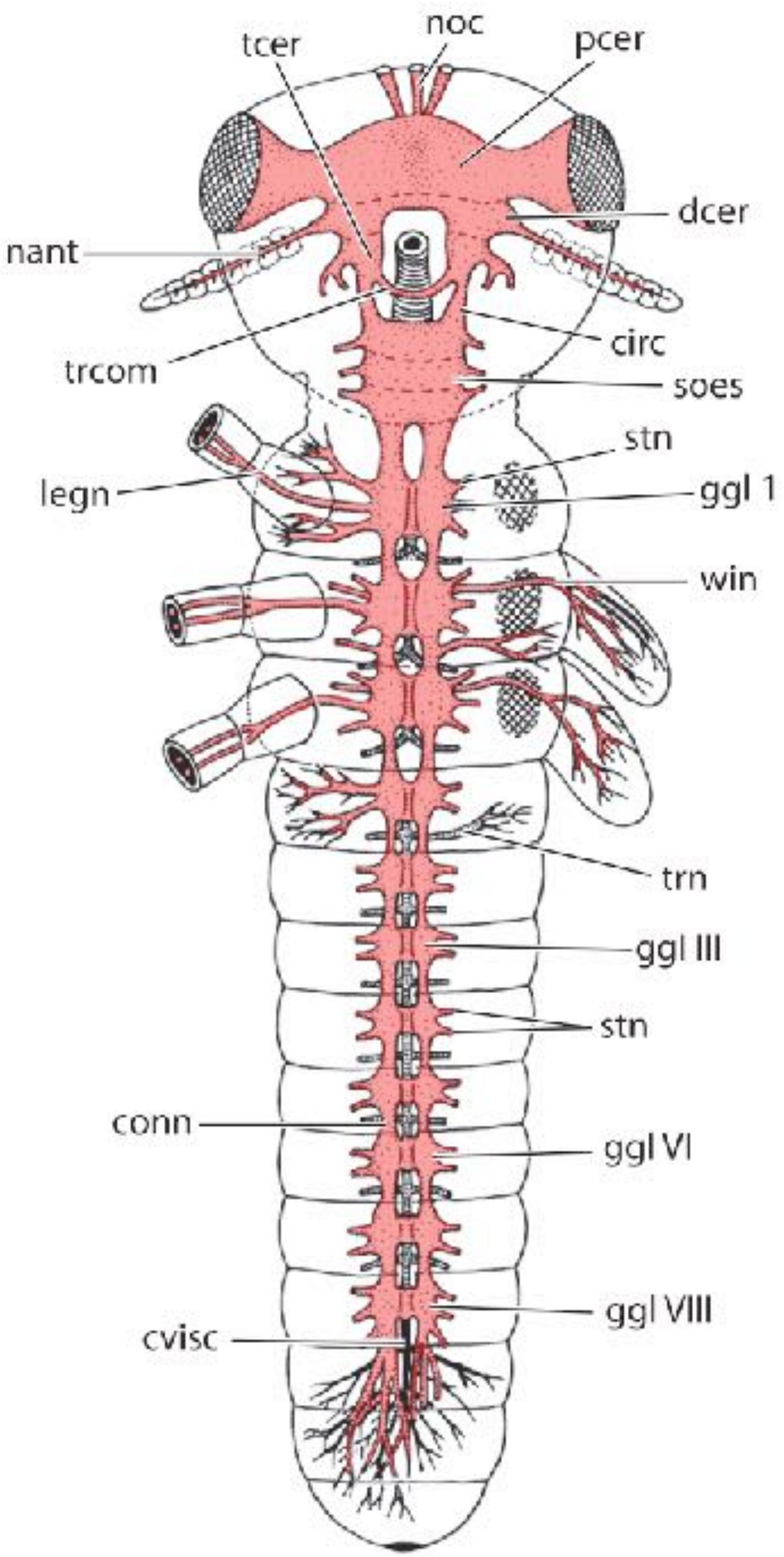
The Class is cosmopolitan in distribution and representatives have been extant since the Devonian Period. The Insecta represent a dominant life form from the viewpoint of numbers of individuals, numbers of Species. length of existence and diversity of life-style.

Anatomical features include; Mandibulate tracheates with three body Tagmata (Head, Thorax, Abdomen), multisegmented Antenna, Thorax composed of three segments, wings primitively present or absent but often secondarily lost and associated with middle and posterior segments of thorax.

Six pairs of legs articulated with and consecutively arranged on each of the thoracic segments. Characterized by a complex life-cycle involving Metamorphosis.



02 Nervous



Nervous system

In its basic design the complex nervous system of Hexapoda is similar to that occurring in other groups of arthropods. It integrates sensory input and internal physiological information and controls the complex locomotor apparatus. It is subdivided into three major elements, the **central nervous system** (**CNS**), the **visceral (sympathetic) nervous system**, and the peripheral nervous system. The main subdivision is the CNS comprising the complex **brain** (**cerebrum**, supraoesophageal ganglion), the **suboesophageal complex** (**suboesophageal ganglion**), and the postcephalic ventral nerve cord or ganglionic chain. The visceral nervous system comprises three subcomponents, the **stomatogastric** (stomodaeal) **nervous system**, the **ventral nerve** (**ventral visceral nervous system**), and the **caudal visceral nervous system**. The peripheral nervous system establishes the connections to the appendages, the body wall, and the organs. A ventral nerve cord with segmental ganglia is arguably an autapomorphy of Arthropoda (with possible reversal in Onychophora). A similar condition occurs in Annelida, the presumptive sistergroup of arthropods.

The **ganglia** of hexapods and euarthropods in general are primarily paired segmental nerve centers. They are a concentration of perikarya (cell bodies) of motoneurons and interneurons and projections connecting different types of nerve cells. The perikarya are always placed at the periphery. The internal layer only consisting of axons is called the **neuropil**. The ganglia are connected by transverse **commissures** and longitudinal **connectives**. Different types of concentration of the ventral nerve cord occur in many groups. The primarily paired ganglia can be more or less completely fused along the median line and also in the longitudinal direction (see below), involving reductions of the commissures and connectives, respectively.

The neurons (nerve cells) are the basic components of the nervous system. They are composed of the perikaryon and two types of projections, a short dendrite which receives stimuli, and a long axon (neurite) which transmits information to another neuron or to effector organs such as for instance muscles. The cell bodies and other parts of the neurons are enclosed by folds of one or several glial cells. Synapses occur only where these folds are absent. The glial cells can enclose an individual axon or several smaller ones. They provide the neurons with nutrients and play an important function in the development of the CNS. The entire system of glial cells is referred to as **neuroglia**. The sheath enclosing the whole nervous system is called the **neurilemma** (perilemma). Its inner cellular layer (**perineurium**) contains glycogen in higher concentration. The external layer or neural lamella is formed by the basement membrane and contains collagen.

Most hexapod neurons are monopolar, i.e. the dendrite and the axon share a single common projection arising from the perikaryon. Peripheral sense cells are bipolar, with a short and usually unbranched distal dendrite and a long proximal axon connected to the CNS. Multipolar neurons occur in ganglia and can be associated with stretch receptors and thermoreceptors. The three main functional types of neurons are the afferent sensory neurons, the efferent motor neurons, and the interneurons (association neurons) which transmit information between other nerve cells. Specialized neuroendocrine cells (**neurosecretory cells**) produce secretions, especially neurohormones.

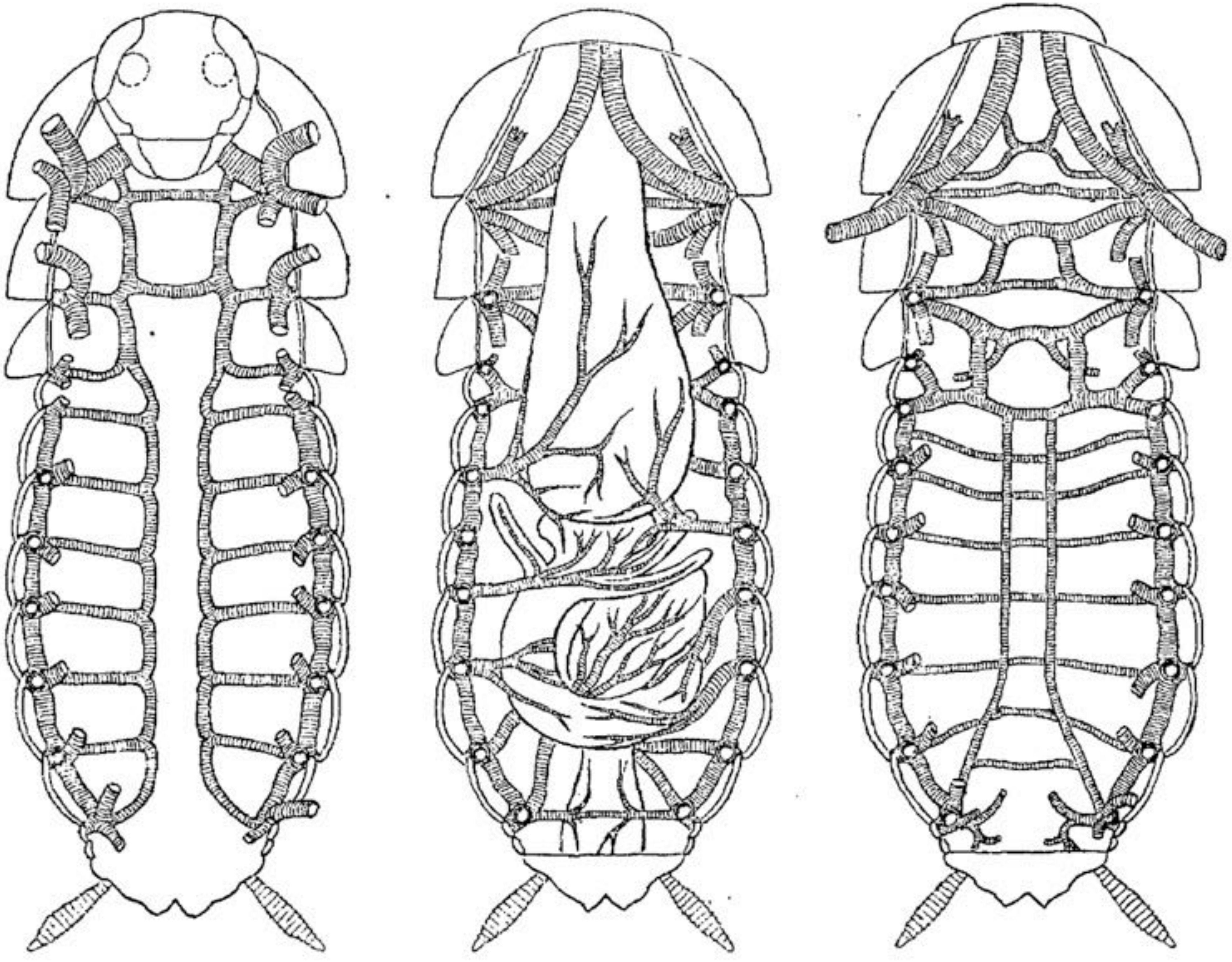
Nervous system, schematized, ventral view. **circ:** circumoesophageal commissure, **cvisc:** caudal visceral nervous system, **conn:** connective, **dcer:** deutocerebrum, **ggl 1/III/VI/VIII:** thoracic and abdominal ganglia, **legn:** leg nerve, **nant:** nervus antennalis, **noc:** ocellar nerve, **pcer:** protocerebrum, **soes:** suboesophageal ganglion, **stn:** stem nerve, **tcer:** tritocerebrum, **trcom:** tritocerebral commissure, **trn:** tracheal nerve, **win:** wing nerve.

03 Respiratory, circulation, and food channel

Gaseous exchange in insects occurs through a system of internal tubes, the tracheal system, the finer branches of which extend to all parts of the body and may become functionally intracellular in muscle fibers. Thus oxygen is carried directly to its sites of utilization and the blood is not concerned with its transport. In terrestrial insects and some aquatic species, the tracheae open to the outside through segmental pores, the spiracles, which generally have some closing mechanism reducing water loss from the respiratory surfaces. Other aquatic species have no functional spiracles, and gaseous exchange with the water involves arrays of tracheae close beneath the surface of thin, permeable cuticle.

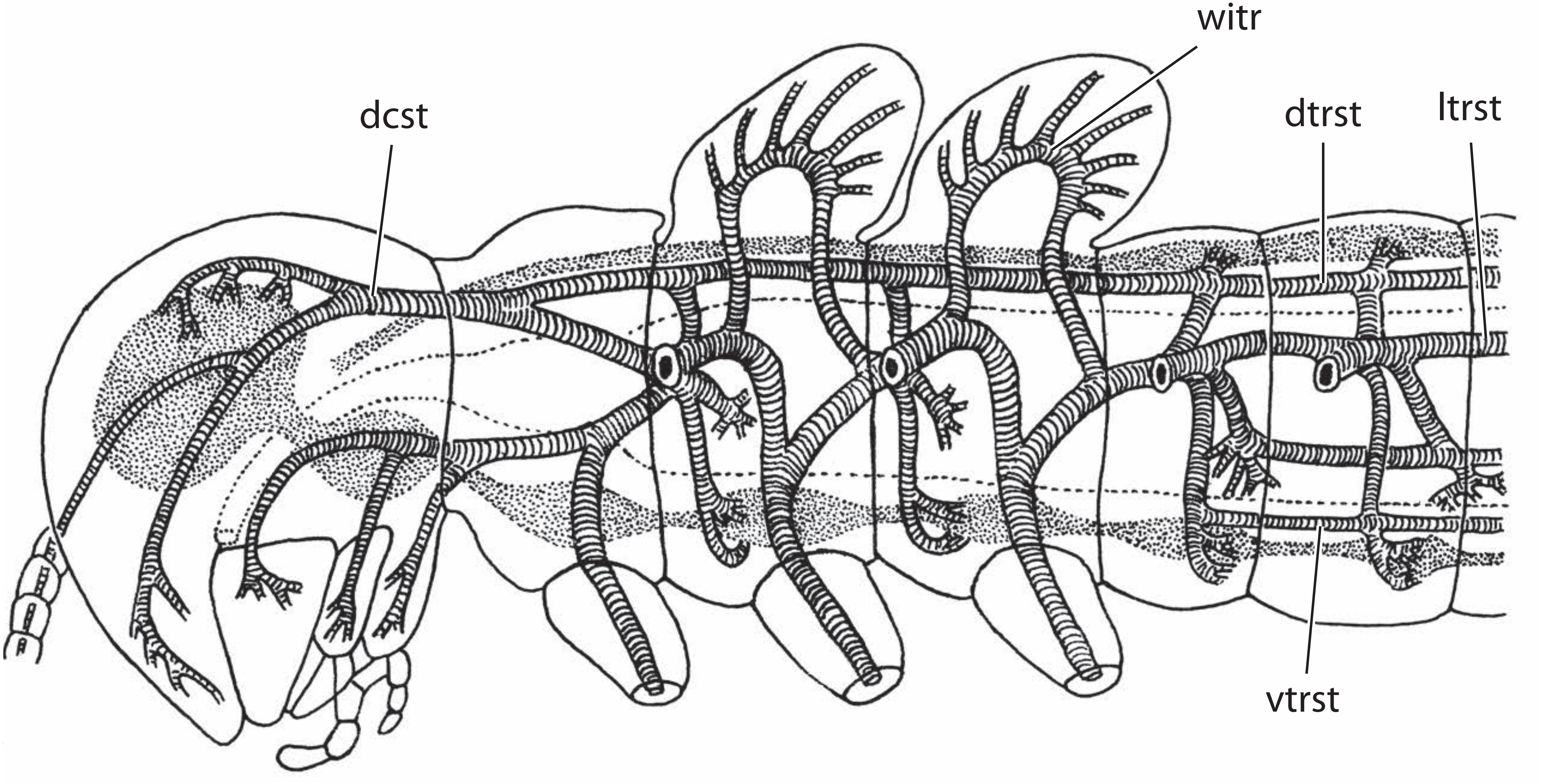
The tracheae are the larger tubes of the tracheal system, running inward from the spiracles and usually breaking up into finer branches, the smallest of which are about 2 µm in diameter. Tracheae are formed by invaginations of the ectoderm and so are lined by a cuticular intima which is continuous with the rest of the cuticle.

A spiral thickening of the intima runs along each tube, each ring of the spiral being called a taenidium. The intima consists of outer epicuticle with a protein/chitin layer beneath it. In the taenidia the protein/chitin cuticle is differentiated as mesocuticle or exocuticle. The chitin microfibrils in the taenidia run round the trachea, while between the taenidia they are parallel with the long axis of the trachea. A layer of resilin may be present beneath the epicuticle.



The taenidia prevent collapse of the trachea if pressure within the tube is reduced. In the wing tracheae of some insects, the taenidia are themselves twisted, giving some elasticity to the wall of the trachea. In places, the tracheae are expanded to form thin-walled airsacs in which the taenidia are absent or poorly developed and often irregularly arranged. Consequently, the airsacs collapse under pressure and they play a very important part in ventilation of the tracheal system as well as having other functions. Airsacs are widely distributed along the main tracheal trunks of many insects.

At various points along their length, especially distally, the tracheae give rise to finer tubes, the tracheoles. There is no sharp distinction between tracheae and tracheoles, but the latter always appear to be intracellular and often retain their cuticular lining at molting, which is not usually true of tracheae. Proximally the tracheoles are about 1µm in diameter, tapering to about 0.1µm or less. They are formed in cells (often called tracheoblasts) which are derived from the epidermal cells lining the tracheae. It is not certain if the tracheoles develop as truly intracellular structures or if they are really extracellular, forming in a deep fold of the plasma membrane of the tracheolar cell and so having the appearance of being intracellular.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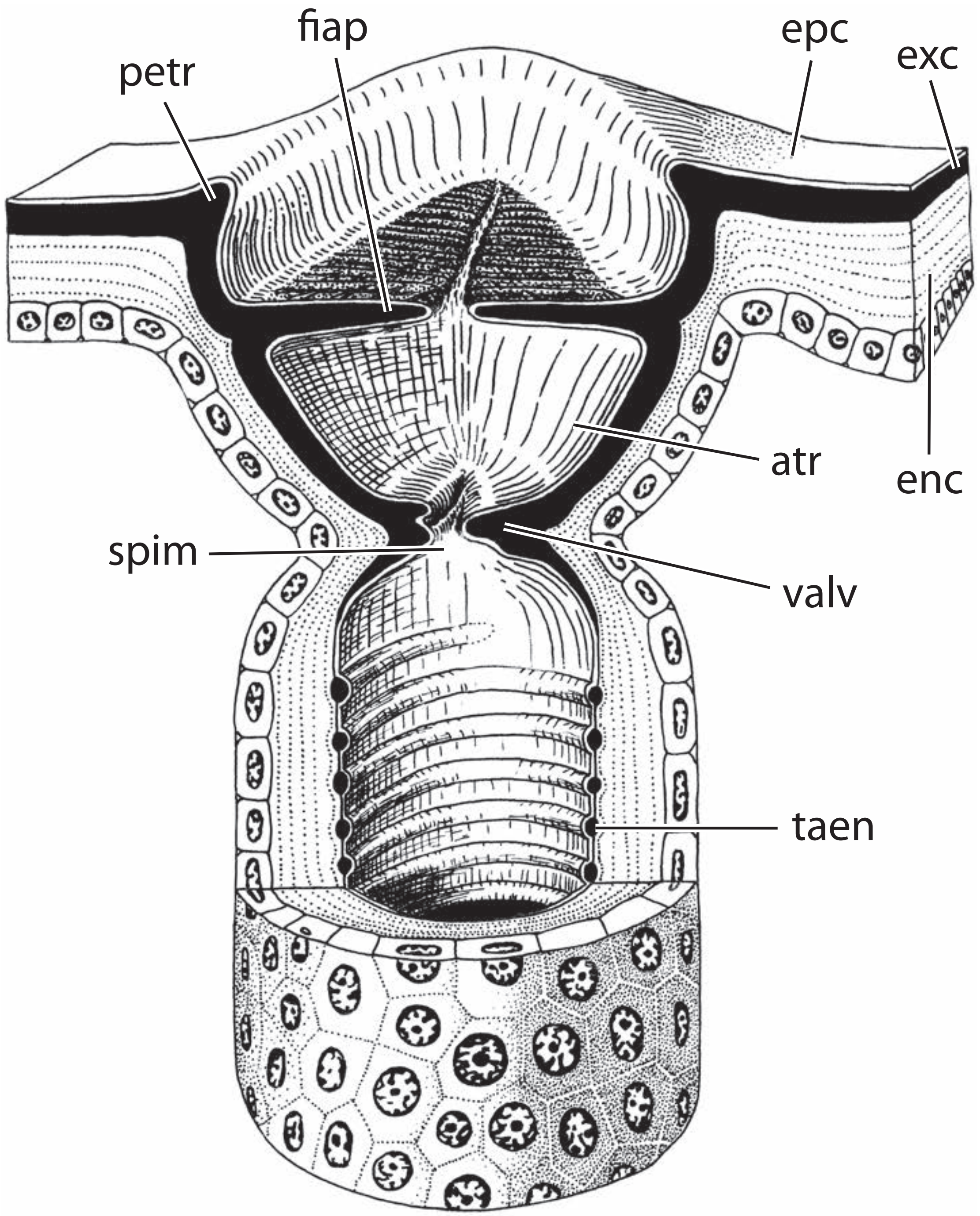
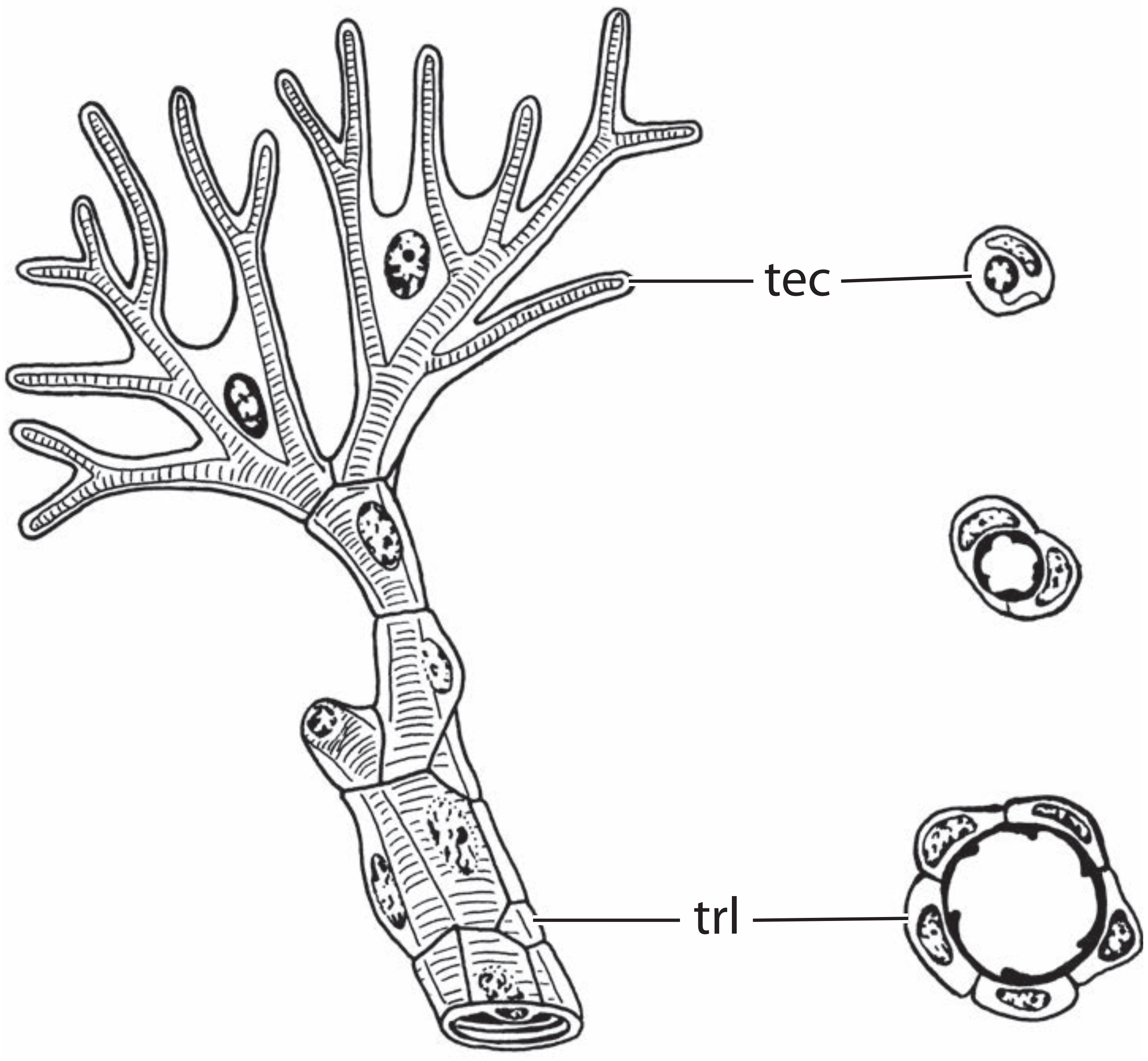
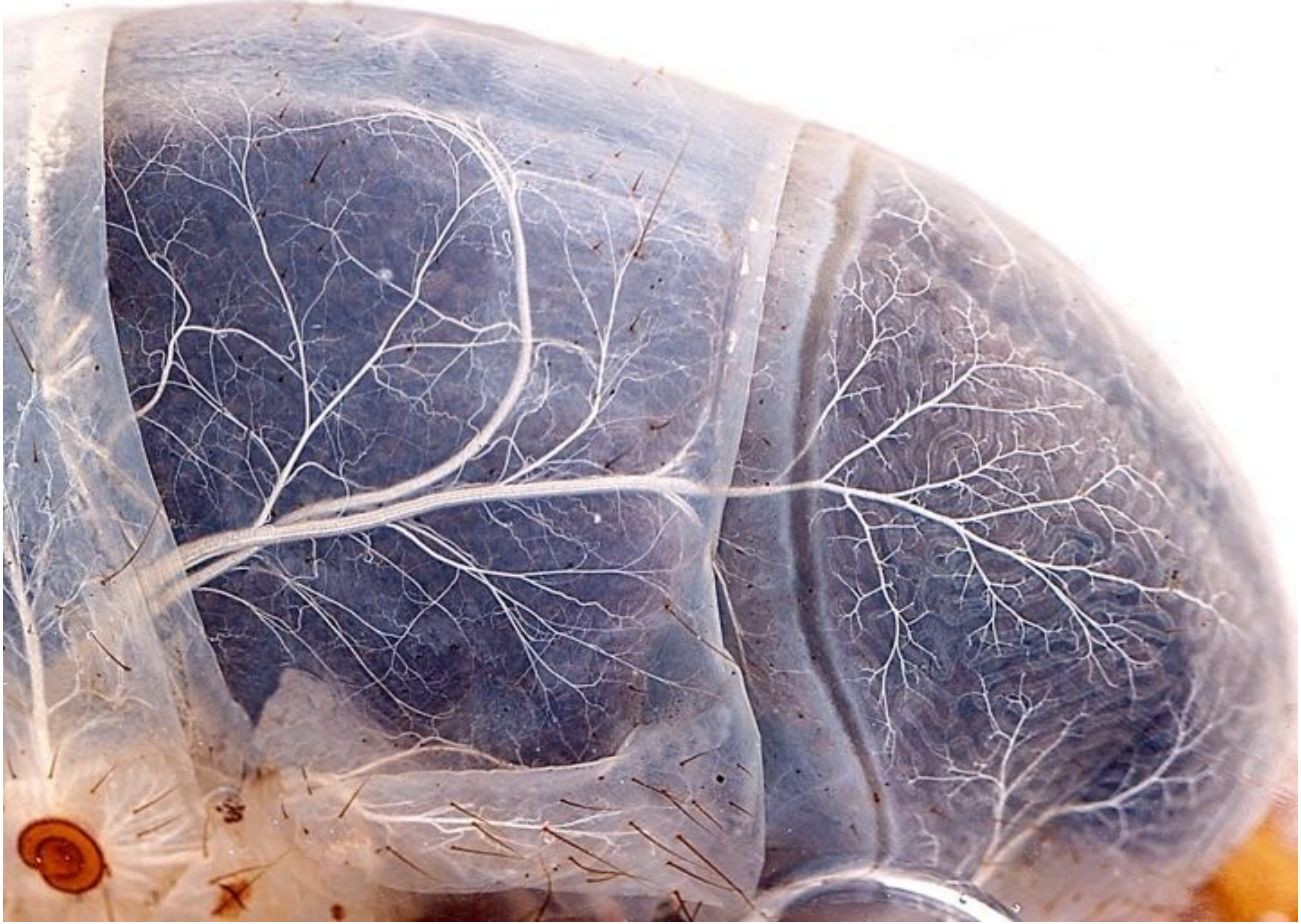
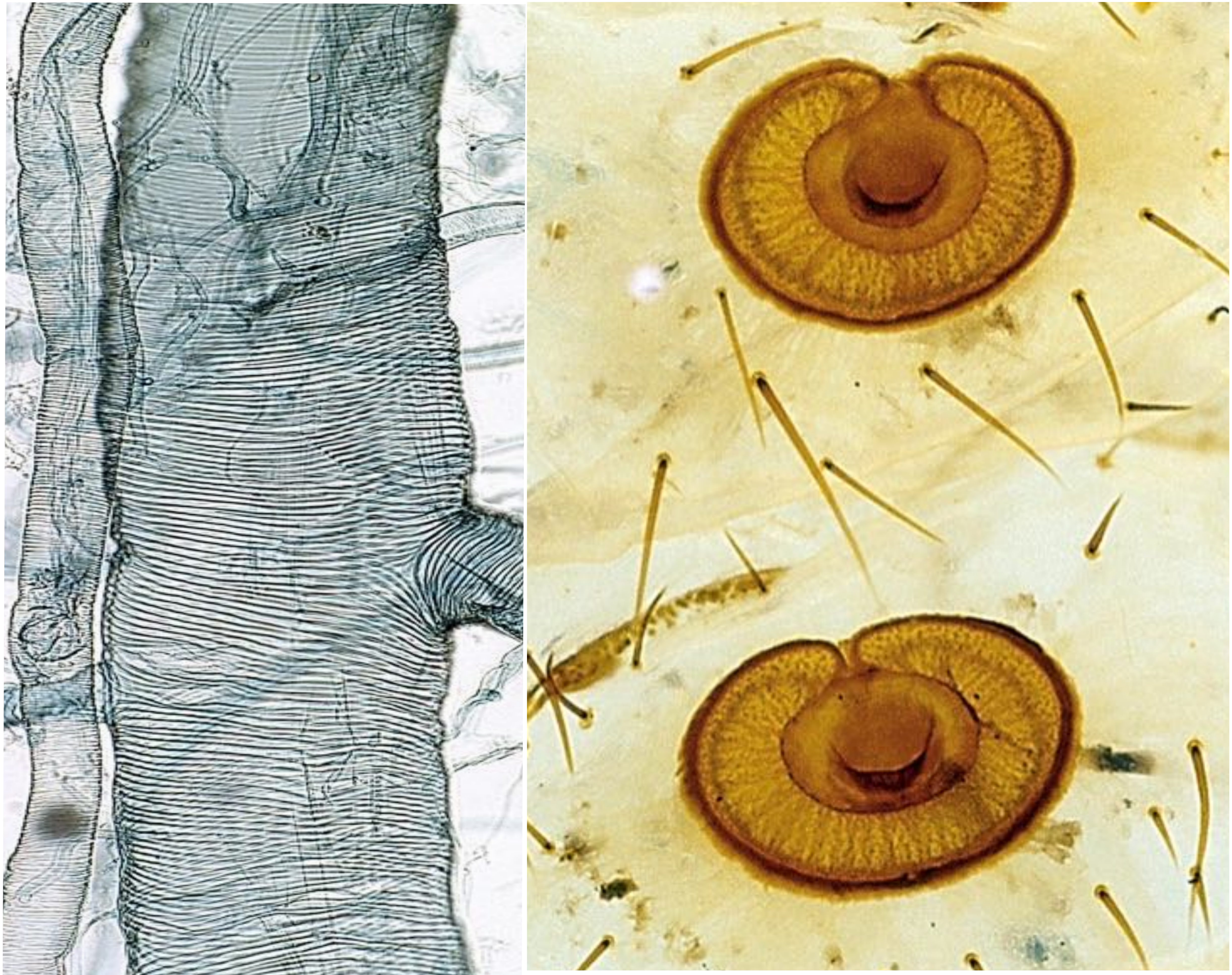


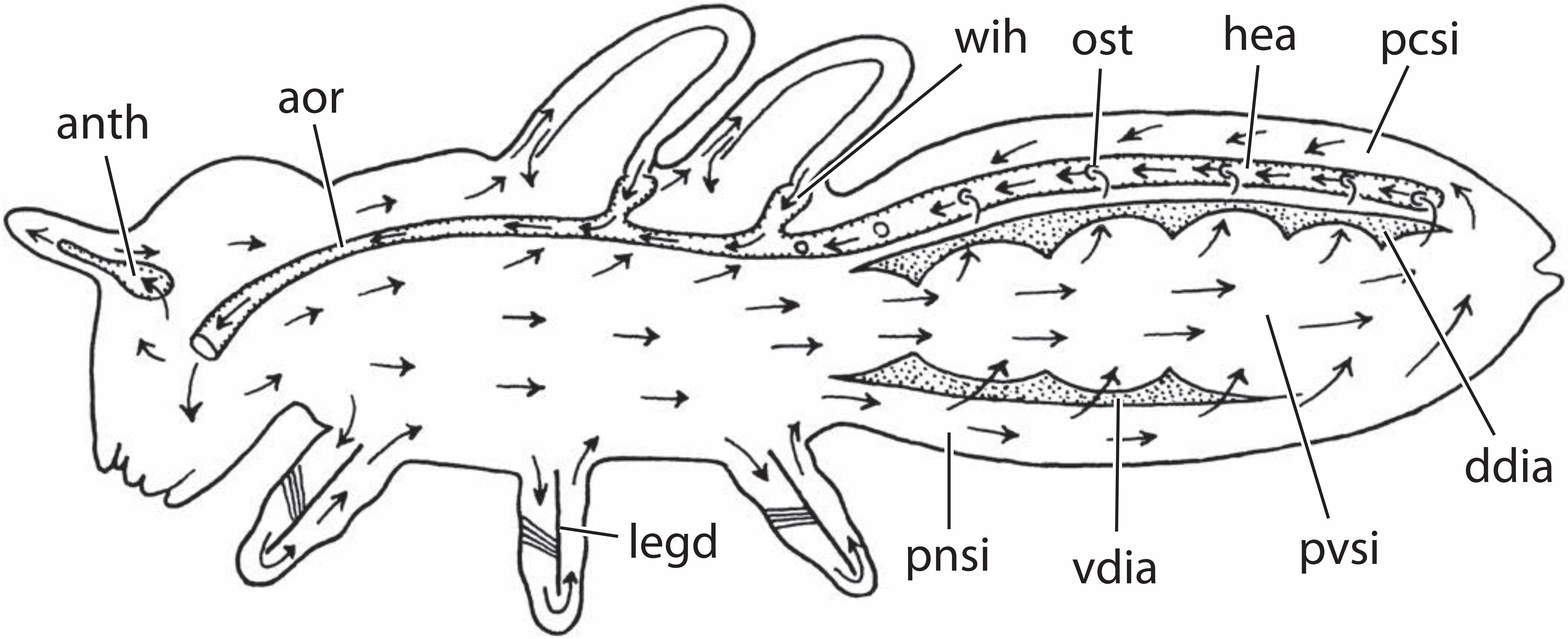
Spiracle. **atr**: atrium, **enc**: endocuticle, **epc**: epicuticle, **exc**: exocuticle, **fiap**: filter apparatus, **petr**: peritreme, **spim**: spiracular mouth, **taen**: taenidium, **valv**: valve.



Distal part of trachea: tracheole and terminal cells. **tec**: terminal cell, **trl**: tracheole.

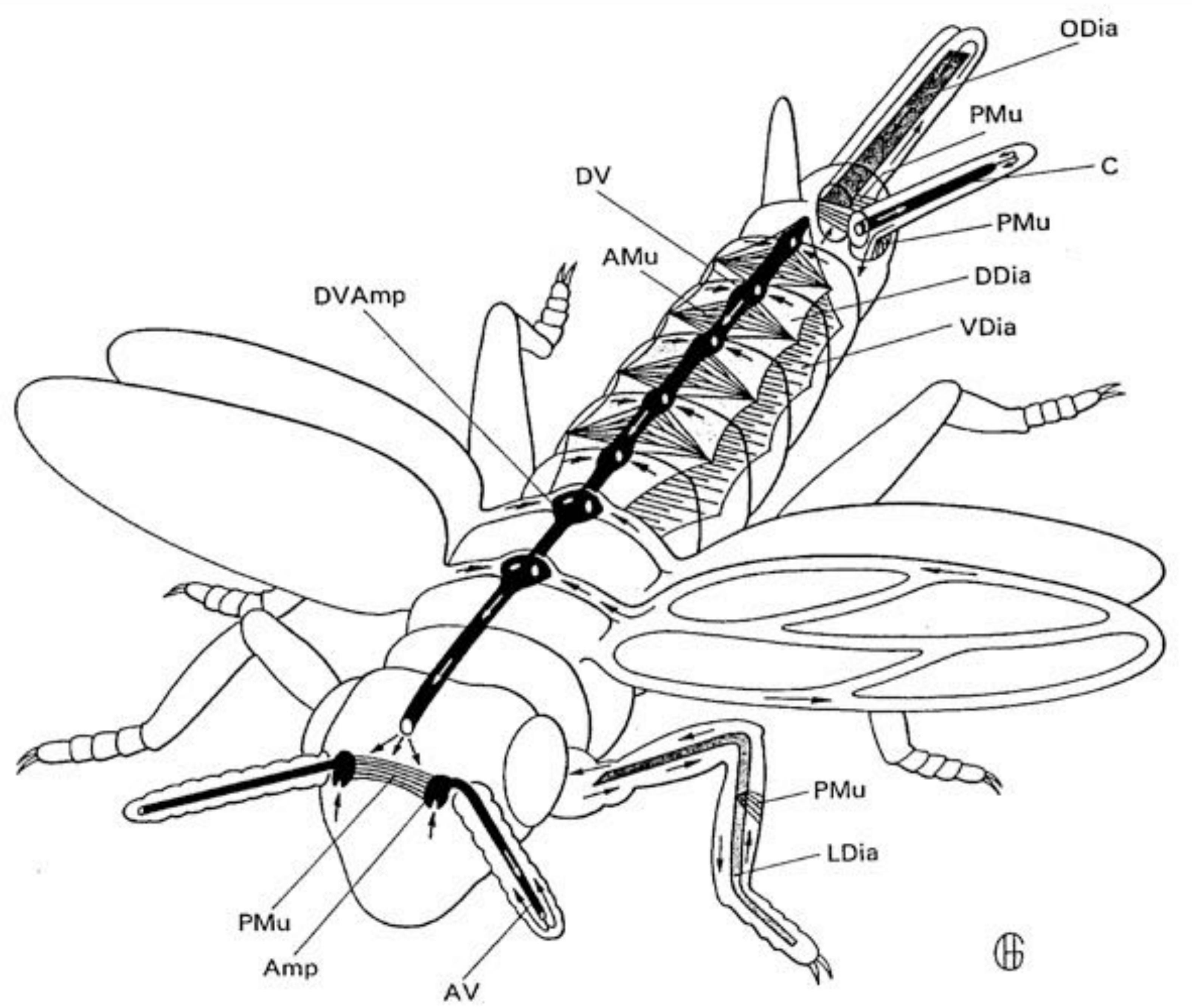






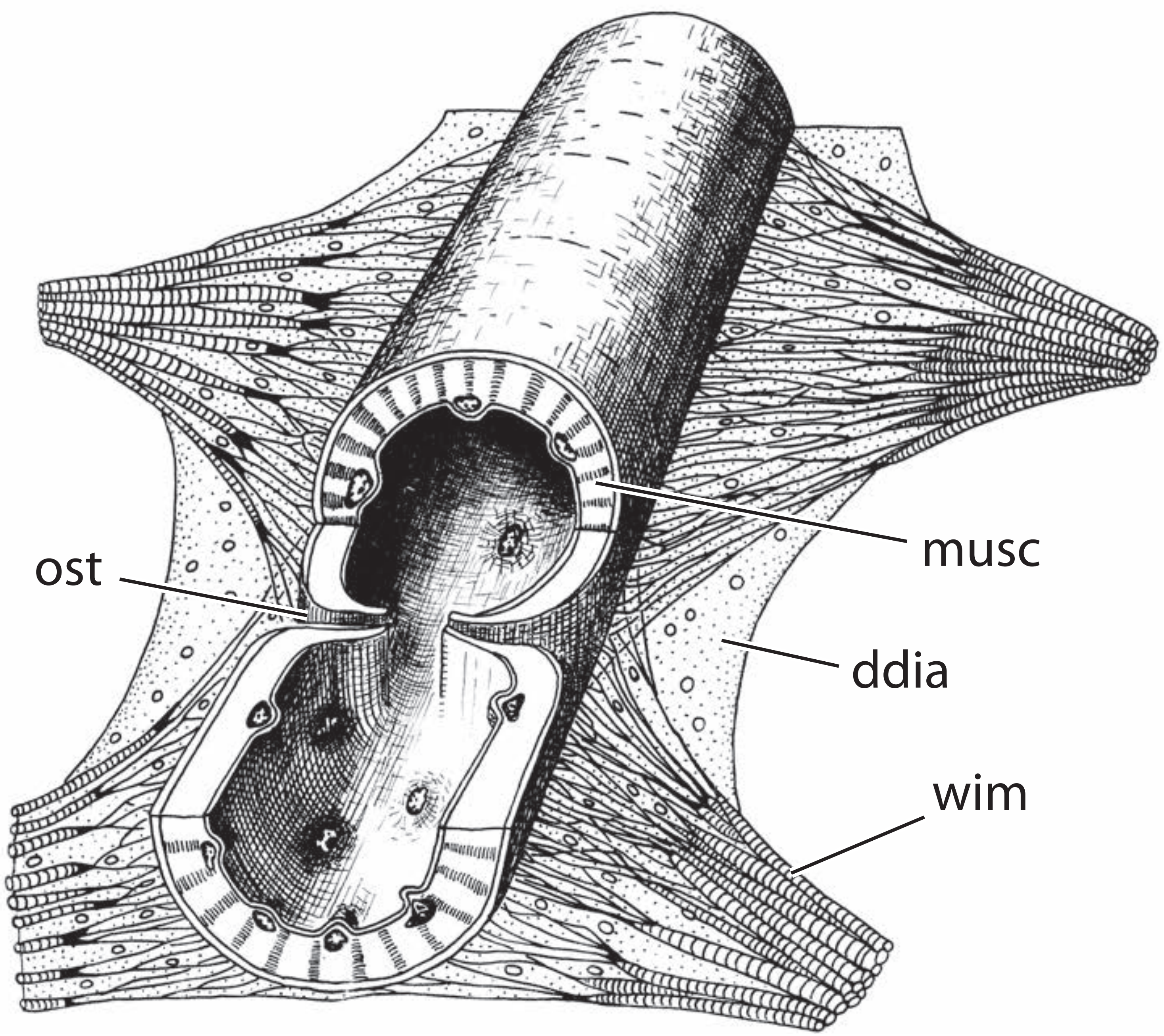
Circulatory system, schematized. **anth**: antennal heart (ampulla), **aor**: aorta cephalica, **ddia**: dorsal diaphragm, **hea**: heart, **legd**: leg diaphragm, **ost**: ostium, **pcsi**: pericardial sinus, **pnsi**: perineural sinus, **pvsi**: perivisceral sinus, **vdia**: ventral diaphragm, **wih**: wing heart.

Insects have an open blood system with the blood occupying the general body cavity, which is known as a hemocoel. Blood is circulated mainly by the activity of a contractile dorsal longitudinal vessel which opens into the hemocoel. The hemocoel is often divided into three major sinuses; a dorsal pericardial sinus, a perivisceral sinus, and a ventral perineural sinus. The pericardial and perineural sinuses are separated from the visceral sinus by the dorsal and ventral diaphragms, respectively. In most insects, the visceral sinus occupies most of the body cavity. The dorsal vessel runs along the dorsal midline, just below the terga, for almost the whole length of the body although in the thorax of adult Lepidoptera and at least some Hymenoptera, it loops down between the longitudinal flight muscles. It may be bound to the dorsal body wall or suspended from it by elastic filaments. Anteriorly it leaves the dorsal wall and is more closely associated with the alimentary canal, passing under the brain just above the esophagus. It is open anteriorly, ending abruptly in most insects, but as an open gutter in orthopteroids. Posteriorly, it is closed, except in larval mayflies (Ephemeroptera) where three vessels diverge to the caudal filaments from the end of the heart. In the honeybee, *Apis*, it forms a spring-like coil in the region of the petiole. The dorsal vessel is divided into two regions: a posterior heart in which the wall of the vessel is perforated by incurrent and sometimes also by excurrent openings (ostia), and an anterior aorta which is a simple, unperforated tube. The heart is often restricted to the abdomen, but may extend as far forwards as the prothorax in cockroaches (Blattodea).

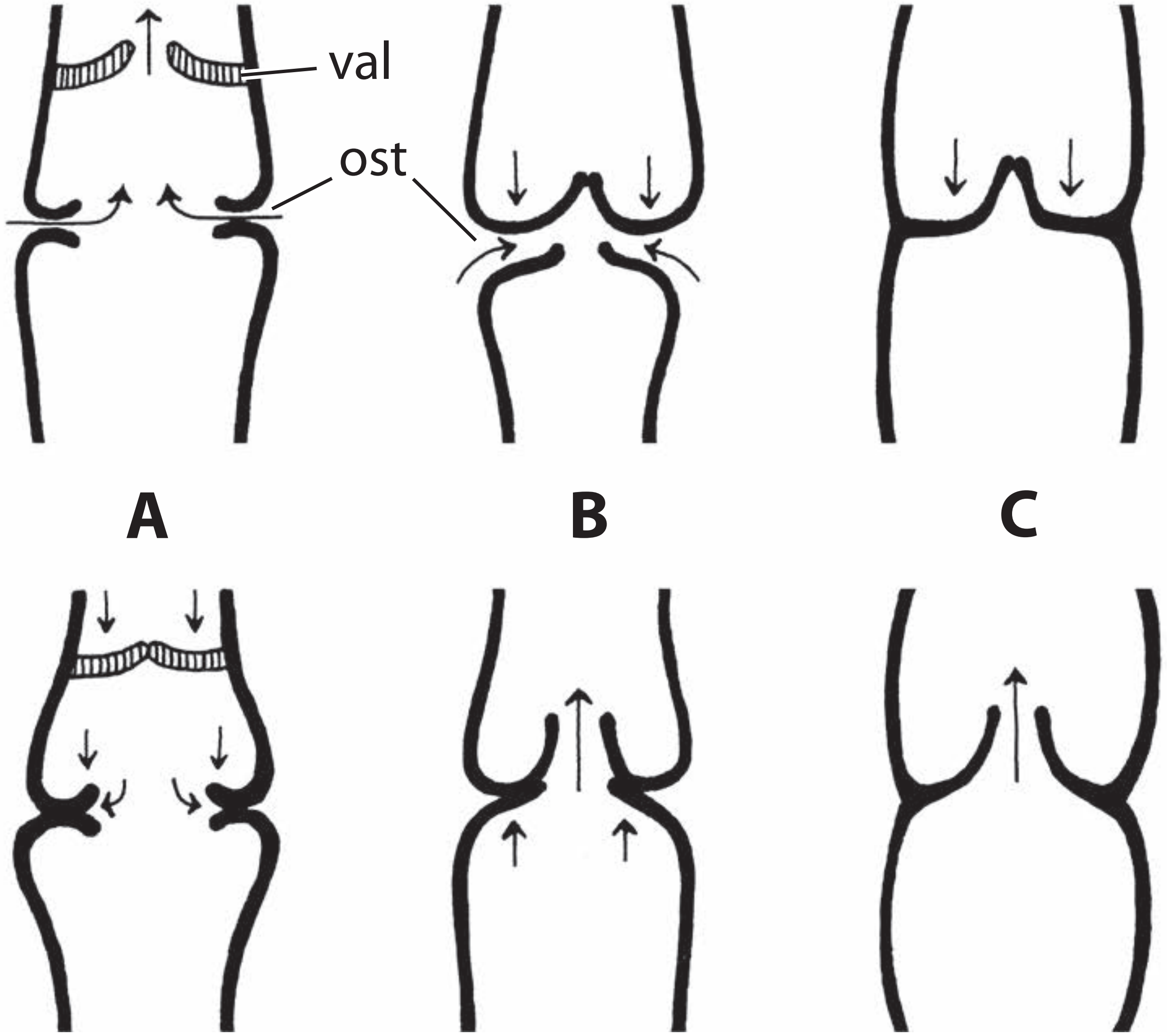


In orthopteroids it has a chambered appearance due to the fact that it is slightly enlarged into ampullae at the points where the ostia pierce the wall. These ampullae are often more prominent in the thorax. In the larvae of dragonflies (Odonata) and the cranefly, *Tipula*, the heart is divided into chambers by valves in front of each pair of incurrent ostia and in some other cases, as in *Cloeon* (Ephemeroptera) larvae, the ostial valves themselves are so long that they meet across the lumen.

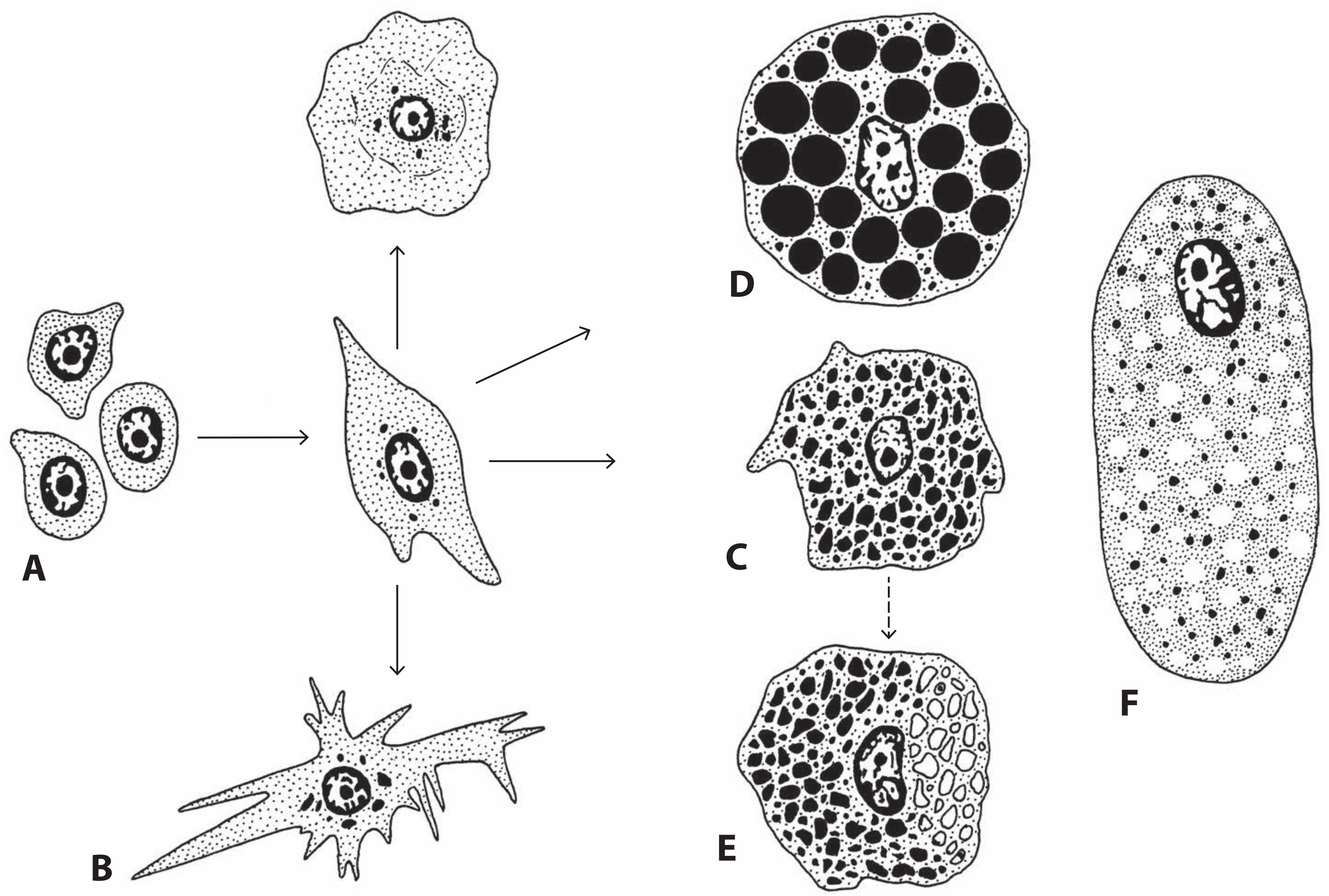
The wall of the dorsal vessel is contractile and usually consists of one or two layers of muscle cells with a circular or spiral arrangement. Longitudinal muscle strands are also present, in Heteroptera, inserting into the wall of the vessel anteriorly and posteriorly; they do not connect with other tissues. The muscles of the heart are sometimes oriented in many different directions, but this appearance may arise through the insertion of the alary muscles into the heart.



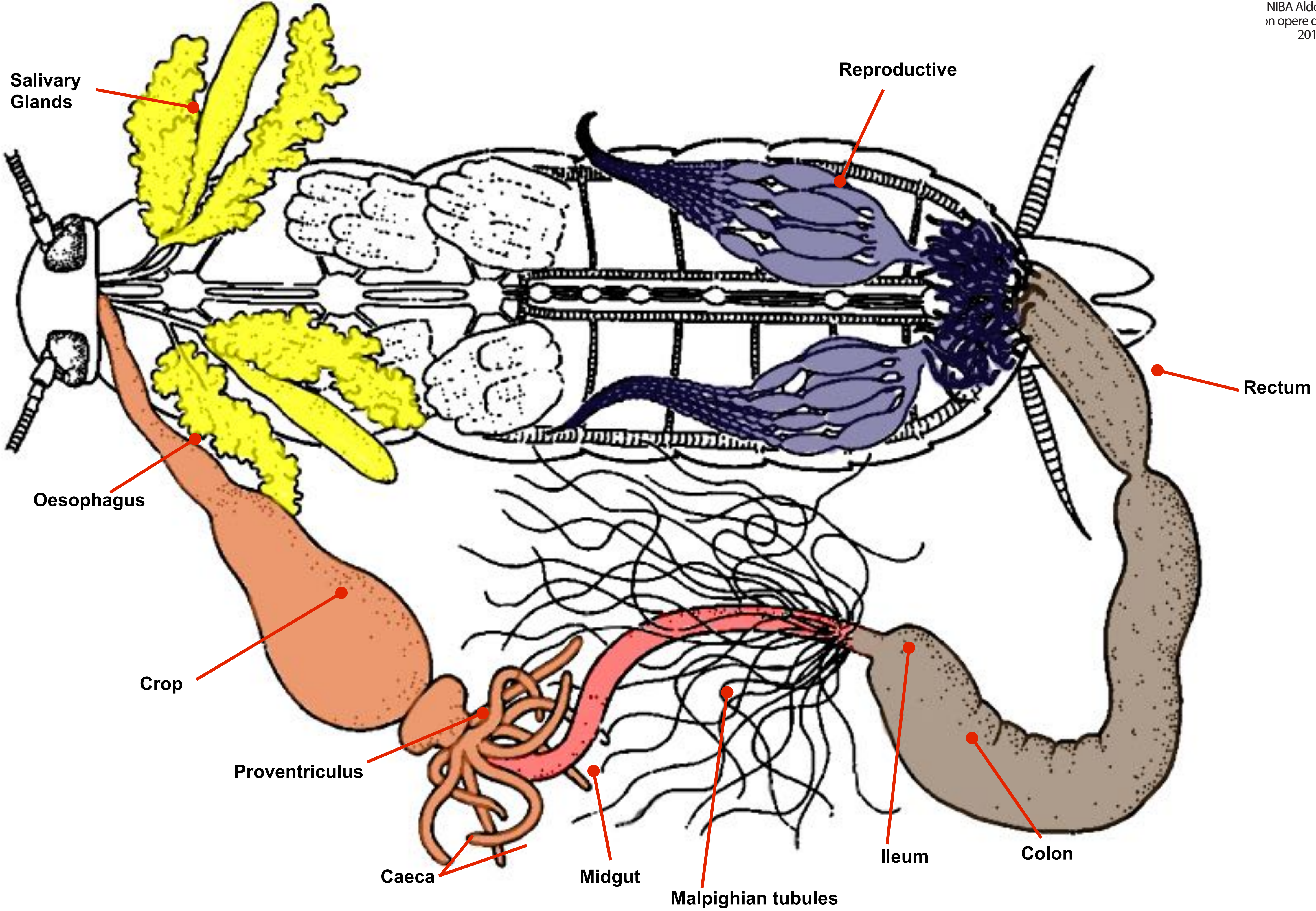
Heart, dorsolateral view, partly opened horizontally. **ddia**: dorsal diaphragm, **musc**: muscularis, **ost**: ostium, **wim**: wing muscles.



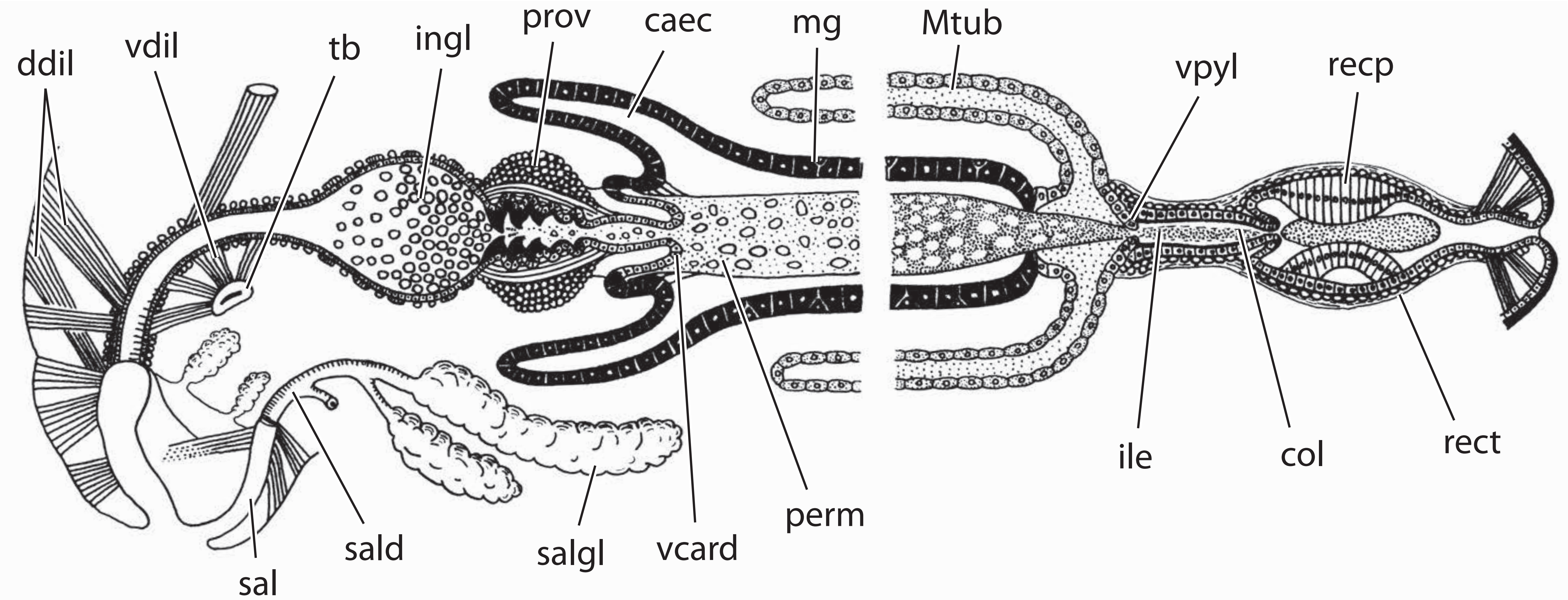
Heart with valves and flow of haemolymph (A–C), schematized. **ost**: ostium, **val**: valve.



Haemolymph cells. A, prohaemocytes; B, plasmatocyte; C, granulocyte; D, sphaerulocyte; E, cystoctyte; F, oenocytoid.

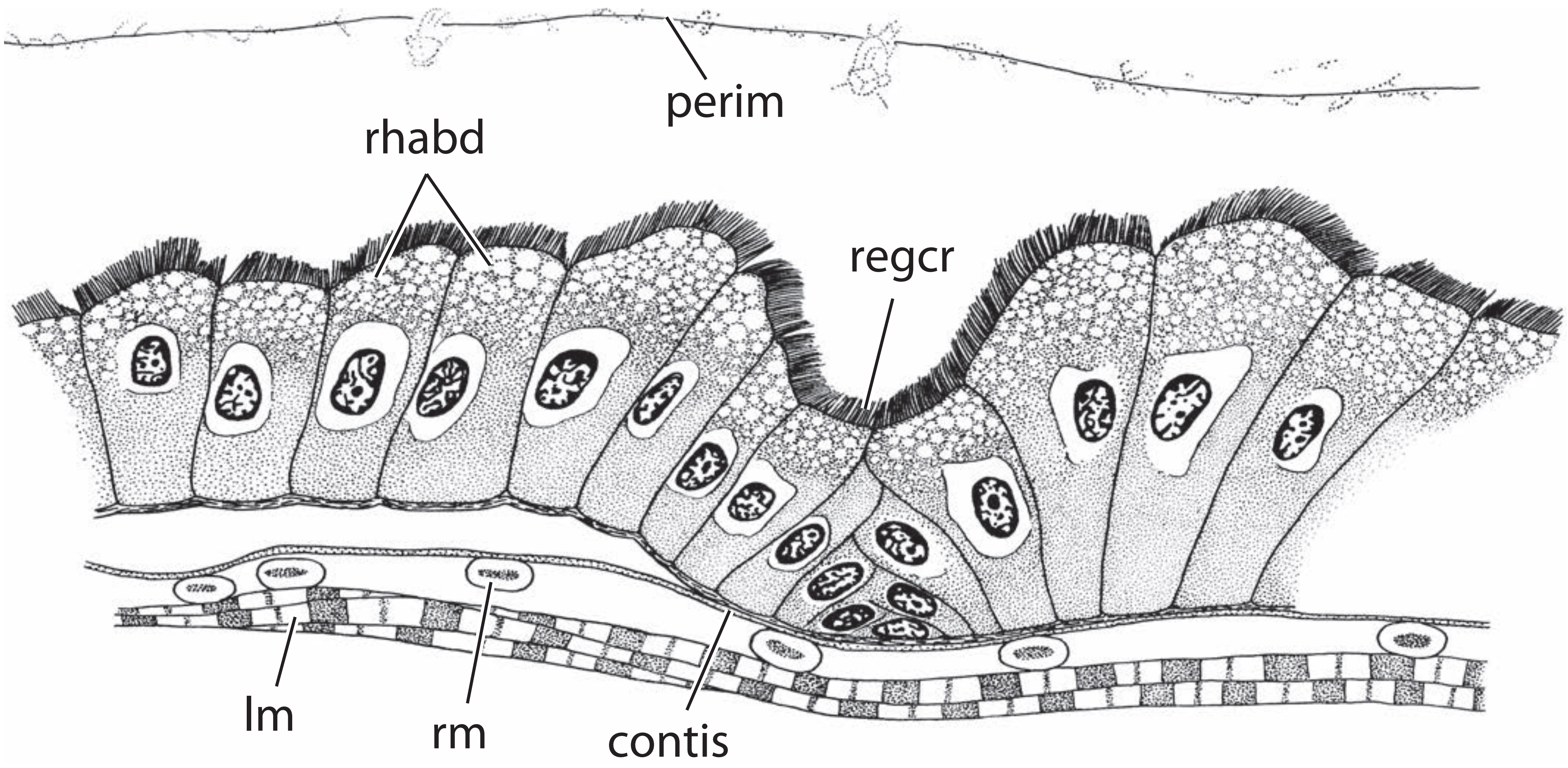


The alimentary canal of insects is divided into three main regions: the foregut, or stomodeum, which is ectodermal in origin; the midgut, or mesenteron, which is endoermal; and the hindgut, or proctodeum, which again is ectodermal. The epithelium of all parts of the gut consists of a single layer of cells. Since the foregut and hindgut are ectodermal in origin, the cells secrete cuticle which is continuous with that covering the outside of the body. The lining cuticle is known as the intima. It is shed and renewed at each molt. Although the midgut does not secrete cuticle, in most insects it does secrete a delicate peritrophic envelope around the food. Usually the gut is a continuous tube running from the mouth to the anus, but in some insects that feed on a fluid diet containing little or no solid waste material the connection between the midgut and the hindgut is occluded. This is the case in some plant-sucking Heteroptera, where the occlusion is between different parts of the midgut, and in larval Neuroptera which digest their prey extraorally. A similar modification occurs in the larvae of social Hymenoptera with the result that the larvae never foul the nest. In these insects a pellet of fecal matter is deposited at the larva–pupa molt.



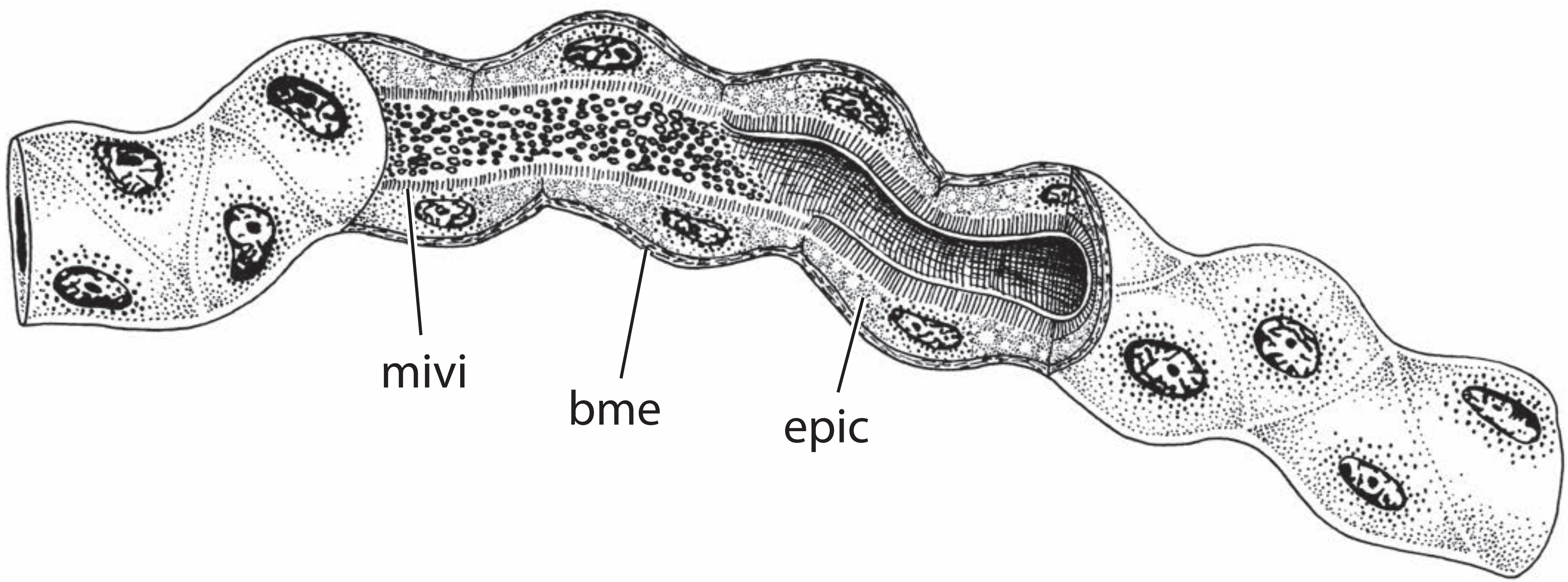
Digestive tract

The digestive tract of hexapods is divided into three main sections with a different ontogenetic origin. The foregut and the hindgut are formed by the ectoderm and therefore coated by an intima, whereas the midgut is of entodermal origin. The epithelium is single-layered. Its external basal lamina is thickened in some groups and then referred to as membrana propria or tunica. It is enclosed by a muscularis formed by circularly arranged fibers (external layer) and longitudinal fibers (internal layer).



Midgut

The border between the ectodermal foregut and the entodermal midgut is clearly marked by the absence of an intima in the latter, by the valvula cardiaca, a ring-shaped fold functioning as a valve, and in some groups by the insertion of a group of more or less extensive midgut caeca, which enlarge the surface of the area involved in secretion and resorption. The caeca can be short papillae or elongate tubes and the number varies between one pair and up to 30. The epithelium is similar to that of the remaining midgut and the main functions are likely surface enlargement and secretion of hydrolases. The midgut is usually distinctly shorter than the foregut. The cells are cuboidal or cylindrical (columnar) and apically lined by microvilli, which greatly enlarge the surface oriented towards the gut lumen (rhabdorium, brush border). Externally a basement membrane is present and a very thin muscularis. Midgut cells are regularly discarded and replaced. The undifferentiated replacement cells lie at the base of the epithelium without contact to the lumen. Sometimes they form large groups, regenerative crypts, which can penetrate the basement membrane and muscularis and reach into the mixocoel.
The secretion is usually apocrinous or merocrinous, but in some cases entire cells disintegrate (holocrinous secretion). The enzymatically digested food is resorbed by way of endocytosis between the microvilli of the midgut cells, usually between cycles of secretion, but in some cases also by specialized non-secretory cells. Another function of the midgut is to metabolize resorbed substances before they are released to the haemolymph (e.g., 20-hydroxy-ecdysone).
The vulnerable midgut epithelium is usually protected by a peritrophic membrane, which is in fact not a membrane but a dense netting of thin cuticular fibrillae. It is continuously produced at the posterior foregut border and dismantled at the posterior end of the midgut by the valvulae pylorica. It can be absent in groups exclusively feeding on fluids. The main functions of the midgut are secretion of digestive enzymes and resorption of food between the microvilli. The active form of ecdysone (20-hydroxy-ecdysone) is also occasionally produced by midgut cells. The hind border is marked by the valvula pylorica and the insertion of the Malpighian tubules.



Excretory organs

Metabolic waste products such as urates can be stored to a certain degree in specific cells of the fat body. Labial glands or midgut cells can be involved in the excretion process and the rectum plays an important role in osmoregulation. However, the Malpighian tubules are clearly the main excretory and osmoregulatory organs. They play an essential role in removing nitrogenous waste from the haemolymph.

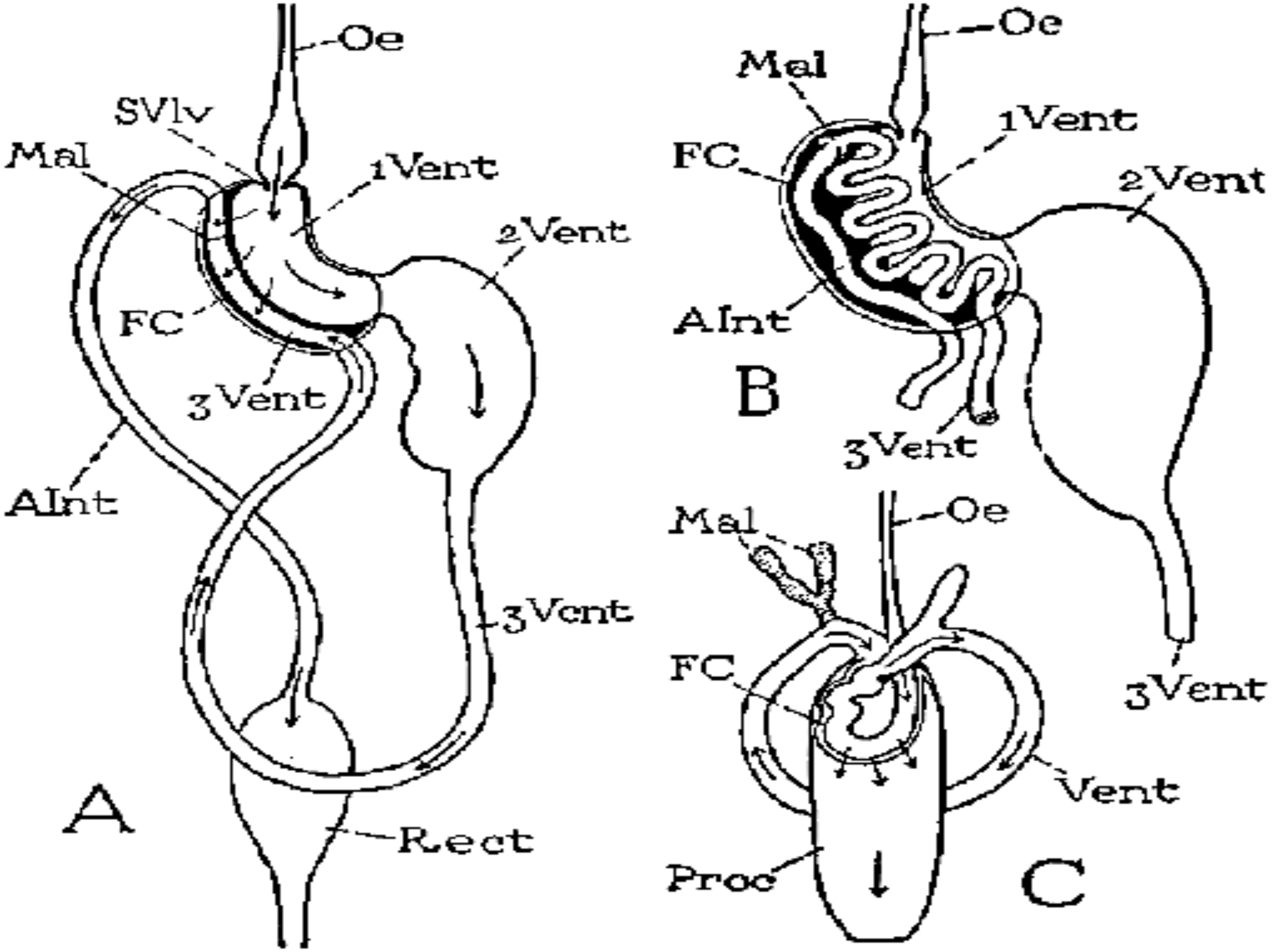
It is disputable whether the Malpighian tubules belong to the groundplan of Hexapoda as they are completely missing in Collembola and aphids and only present as short papillae in Protura and Diplura (partim, missing in Japyx). The number varies strongly between the orders. Ten or 12 are present in Archaeognatha and usually 4–8 in Zygentoma. High numbers occur in some polyneopteran groups (ca. 100 in Mantodea and roaches) and ca. 50 are present in some groups of Hymenoptera. A low number (4–8) is characteristic for Acercaria and Holometabola.

The Malpighian tubules of Insecta are more or less thin, tube-like structures originating from the pylorus at the midgut-hindgut border. They are usually unbranched and floating freely in the haemolymph. The apical parts are branched, inflated or connected pairwise in few groups. The single-layered epithelium is similar to that of the midgut. Often two cell types occur, primary cells and stellate cells. A basement membrane covers the external (basal) surface of both types and the internal (apical) surface is covered by microvilli (rhabdorium) as it is the case in the midgut. The distribution and density can vary in different regions and is often lower and more scattered in the case of the stellate cells. An additional surface enlargement is caused by multiple folds of the basal cell membrane, the basal labyrinth.

The passage of excretion products from the haemolymph to the lumen of the Malpighian tubules is partly a passive diffusion (urea, amino acids) but active pumping mechanisms using adenosine triphosphate (ATP) are also involved. ATP is produced by numerous mitochondria in the folds of the basal labyrinth. Clear pre-urine is formed in the distal area of the tubules. Concrement vacuoles are produced by the endoplasmatic reticulum of the cells and are concentrated in the proximal region of the tubules. The cells of the proximal regions re-absorb water from the lumen which likely results in the formation of crystals of uric acid and other substances. A basal ampulla lacking typical microvilli is present in different groups. Its elongated cells are extend into the lumen of the pylorus and are also involved in the water re-absorption.

The excretions of most hexapods mainly consist of uric acid, but they can also contain ammonia (mainly aquatic insects and carnivorous flies), urates, urea, pteridines, amino acids, hypoxanthine, allantoin and allantoic acid. The rectal papillae play an important role in the water re-absorption before the waste is deposited via the anus.

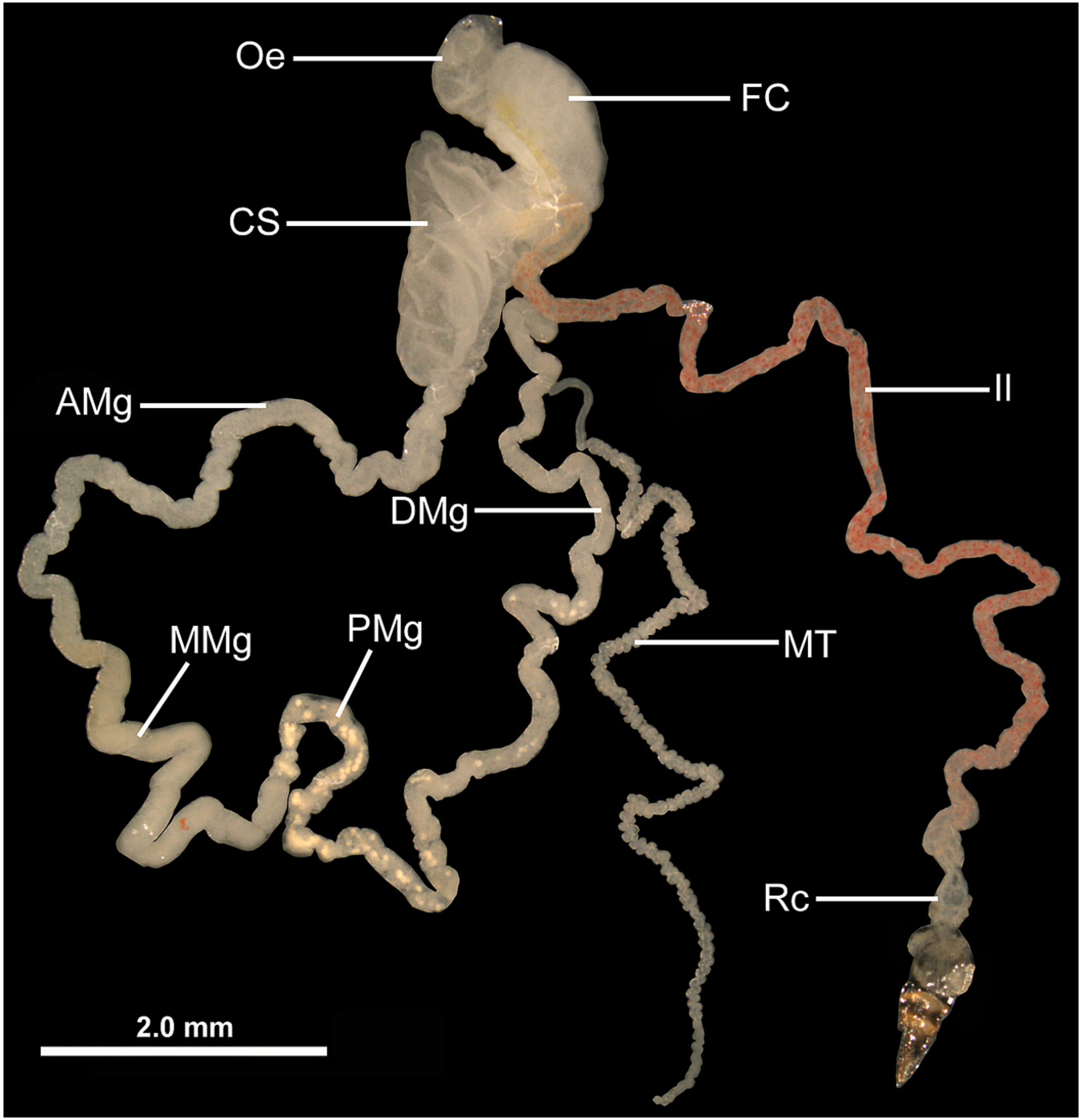
Filter chambers



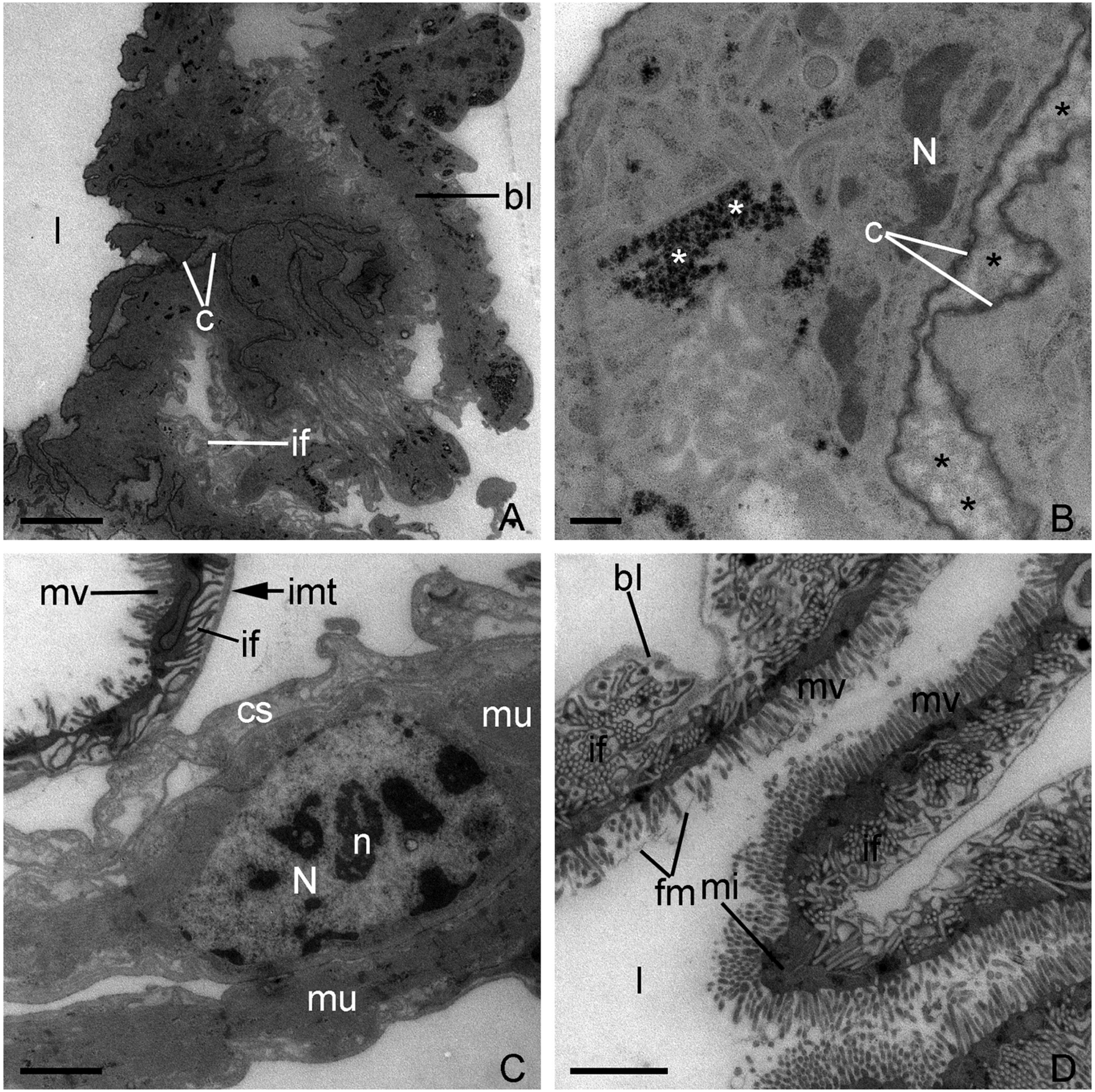
As plant material is not generally very nutritious, having at most 4% of its dry weight as nitrogen, there are two options open to herbivorous bugs. They can consume large volumes or grow slowly. The sap of phloem vessels, fed on by the great majority of herbivorous bugs, usually contains much less than 0.5% weight to volume of soluble nitrogen, but up to 9 or 10% weight to volume of sugars. Xylem sap, fed on by cicadas, froghoppers, and some leafhopper species, is even poorer in nutrients than phloem sap, and some bugs that specialize on this diet may take anything from several months to many years to complete their nymphal development.

A modification of bug's guts seen in many sap suckers, such as the Cicadidae, Cercopidae, some Cicadellidae, and virtually all the coccoid families, is the filter chamber, formed by the intimate association of epithelial tissues from the rear of the midgut or front of the hindgut with those of the anterior foregut. This allows large amounts of water and low molecular weight molecules to bypass the midgut entirely and pass straight into the rectum while the rest of the food carries on through the midgut to be processed more efficiently.

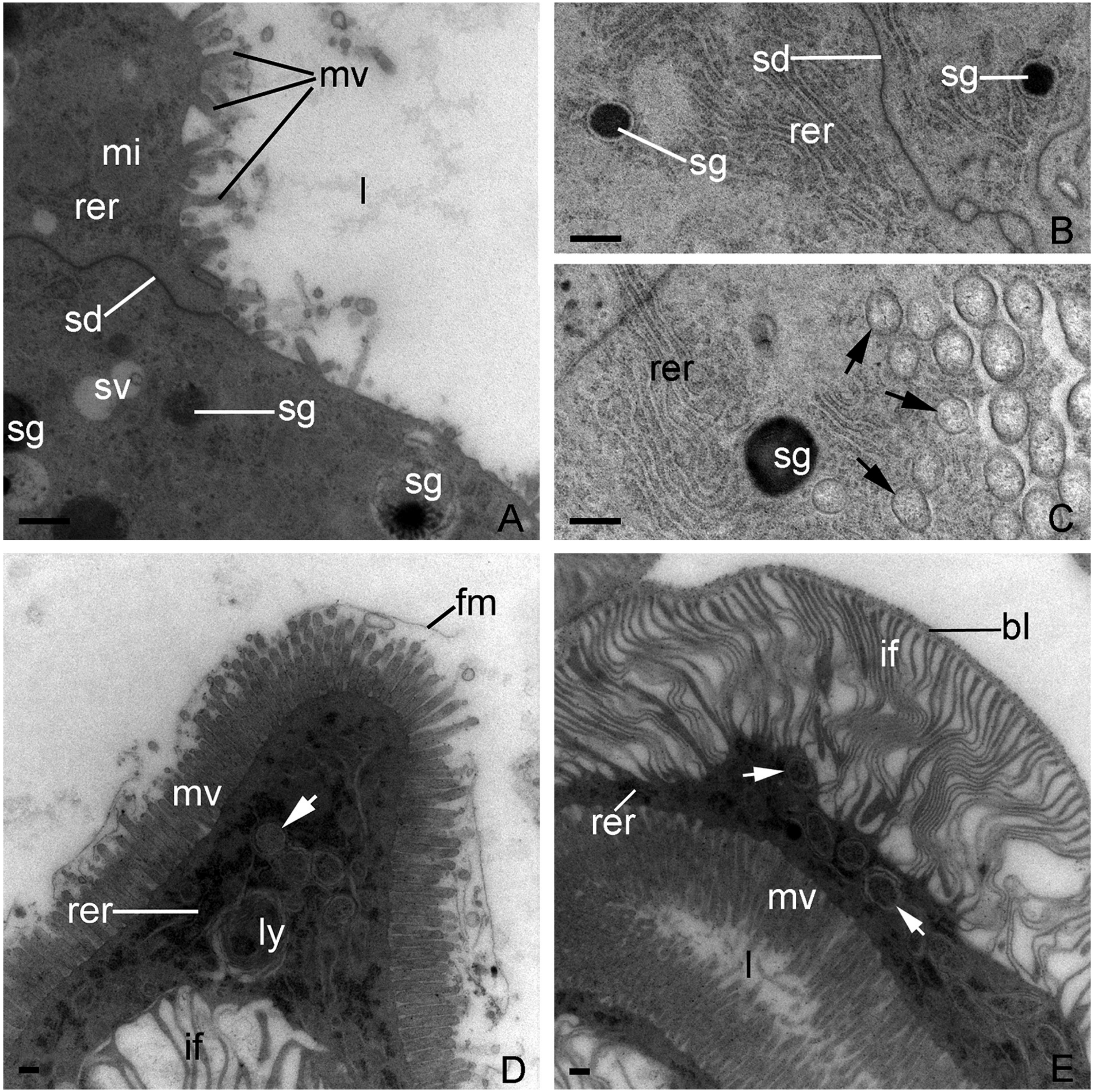
Some heteropteran bugs rely on symbiotic microorganisms to provide them with essential nutrients, and these may be contained within special bodies in the haemocoel or inside the lumen of the midgut. In blood feeding species, bacteria are responsible for providing the bugs with B vitamins. However, auchenorrhynchan and sternorrhynchan bugs, that feed generally on a diet low in nutrients, are especially well known for their bacterial (Proteobacteria) symbionts, which are contained inside special cells called mycetocytes. The myctetocytes, which may be aggregated into bodies known as mycetomes, are free in the haemolymph of the body cavity or associated with the fat body. The symbionts are important in the recycling of nitrogen, providing their hosts with vitamins, certain essential amino acids, such as tryptophan, which are absent from the diet, and certain lipids, such as the sterols, which insects are unable to manufacture for themselves and are vital to the production of the insect moulting hormone, ecdysone. The symbionts of a few bug groups have been examined. Aphid symbionts belong to the Buchnera aphidicola.complex and these differ from those seen in whiteflies or scale insects. The success and radiation of sap feeding auchenorrhynchan and sternorrhynchan bug was made possible by the acquisition of bacterial symbionts.



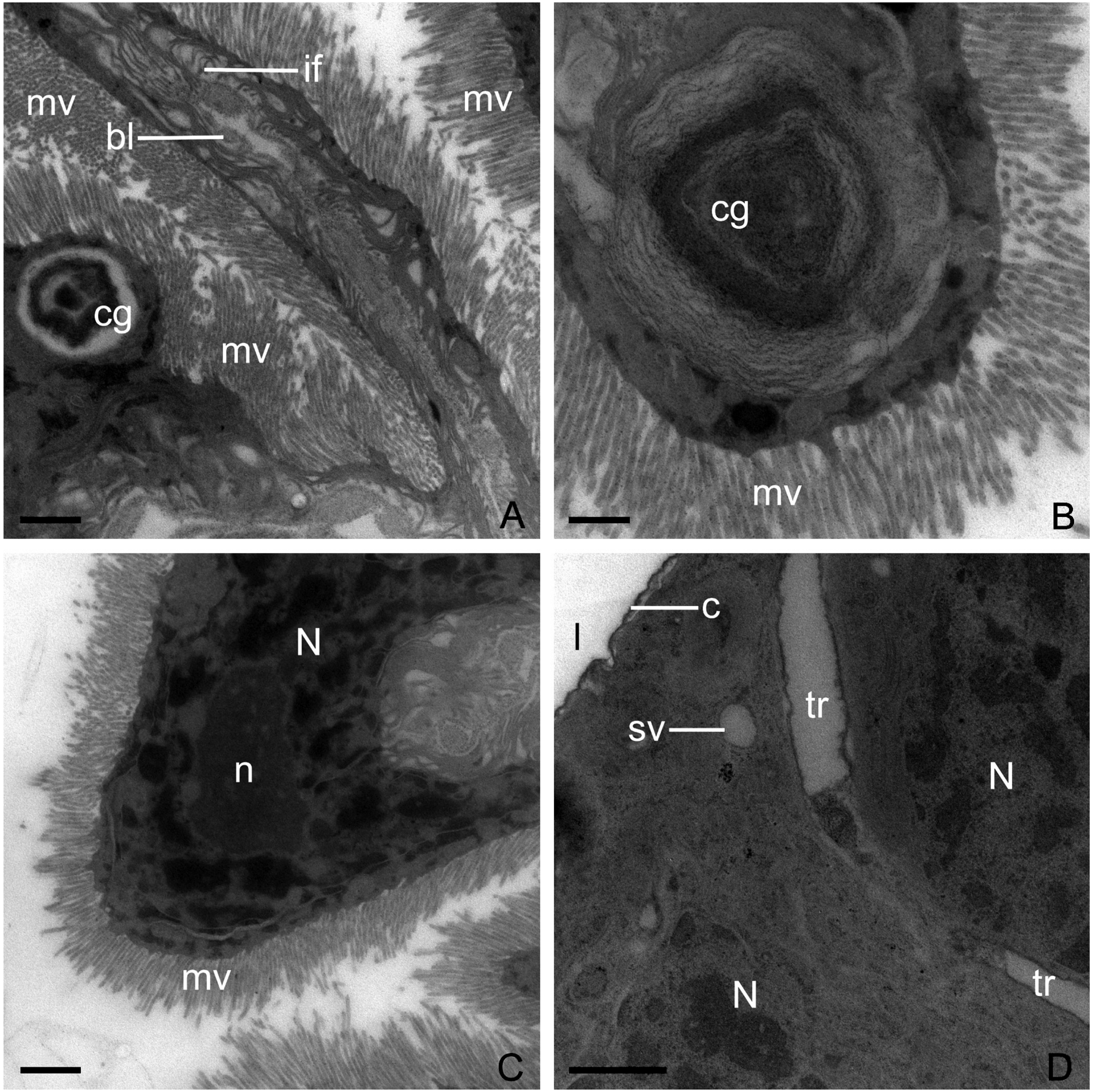
General structure of alimentary canal of *Lepyronia coleopterata*, with one Malpighian tubule left and the other three tubules removed. **AMg**, anterior tubular midgut; **CS**, conical segment; **DMg**, distal tubular midgut; **FC**, filter chamber; **Il**, ileum; **MMg**, mid-midgut; **MT**, Malpighian tubule; **Oe**, esophagus; **PM**g, posterior tubular midgut; **Rc**, rectum.



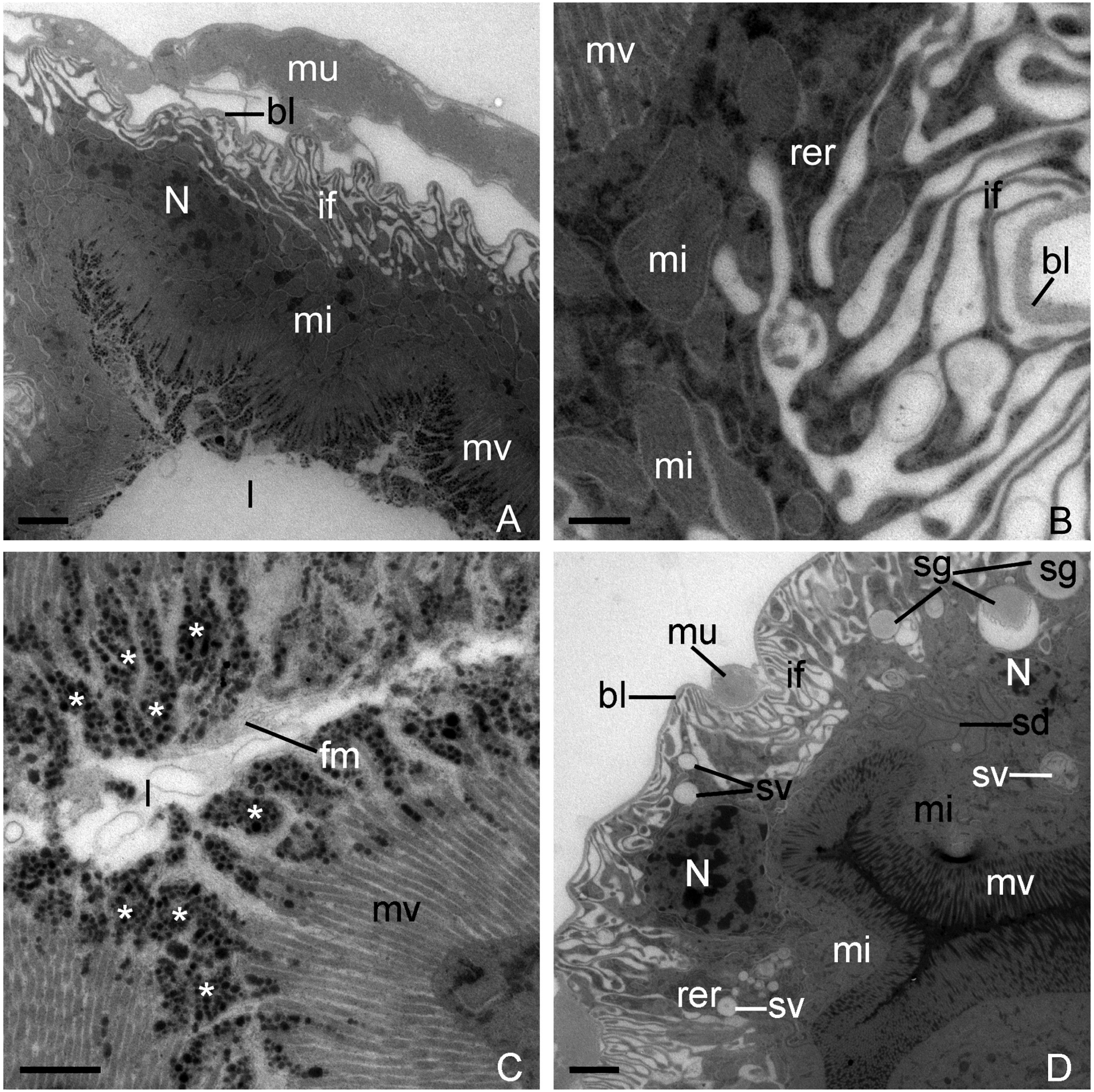
Transverse section of esophagus lined with a convoluted cuticle (c) facing the lumen (l), thick basal lamina (bl) and basal infoldings (if) are also visible. (B) Detail of the cytoplasm of the esophagus, with aggregations of virus-like fine granules (white asterisks), a thick cuticle (c) and elongate nuclei (N). Secretions (black asterisks) exist in the lumen. (C) Cells of cellular sheath (cs), which are externally surrounded by well-developed circular muscles (mu) containing nuclei (N) with evident nucleoli (n). Basal infoldings (if) and apical microvilli (mv) of the cells of the proximal Malpighian tubule (imt) (arrow) are also obvious. (D) Transverse section of the anterior extremity of the midgut. Filamentous materials (fm) coat the apical microvilli (mv) facing the lumen (l). Basal infoldings (if) cytoplasm. bl, basal lamina. Scale bars: 5.0 mm in (A); 0.5 mm in (B); 2.0 mm in (C, D).



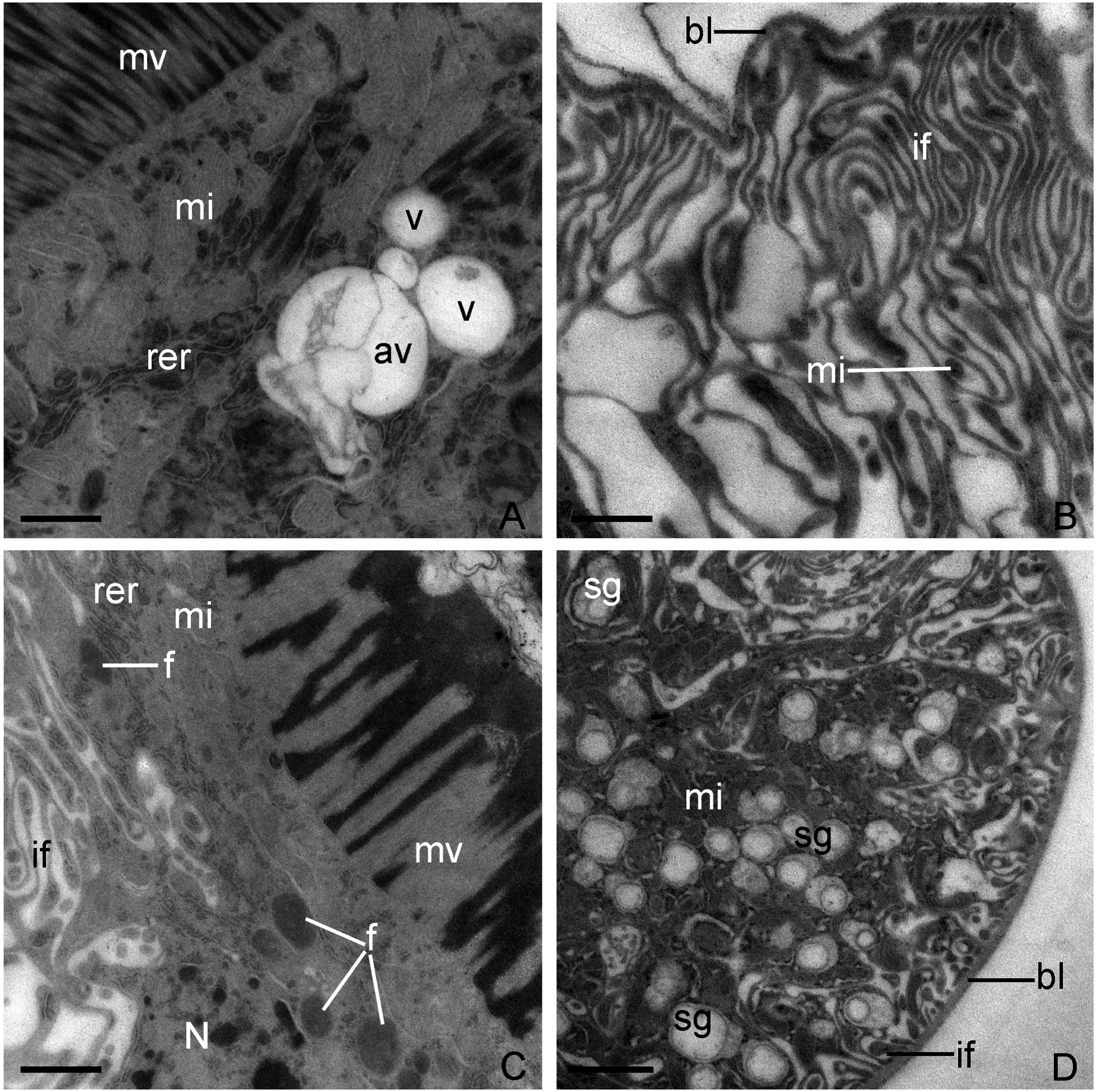
The apical region of the large cuboidal cells of the anterior extremity of the midgut (filter chamber proper). Rough endoplasmic reticulum (rer), septate desmosomes (sd), mitochondria (mi), sparse microvilli (mv), secretory vesicles (sv), and electron-dense secretory granules (sg) are visible. (B) Cytoplasm of the large cuboidal cells of the anterior extremity of midgut (filter chamber proper) contains extensive rough endoplasmic reticulum (rer) and secretory granules (sg) of electron-dense center and electron-lucent pe- riphery. (C) Large cuboidal cells of the anterior extremity midgut (filter chamber proper), showing extensive rough endoplasmic reticulum (rer), electron-dense secretory granules (sg) and microorganisms (arrows). (D) Transverse section of the posterior extremity of the midgut. Regularly-arranged microvilli (mv) are evident. Filamentous materials (fm) cover the apex of apical microvilli. Basal plasma membrane invaginates into wide infoldings (if). The cytoplasm contains microorganisms (arrow), lysosome-like structures (ly) and rough endoplasmic reticulum (rer). (E) Transverse section of the proximal Malpighian tubule, showing well-developed and regularly-arranged basal infoldings (if) and apical microvilli (mv). Scattered rough endoplasmic reticulum (rer) and microorganisms (arrows) are also seen in the cytoplasm. bl, basal lamina; l, lumen; Scale bars: 0.5 mm in (A, B, C); 0.2 mm in (D, E).



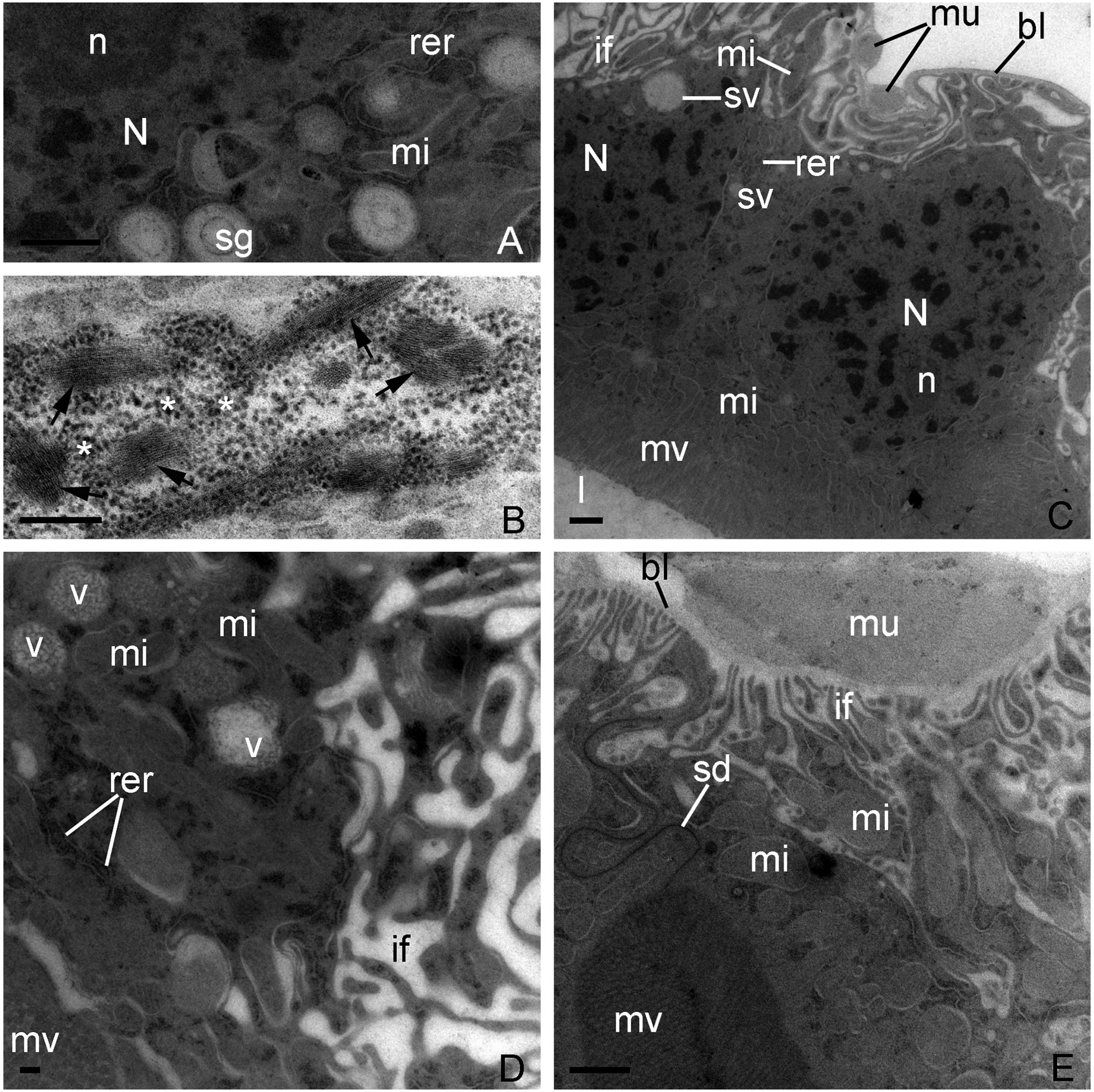
Transverse section of the proximal Malpighian tubule, showing concentric granules (cg) with different electron-density from the center to the periphery. (B). Apical area of the cells of the proximal Malpighian tubule. Concentric granules (cg) with filamentous periphery are shown. (C) Cells of the proximal Malpighian tubule contain large nuclei (N) with evident nucleoli (n). The apical microvilli (mv) are dense and long. (D) The internal proximal ileum is lined with a layer of cuticle (c) facing the lumen (l), and its cytoplasm contains large nuclei (N) and secretory vesicles (sv). Tracheoles (tr) are well-developed and penetrate into the plasma membrane. bl, basal lamina; if, infoldings of the basal plasma membrane; mi, mitochondria. Scale bars: 1.0 mm in (A, C); 0.5 mm in (B); 2.0 mm in (D).



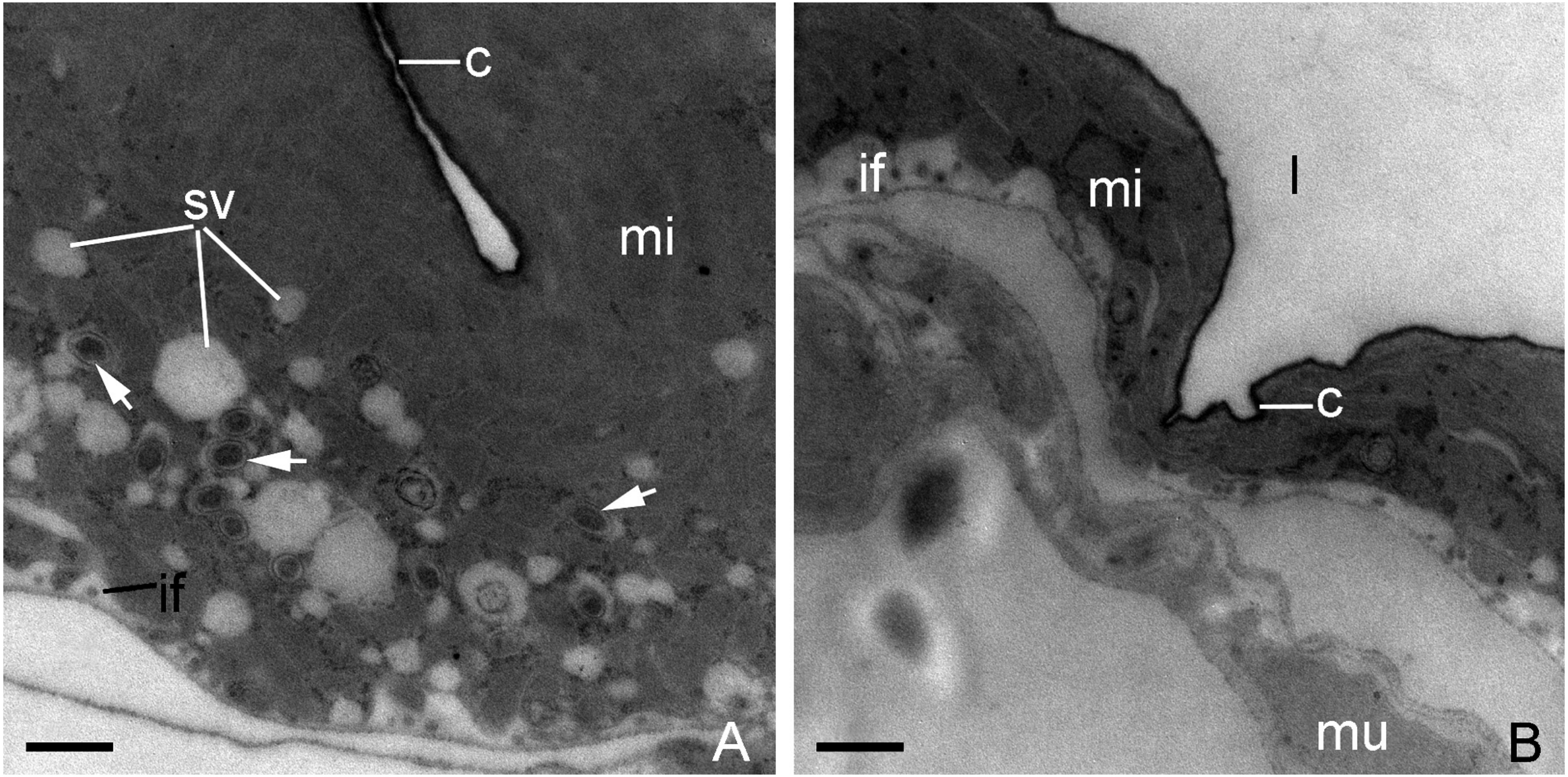
Transverse section of the conical segment, showing well-developed circular muscles (mu) that envelope the cells, which have well-developed basal infoldings (if) and dense microvilli (mv). Nuclei (N) and abundant mitochondria (mi) are observed in the cytoplasm. (B) High magnification of the basal area of the conical segment cells. Basal plasma membrane invaginates into wide infoldings (if) extending to scattered rough endoplasmic reticulum (rer). Mitochondria (mi) of different shapes exist among the rough endoplasmic reticulum. (C) High magnification of the apical region of the conical segment cells. Filamentous materials (fm) and abundant electron-dense fine granules (asterisks) cover the apex of apical microvilli (mv). (D) Transverse section of the anterior tubular midgut. Cells with well-developed basal infoldings (if) contain abundant mitochondria (mi). Secretory vesicles (sv) and secretory granules (sg) are also evident in the cytoplasm. Microvilli (mv) are dense and regularly-arranged. Nuclei (N) and rough endoplasmic reticulum (rer) scatter in the cytoplasm. l, lumen; mu, muscles; bl, basal lamina; sd, septate desmosomes. Scale bars: 2.0 mm in (A, D); 0.5 mm in (B); 1.0 mm in (C).



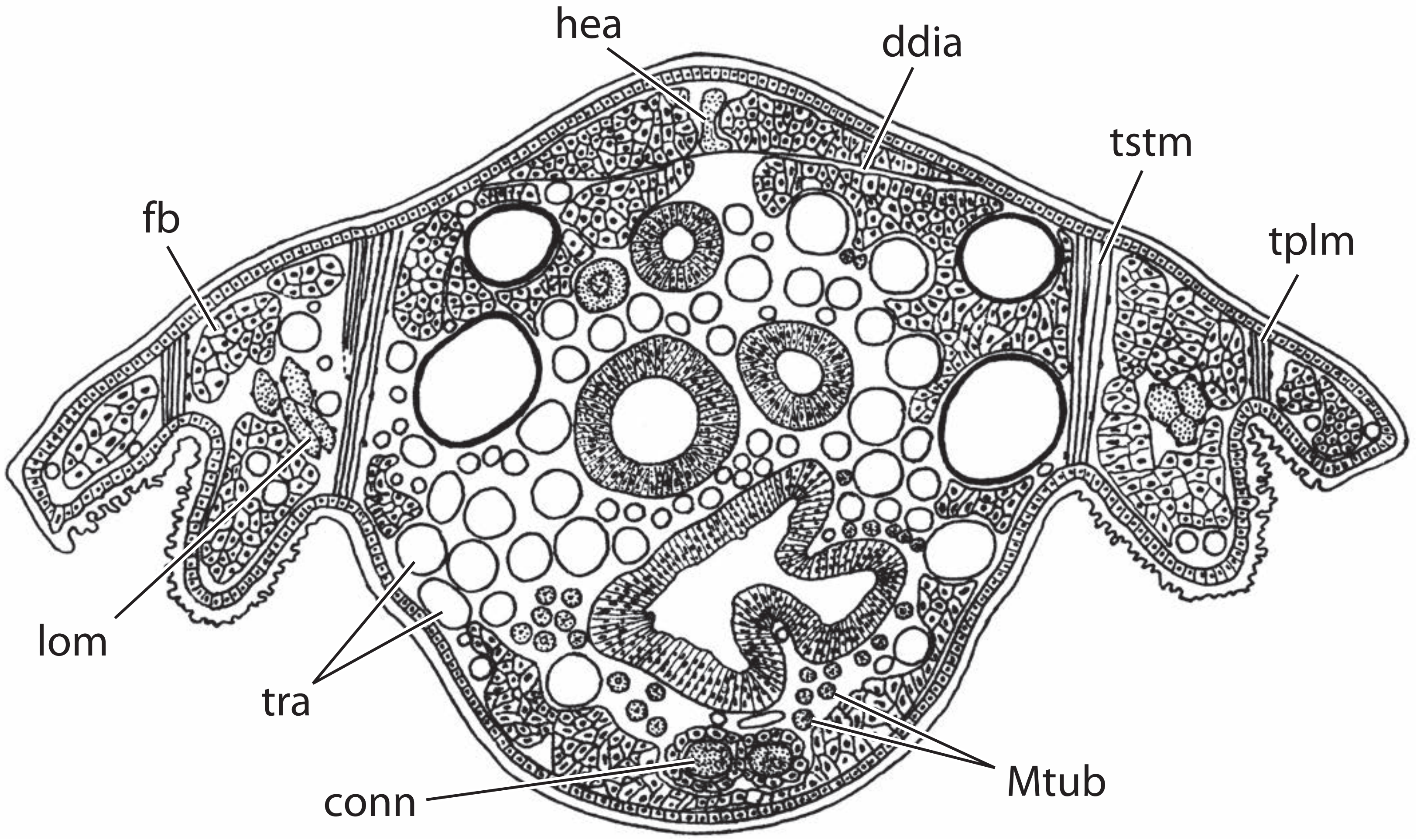
Electron micrographs of the tubular midgut. (A) Detail of the apical region of the cells of anterior tubular midgut, showing autophagic vacuoles (av) and small vacuoles (v). The cytoplasm contains abundant mitochondria (mi) and scattered elements of rough endoplasmic reticulum (rer). Long apical microvilli (mv) are regularly- arranged and dense. (B) Basal region of mid-midgut cells, showing well-developed basal infoldings (if) associated with mitochondria (mi). (C) Apical parts of the cells of the mid-midgut. The cytoplasm contains ferritin-like granules (f), mitochondria (mi) and sparse rough endoplasmic reticula (rer). The apical microvilli are long but sparse, and some of them are ruptured. (D) The first cellular type of the posterior tubular midgut. Shallow and bulb-shaped basal infoldings (if) are visible. Cytoplasm filled with secretory granules (sg) and mitochondria (mi). The secretory granules are electron-lucent in center and electron-dense at periphery. bl, basal lamina; N, nuclei. Scale bars: 1.0 mm in (A, B, C); 2.0 mm in (D).



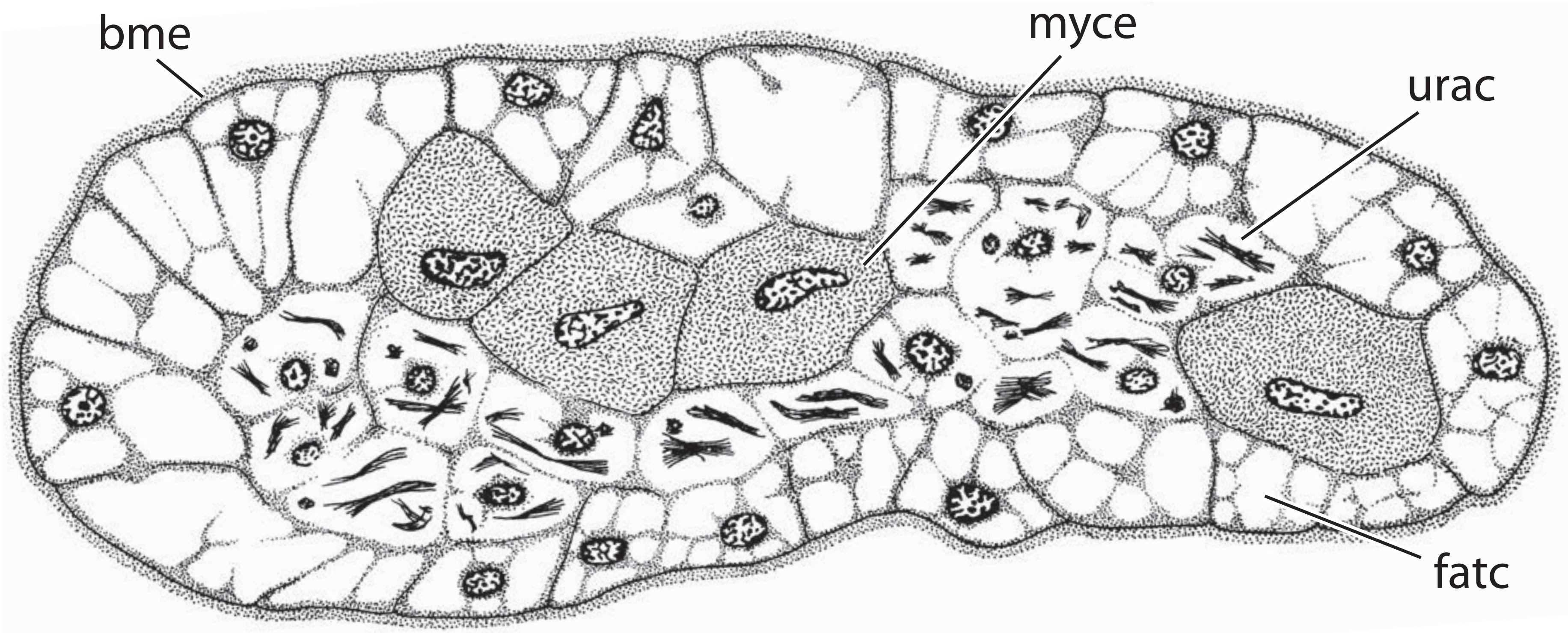
Detail of the cells of the posterior tubular midgut, showing elongated mitochondria (mi), secretory granules (sg), rough endoplasmic reticulum (rer), and nuclei (N) with evident nucleoli (n). (B) High magnification of the first cellular type of the posterior tubular midgut, showing aggregations of fine granules (asterisks) and mitochondria with cristae (arrows). (C) The second cellular type of the posterior tubular midgut features well-developed basal infoldings (if) and regularly-arranged microvilli (mv). Cytoplasm contains abundant mitochondria (mi), secretory vesicles (sv), nuclei (N) with small nucleoli (n), and scattered elements of rough endoplasmic reticulum (rer). (D) Detail of the second cellular type of posterior tubular midgut. Cells with well-developed basal infoldings (if) possess numerous mitochondria (mi), vesicles (v) filled with fine granular materials, and sparse rough endoplasmic reticulum (rer). (E) Transverse section of the distal tubular midgut. Cells possess well-developed basal infoldings (if) and dense microvilli (mv), and their cytoplasm is packed with mitochondria (mi). sd, septate desmosomes; bl, basal lamina; l, lumen; mu, muscles. Scale bars: 1.0 mm in (A, C, E); 0.5 mm in (B); 0.2 mm in (D).



Transverse section of the hindgut, showing a cuticle (c) lining the surface of the hindgut lumen. (A) The ileum cells contain numerous secretory vesicles (sv) and abundant mitochondria (mi). Double-membraned microorganisms (arrows) are visible among the secretory vesicles. (B) Cytoplasm of the rectum cell contains abundant mitochondria (mi). if, infoldings of basal plasma membrane; l, lumen; mu, muscles. Scale bars: 1.0 mm in (A, B).



Abdomen with fat body lobes and other internal organs. Abbr.: conn: connective of ventral nerve cord, ddia: dorsal diaphragm, fb: fat body, hea: heart, lom: longitudinal muscle, Mtub: Malpighian tubule, tplm: tergopleural muscle, tra: trachea, tstm: tergosternal muscle.

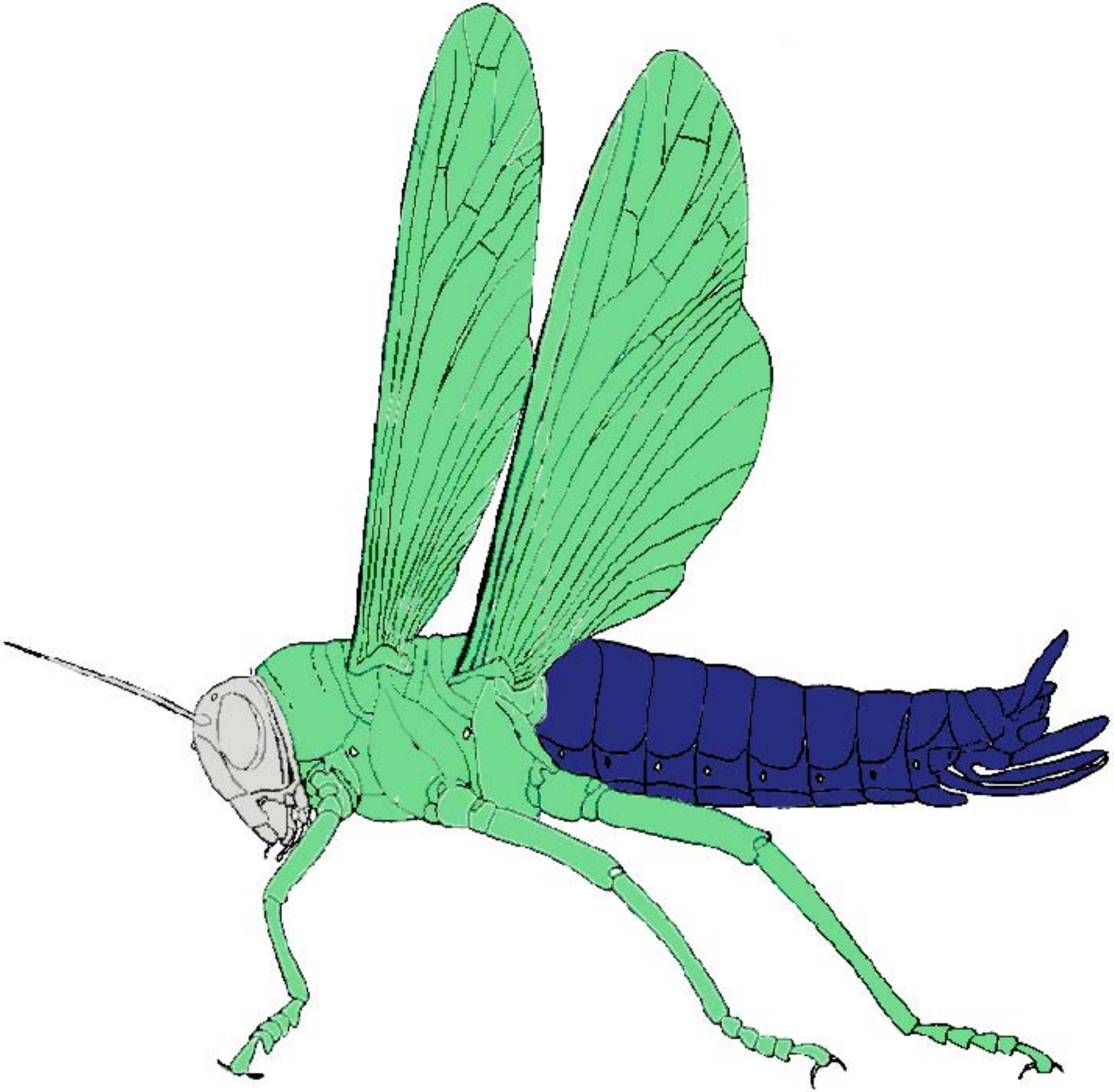


Fat body lobe. **bme:** basement membrane, **fatc:** fat cell, **myce:** mycetome, **urac:** urate cell.

Fat body

The fat body or corpus adiposum occurs as a diffuse organ, but its presence as a voluminous organ mainly concentrated in the abdomen. With its capacity to mobilize energy-rich substances efficiently it was probably an important prerequisite for the evolution of flight, likely the most important innovation in the evolution of Hexapoda. The fat body is a diffuse, ill-defined organ. It is highly variable in its shape, extension and histological properties among taxa, and also depending on the developmental stage and physiological condition of an hexapod. It is composed of small whitish lobes of sheets or ribbons of cells which are immersed in the haemolymph. Other organs, especially in the abdomen, are embedded in the complex 3-dimensional system formed by the fat body lobes (e.g., salivary glands, tracheae, ovarioles). Sometimes, especially in caterpillars and other holometabolan larvae, it shows a division into an inner visceral layer around the digestive tract and an outer parietal layer more closely associated with the integument. It is a multifunctional organ and plays a highly important role in the metabolism of hexapods. It is primarily designed to synthesize and store energy-rich substances such as glycogen, fat and protein. An important function, as pointed out above, is to mobilize these products very efficiently, for instance in the context of flight or specific development stages (e.g., metamorphosis). The dominant cell type in the fat body is the trophocyte. These cells are responsible for the main functions of storage, mobilization of energy-rich substances and synthesis. Their size and contents (e.g., small droplets of lipids, albuminoids) are indicators of the developmental stage, active tissue formation or starvation. They are involved in the metabolism of carbohydrates, lipids and nitrogenous compounds. They synthesize the active form of ecdysone (20-hydroxy-ecdysone) and also sugar and proteins (e.g., vitellogenin, storage proteins) of the haemolymph. The fat body can also play a role in excretion, especially in Collembola, which lack Malpighian tubules. Metabolic waste is stored as spherules of urates (including uric acid) in specific urate cells, the urocytes. Fat body cells can also contain endosymbiotic microorganisms, mostly bacteria, but sometimes also yeasts or fungi. In certain aphids (Aphidoidea) endosymbionts can occur in all fat body cells, whereas they occur only in specific mycetocytes in roaches and certain scale insects (Coccoidea). The specialized mycetocytes are free of reserve substances and excretion products and can be scattered over the entire fat body or concentrated in small groups (mycetomes) in the central region of fat body lobes. The symbionts provide the hosts with vitamins and other substances the hexapods cannot produce themselves. Some symbionts can make use of uric acid for their own protein synthesis. An important function of the fat body in immatures is the production of energy-rich yolk proteins as a preparation for the molt to the adult stage. In some holometabolan groups (Lepidoptera, Diptera) the larval fat body dissolves completely during the metamorphosis and is replaced by an adult fat body formed by cells kept at an embryological stage in the larva. In the highly specialized beetle family Lampyridae and some closely related elateroid groups the fat body or specialized regions of it form luminous organs. Light emission is caused by oxidation of luciferin involving the enzyme luciferase and adenosine triphosphate (ATP) as an energy source. The species specific pattern of light flashes is triggered by nervous impulses.

04 Abdomen



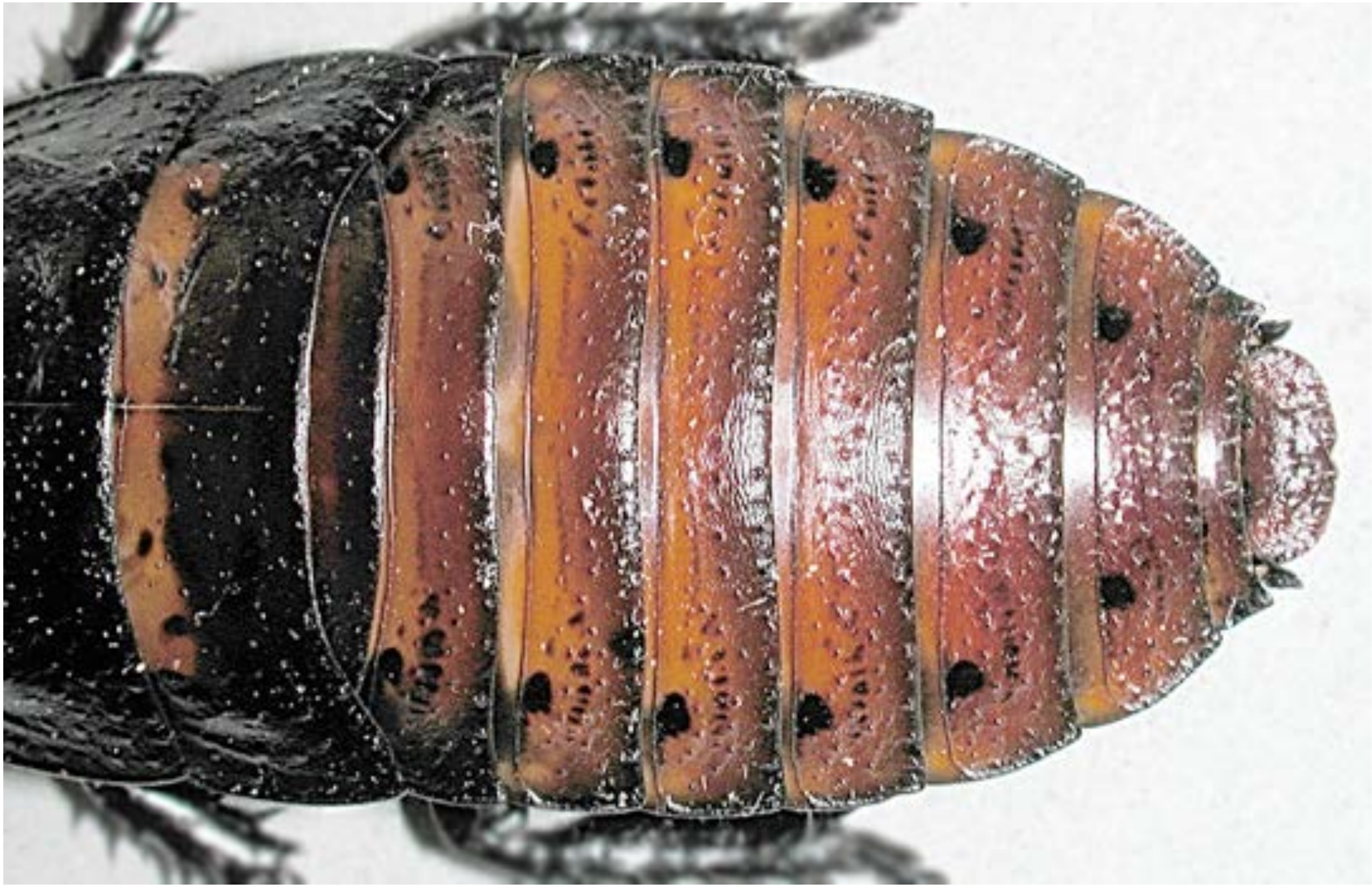
The Abdomen is the third or posterior-most Tagma of the insect body. The abdominal Groundplan is composed of 11 segments, with a trend of reduction in number of segments in higher Orders of insects. In many insects, the abdomen is less strongly sclerotized than the head or Thorax.

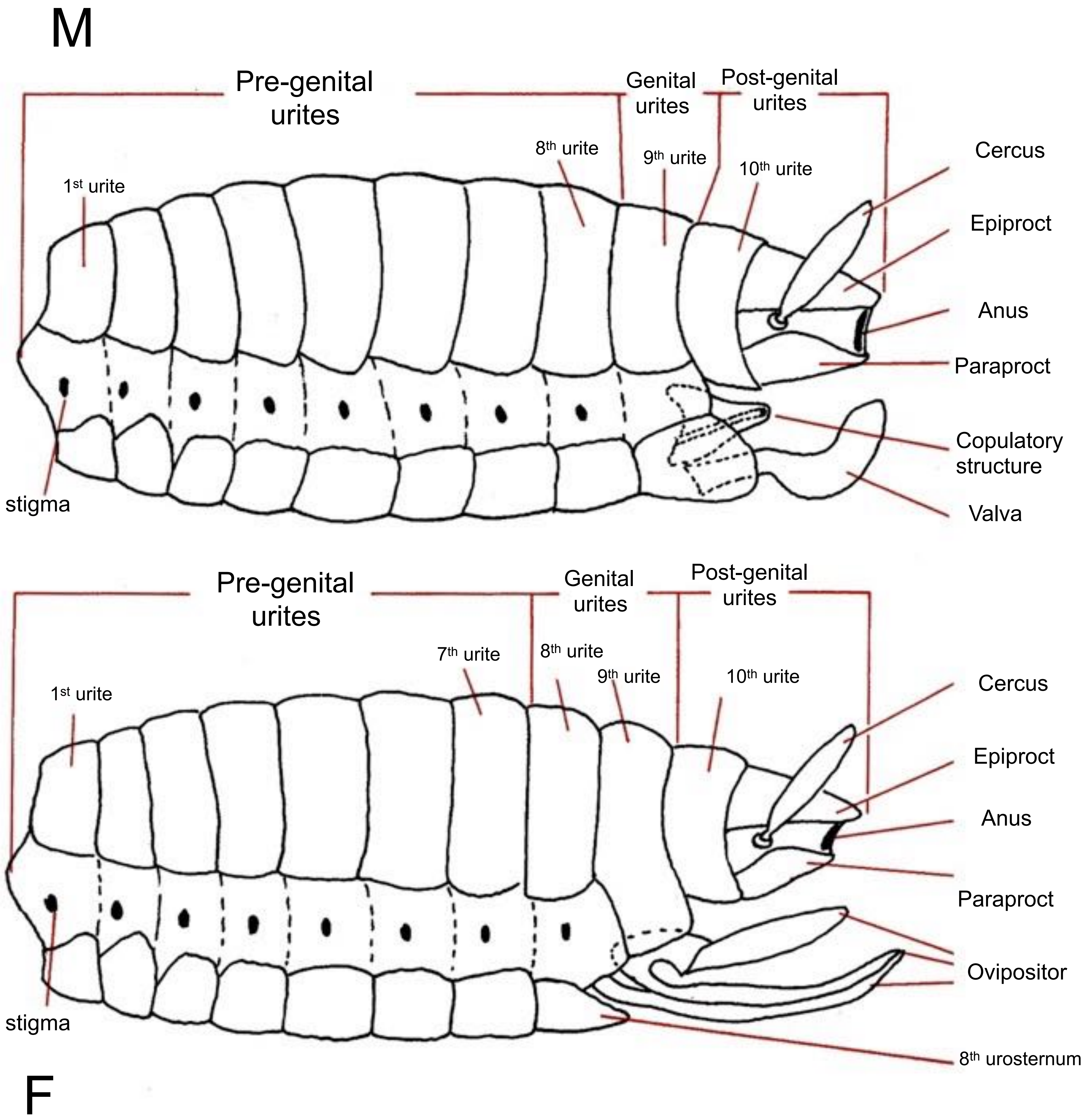
Each abdominal segment consists of a sclerotized Tergum, Sternum and sometimes a Pleurite. Terga are separated from each other and from the adjacent Sterna or Pleura by membrane. Spiracles occur in the pleural area.

Some insects bear a sclerite (Laterotergite) in the pleural area. Ventral sclerites are sometimes called 'Laterosternites.' Spiracles are often situated in the definitive Tergum, Sternum, Laterotergite or Laterosternite. The Abdomen is more conspicuously segmented than the head or Thorax.

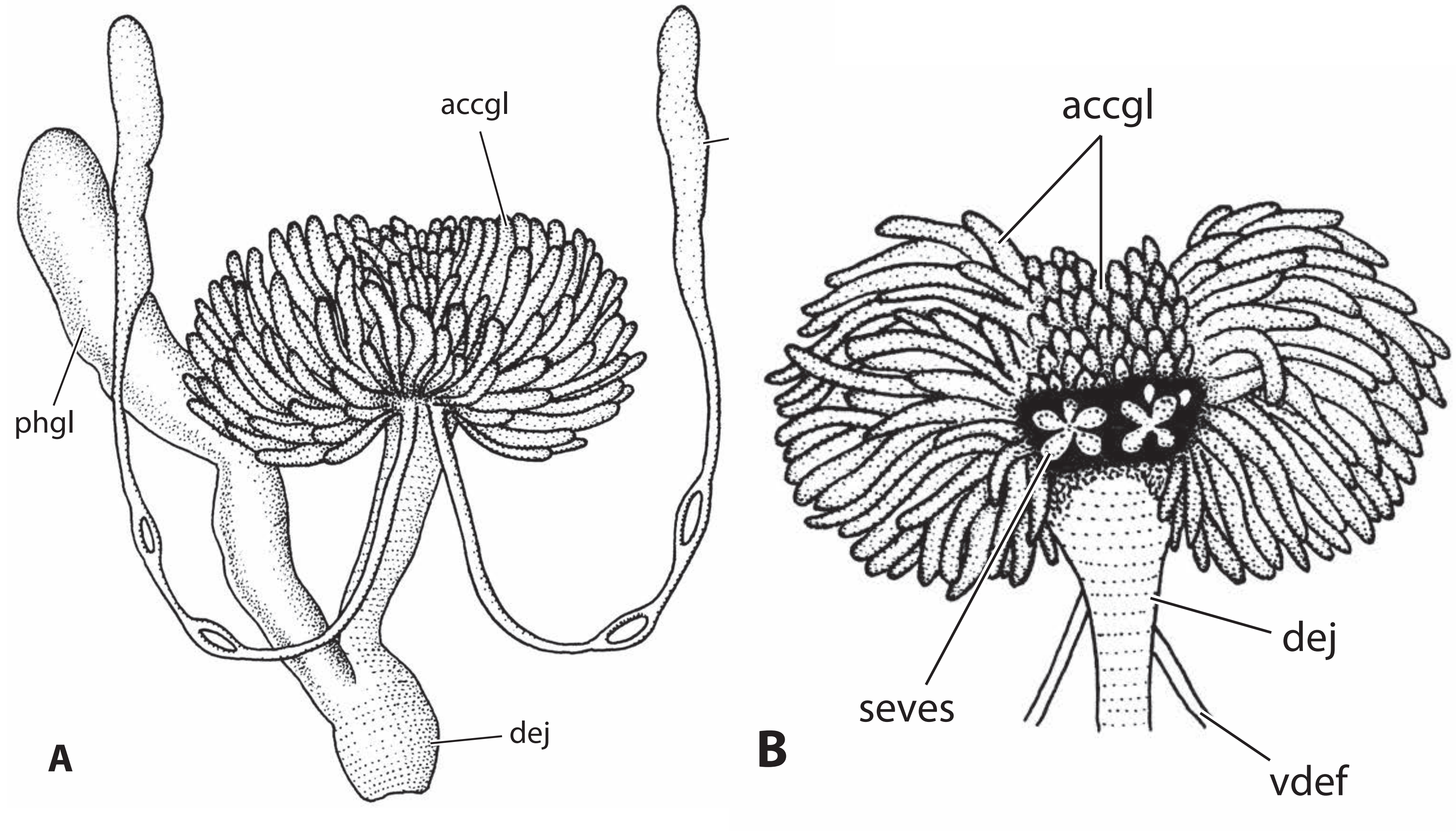
Abdominal segmentation is evident and serially uniform. Typically abdominal Terga show secondary segmentation with the posterior part of a segment overlapping the anterior part of the segment behind it. Functionally, this overlap prevents damage or injury to the animal while it moves through the environment, particularly in confined spaces. Secondary segmentation with associated membrane permits rapid change in size (volume) because the Abdomen must accommodate change in size associated with respiration, digestion and production of gametes. Superficially, the Abdomen is the least specialized body Tagma, but notable exceptions include scale insects (Coccidae , Diaspididae). Most Pterygota lack abdominal appendages except Cerci, and external genitalia and pregenital appendages in adult Apterygota and larval Pterygota. Pregenital segments in a male are 1-8; pregenital segments in a female are 1-7.

The adult's Abdomen is primarily responsible for digestion, defense, respiration (predominantly), excretion and reproduction. These activities are conducted in different areas of the Abdomen. In most insects, the anterior area is predominantly involved with digestion and an accumulation of waste in some insects. Gas exchange during respiration occurs generally over the entire Abdomen, with one pair of spiracles per segment. The posterior abdominal area is predominantly involved with reproduction and excretion.

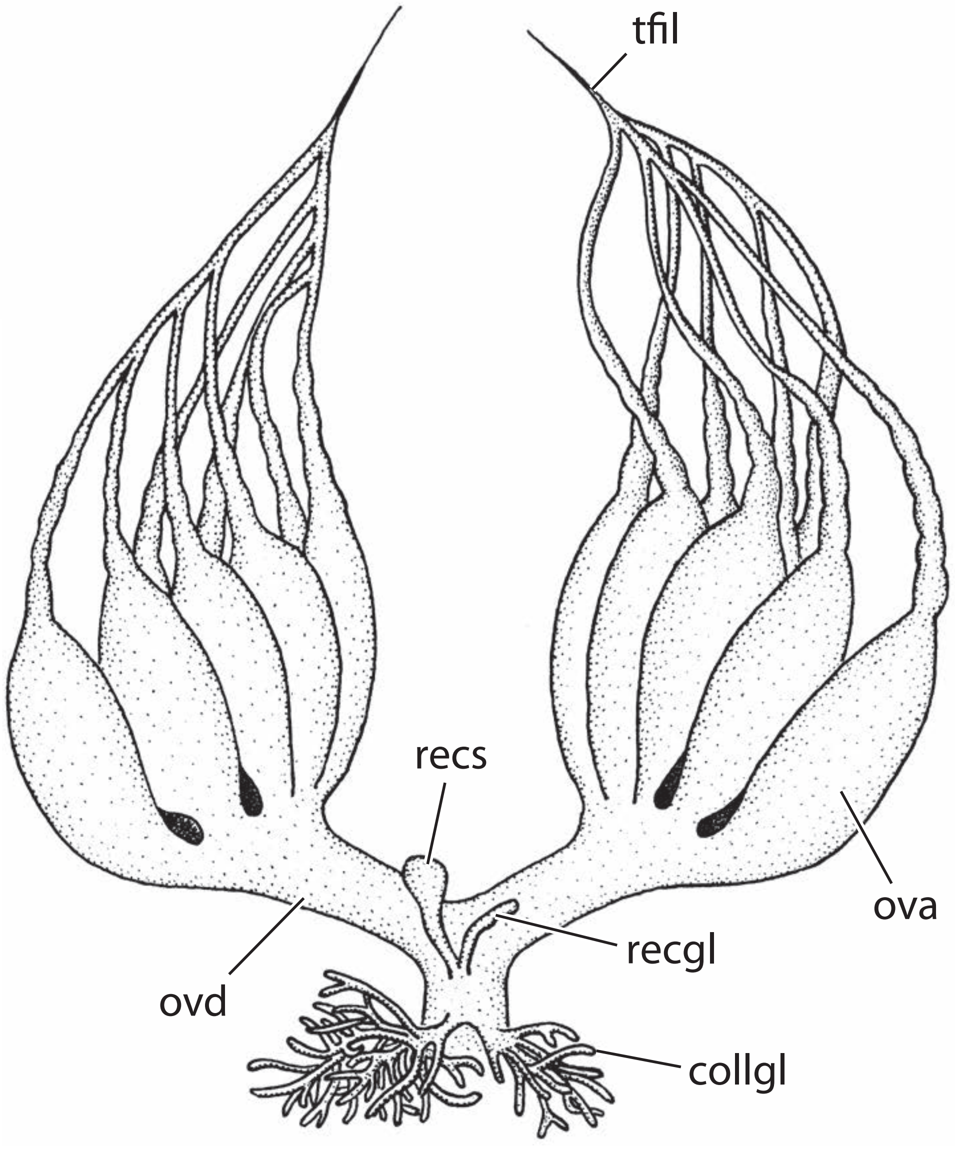




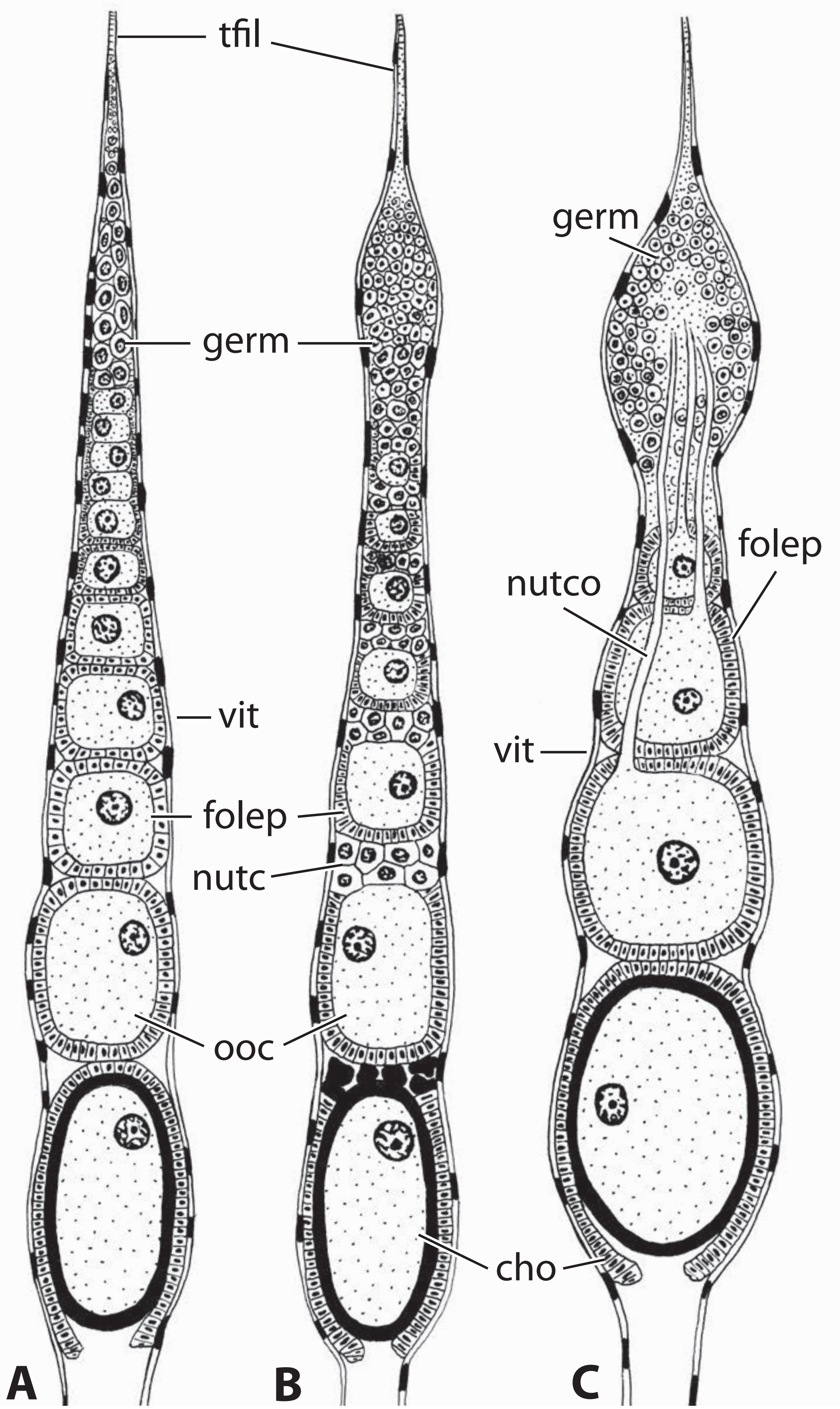
The insect abdomen is more obviously segmental in origin than either the head or the thorax, consisting of a series of similar segments, but with the posterior segments modified for mating and oviposition. In general, the abdominal segments of adult insects are without appendages except for those concerned with reproduction and a pair of terminal, usually sensory, cerci.
Pregenital appendages are, however, present in Apterygota and in many larval insects as well as in non-insectan hexapods. Aquatic larvae often have segmental gills, while many holometabolous larvae, especially amongst the Diptera and Lepidoptera, have lobe-like abdominal legs called prolegs.



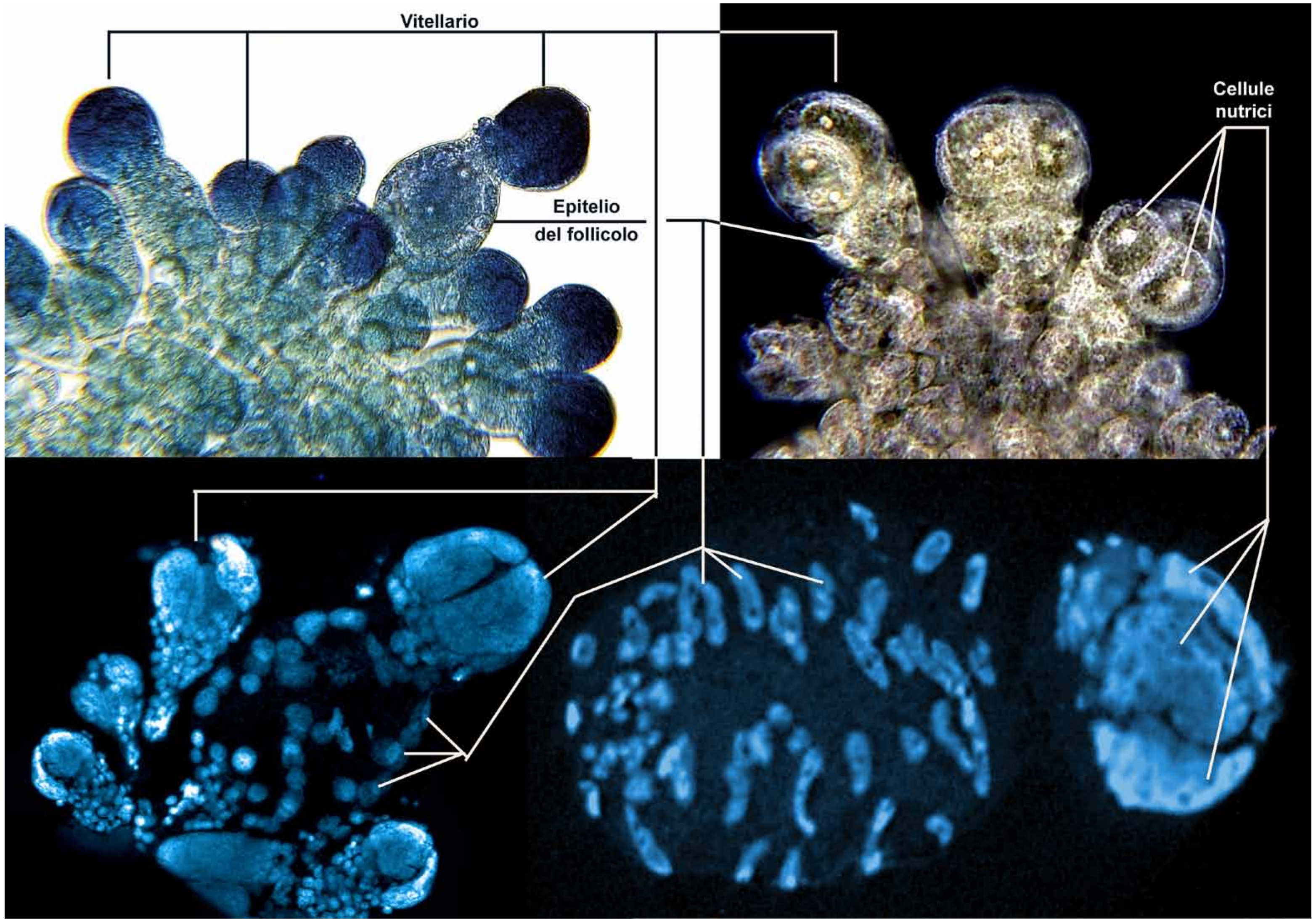
Ovaries and associated structure. collgl: collateral glands, **ova:** ovarioles, **ovd:** oviduct, **recs:** rectal sac, **recgl:** rectal gland, **tfil:** terminal filament.



Male internal reproductive organs of Blattodea. **A:** dorsal view; **B:** accessory gland, ventral view. **accgld:** accessory gland, **dej:** ductus ejaculatorius, **phgl:** phallic glands, **seves:** seminal vesicles, **test:** testes, **vdef:** vas deferens.



Ovariole types. A: panoistic; **B:** polytrophic (meroistic); **C:** telotrophic (meroistioc). **cho:** chorion, **folep:** follicle epithelium, **germ:** germarium, **nutc:** nutritive cell, **nutco:** nutritive cord, **ooc:** oocyte, **tfil:** terminal filament, **vit:** vitellarium.



Male and female internal genital organs

The main elements of the male internal genital organs are the **testes**. They are always paired but in few lineages secondarily connected. The testes are usually composed of a series of sperm producing **follicles** (tubes). More than 100 of these subunits can be present per testis in some groups (e.g., Acridiidae), but only one tubular follicle is present in non-polyphagan beetles, and only one sac-shaped structure in Diptera and some entognathous hexapods. The wall of the follicles is a thin epithelium, in some groups with two layers of cells on a basal lamina. The primordial germ cells are usually located in the apical region. The entire structure is enclosed in a sheath of connective tissue in many cases. The shape of the testes can vary considerably among hexapod lineages. They can be fan-shaped, divided into several small lobes, or tubular.

The sperm cells are released into the paired mesodermal **vasa deferentia**, which are often enlarged proximally, thus forming **vesiculae seminales** functioning as sperm storage organs. In almost all groups they unite to form an unpaired ectodermal **ductus ejaculatorius**. In most cases it leads to an intromittent organ (absent in entognathous hexapods, simple in Archaeognatha and Zygentoma), with the gonopore usually placed in the membrane connecting sternites IX and X. The epithelium of the ductus ejaculatorius is one-layered and as a structure of ectodermal origin covered by a thin intima. In some groups it is equipped with a strongly developed muscularis and forms a simple sperm pump for spermatozoa contained in liquid. In Ephemeroptera the ductus ejaculatorius is lacking. The vasa deferentia lead directly to the paired gonopores and copulatory organs. In Dermaptera the ductus is paired, but vestigial on one side in some species.

In some groups the epithelium of the vasa deferentia has a glandular function, but they usually form tubular diverticula differentiated as mesodermal **accessory glands** (mesadenia). In some nematoceran groups (Diptera) parts of the ectodermal ductus ejaculatorius are enlarged and modified as accessory glands (ectadenia). Ectodermal accessory glands also occur in Coleoptera and Heteroptera, and both types can be present in some species of these orders. The secretions of the accessory glands play an important role in formation of the spermatozoa (sperm packages). Their shape and also the number can vary strongly.

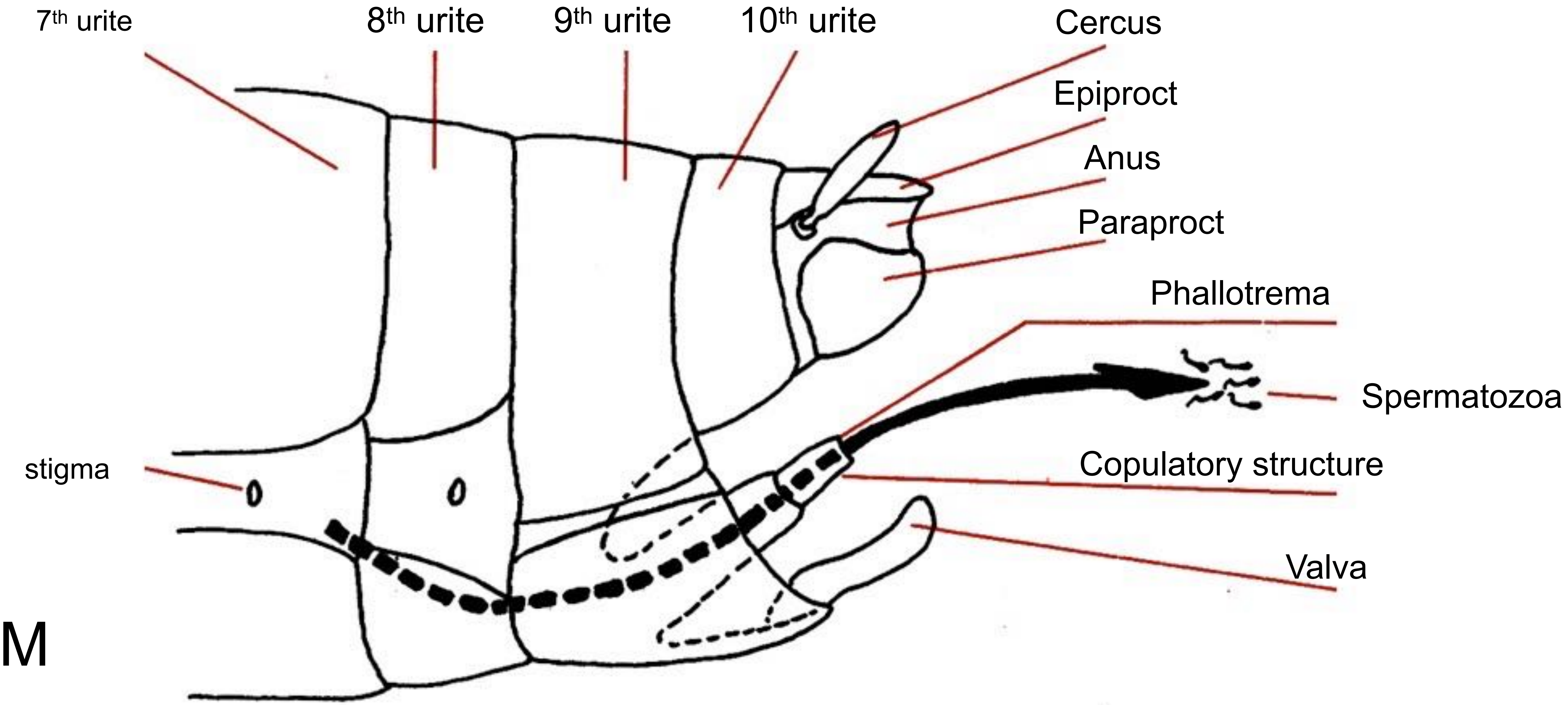
The main elements of the internal female genital apparatus are the paired ovaries, each of them composed of several or many **ovarioles** or **egg tubes** in almost all groups. The number and arrangement varies. Only one pair of sack-shaped elements with unclear homology is present in Collembola, Campodeoidea (Diplura) and Protura. The ovaries of vivipaous dipterans (e.g., Hippoboscidae) contain only two ovarioles. Four per ovary are present in smaller orthopterans but more than 100 in larger species. The ovarioles are usually arranged as a bundle, but a serial arrangement occurs in some lineages, such as for instance Archaeognatha, Zygentoma and Ephemeroptera. Botrydoid ovaries with many small ovarioles are characteristic for Coccoidea (Sternorrhyncha) and also occur in nematoceran groups of Diptera. Atypical horseshoe-shaped ovaries (distally connected) with numerous finger-shaped ovarioles are present in Plecoptera (autapomorphy). A common sheath of the ovaries is usually absent, but occurs in Diptera.

The typical ovarioles are tube-like, apically tapering structures forming a cluster on both sides. They are enclosed by an external ovariole sheath or **tunica externa**, and an internal **tunica propria**, an elastic basal lamina. In the **germarium** the primordial germ cells are formed and the first meiotic divisions take place. It is almost always located in the distal part but laterally in the atypical ovaries of Collembola. When the **oocytes** (immature egg cells) leave the germarium they are clothed by **follicle cells**. In the proximal **vitellarium** yolk is produced and the **oocytes** increase in size. Apically the ovarioles bear thin terminal filaments, with a cellular core covered by the tunica propria. They are often connected distally, thus forming a suspensory ligament. In some groups the ligaments of both sides merge, or they are attached to the body wall or the dorsal diaphragm.

Three different types of ovarioles can be distinguished. The **panoistic** ovariole lacks nurse cells. All primordial germ cells develop as **oocytes**. The nutrition is provided by the **follicle epithelium** of the ovarioles. In polytrophic or telotrophic **meroistic** ovarioles some priordial germ cells form nurse cells (**trophocytes**) and others oocytes. In the **polytrophic** type each oocyte is enclosed by follicle cells. In **telotrophic** type trophic tissue is present and oocytes, and prefollicular tissue in the apical region. The trophocytes are confined to the germarium and enclose a central trophic core in this region. The advancing oocytes are connected to the trophic core by thin nutritive cords.

At their base the ovarioles are usually connected with a common **calyx** by narrowed stalk-like pedicels. From there the mature oocytes enter the paired **oviducts**. Their epithelium of cubic or columnar cells on a basal lamina is usually enclosed by a thin muscularis. In almost all groups they join an unpaired median **oviduct**. Due to its ectodermal origin its inner surface is coated by a thin intima. Externally it is usually covered by thin layers of circular and longitudinal muscles. The **gonopore** (usually unpaired, paired in Ephemeroptera) at the posterior end of the oviduct releases the eggs into a more or less extensive genital chamber in most groups. This can form a specifically shaped diverticulum or pouch, the **bursa copulatrix**, which receives the male intromittent organ during copulation. In other cases only a more or less narrow tube-like **vagina** is present, with the **vulva** as its terminal opening. In viviparous dipterans, the genital chamber forms an “uterus”. From the female genital tract eggs enter the basal part of an ovipositor in most groups. A **spermatheca** or **receptaculum seminis** is present in many groups and usually unpaired. Its insertion is a landmark for separating the median oviduct from the vagina. Its internal surface is coated with a thin intima. Spermatozoa can be stored in the spermatheca until they are used for fertilization. In most cases it comprises a more extensive pouch-like part and a narrow **spermathecal duct**, connecting it to the bursa copulatrix or vagina. Tubular ectodermal **spermathecal glands** are connected to the duct occur in different groups. Paired ectodermal **accessory glands** are almost always associated with the female genital tract (absent in Grylloblattodea) and more than one pair is present in some groups. They usually produce substances coating and protecting the eggs or enabling the females to glue them on specific substrates. The function of the secretions varies in different lineages.

Schematic side view of male terminalia



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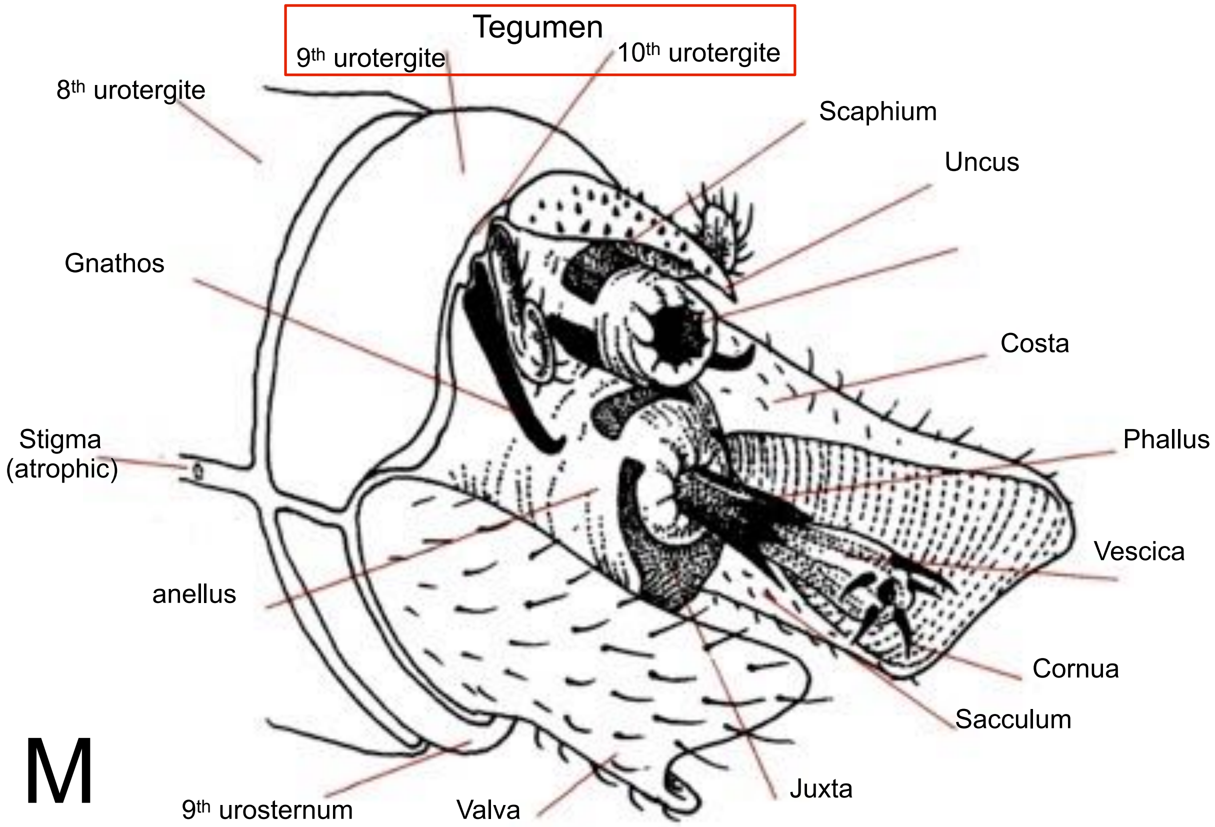
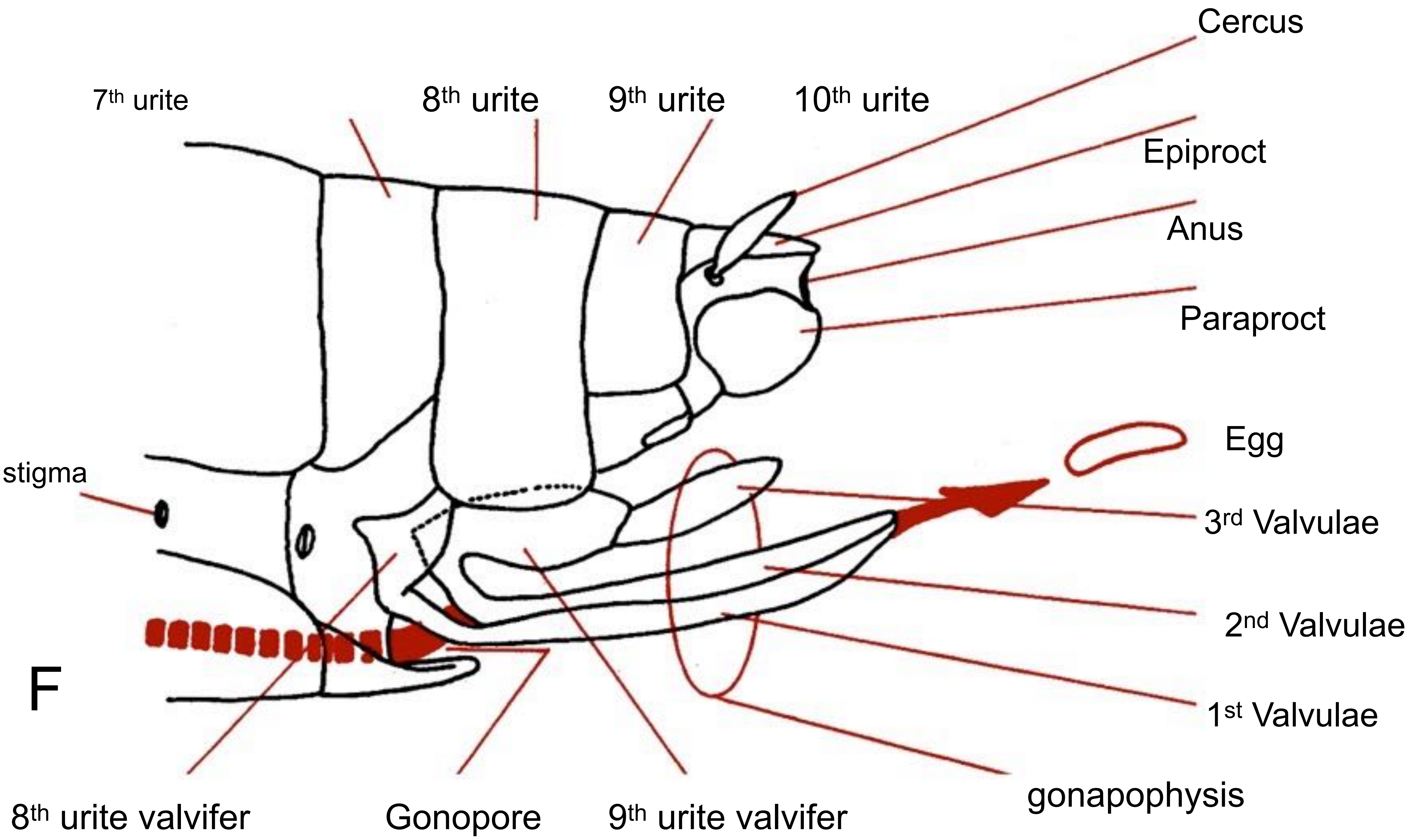
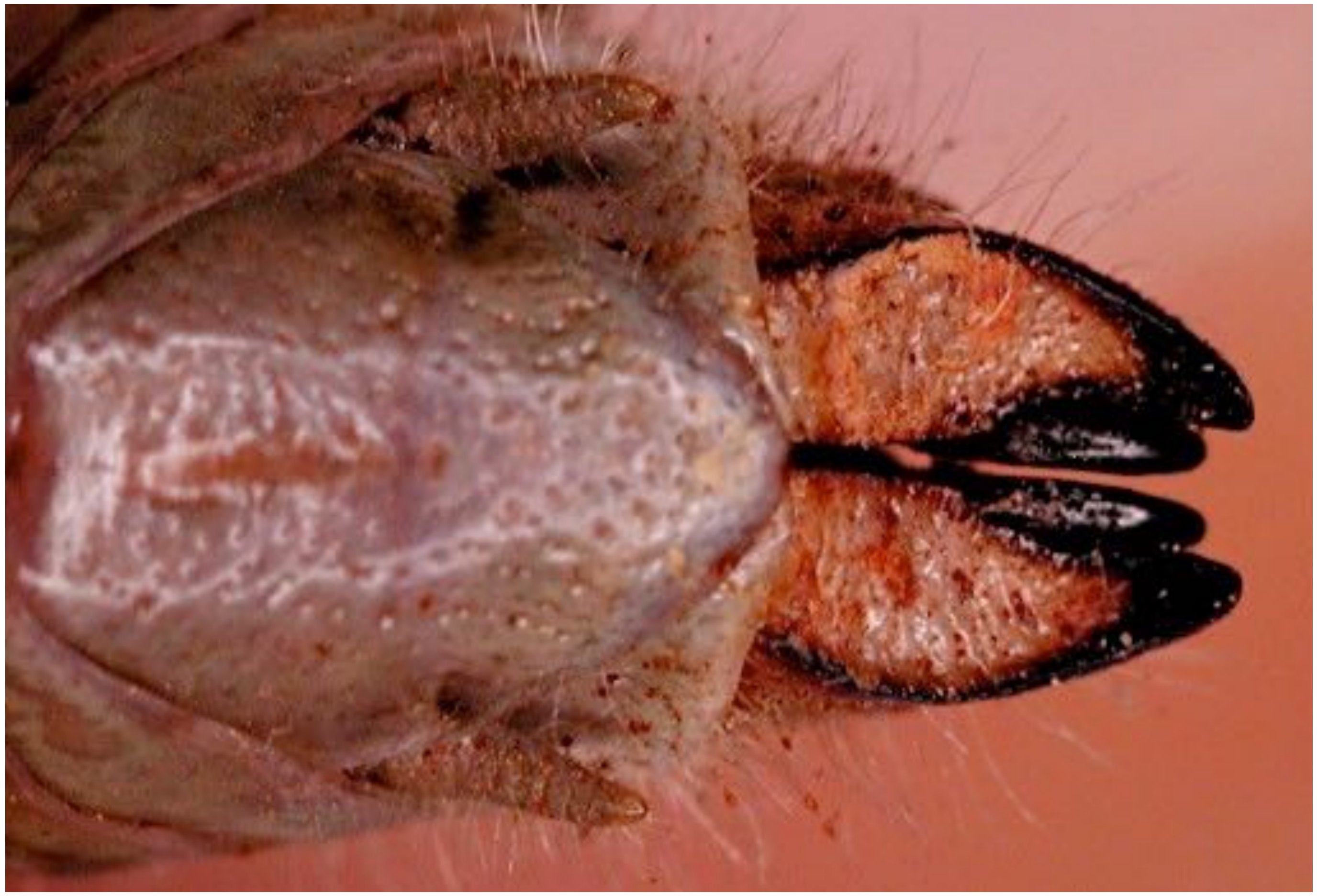
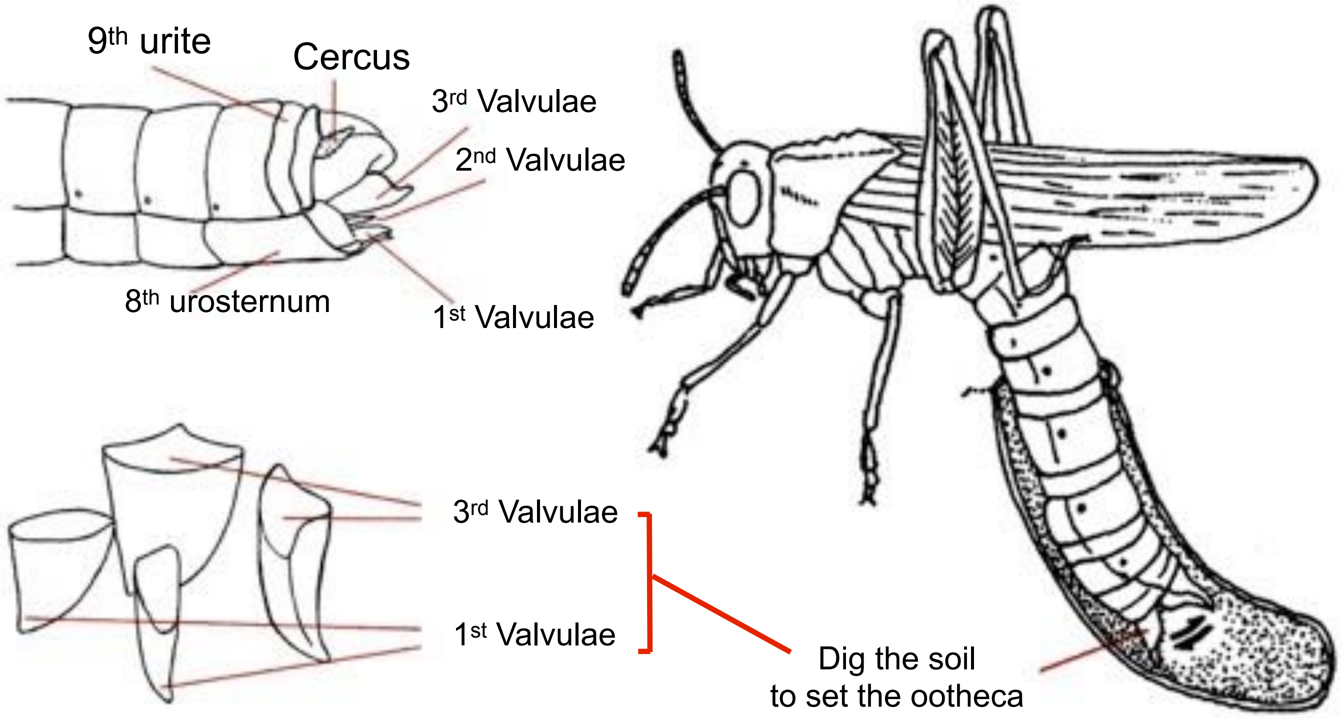

Tegumen
9th urotergite
10th urotergite
8th urotergite
Scaphium
Uncus
Gnathos
Costa
Stigma
(atrophic)
Phallus
Vescica
anellus
Cornua
Sacculum
M
Juxta
9th urosternum
Valva

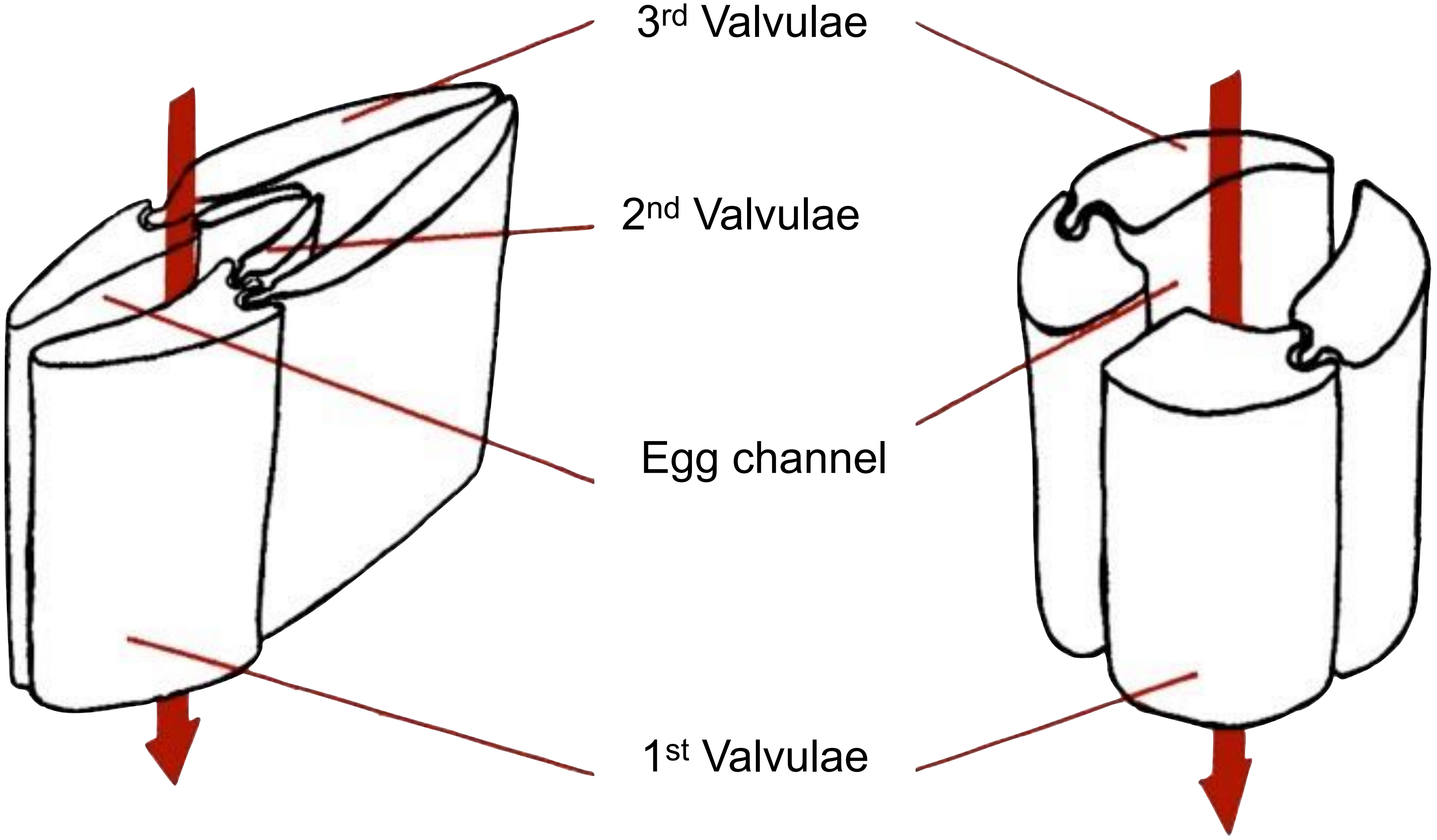
Schematic side view of female terminalia with gonapophysis (three pairs). The ovipositors derives from abdominal appendages.






9th urite
Cercus
3rd Valvulae
2nd Valvulae
8th urosternum
1st Valvulae
3rd Valvulae
1st Valvulae
Dig the soil
to set the ootheca

Valvulae arragment to create the egg channel



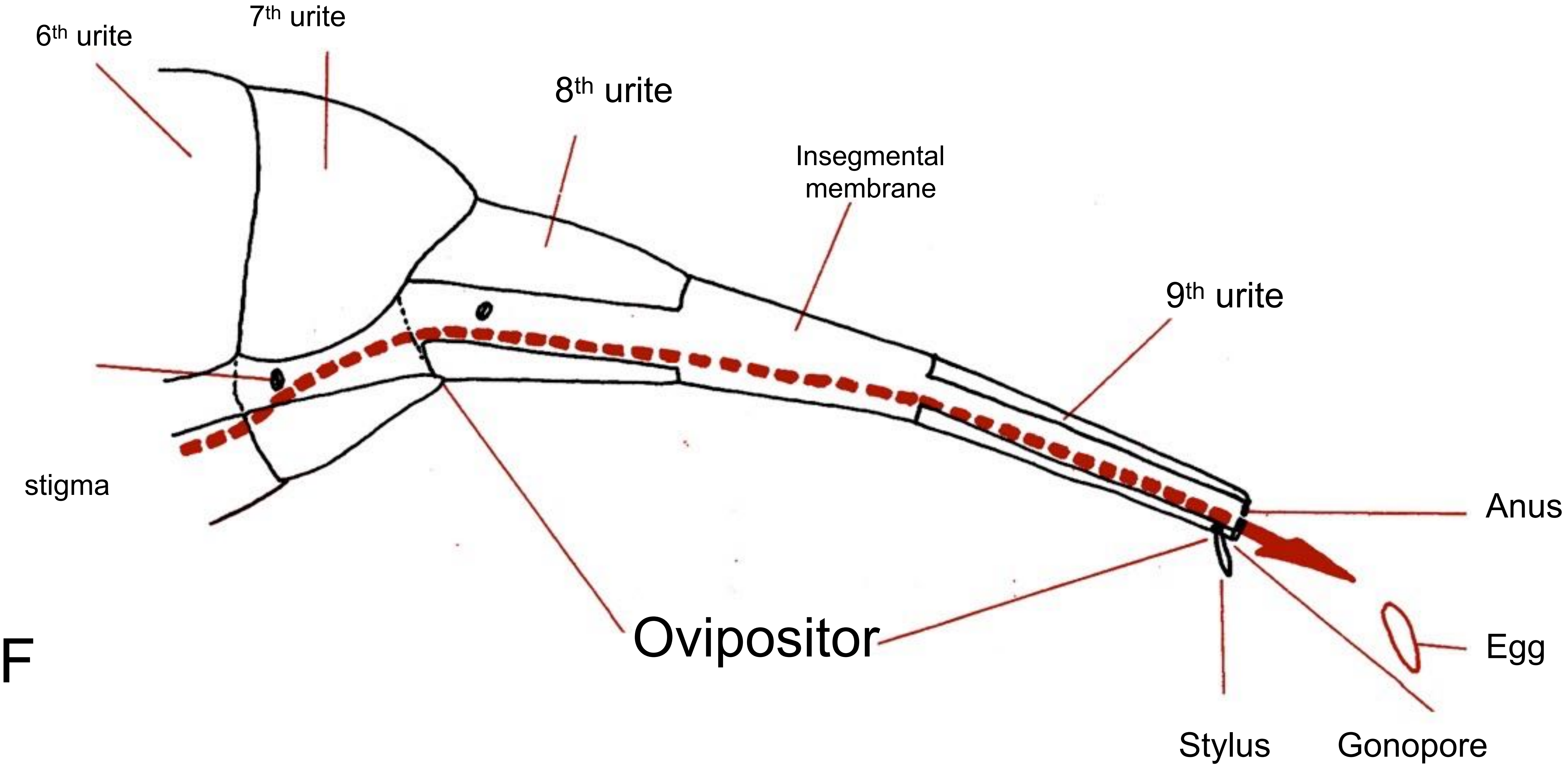
3rd Valvulae

2nd Valvulae

Egg channel

1st Valvulae

Schematic side view of female terminalia without gonapophysis



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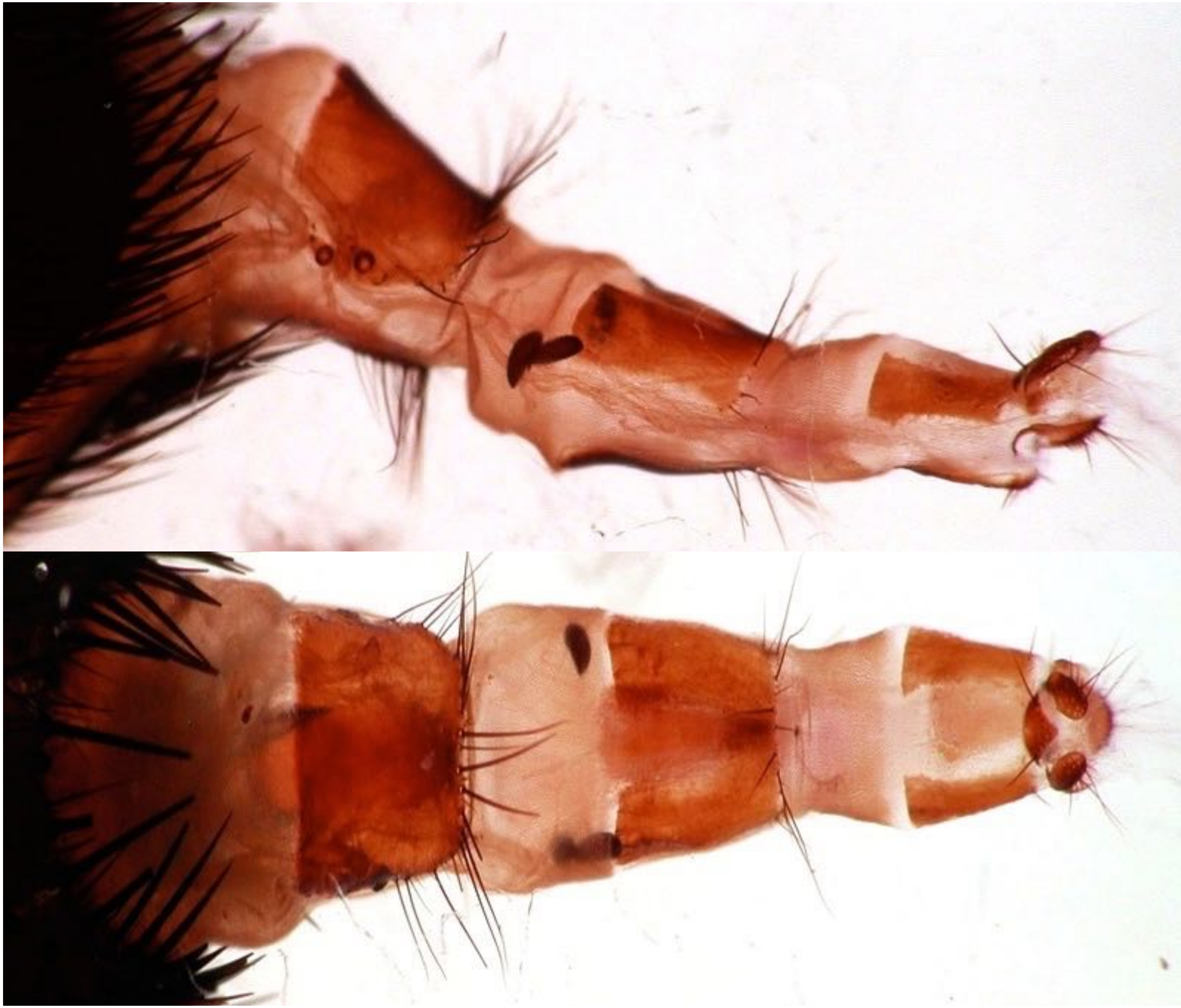


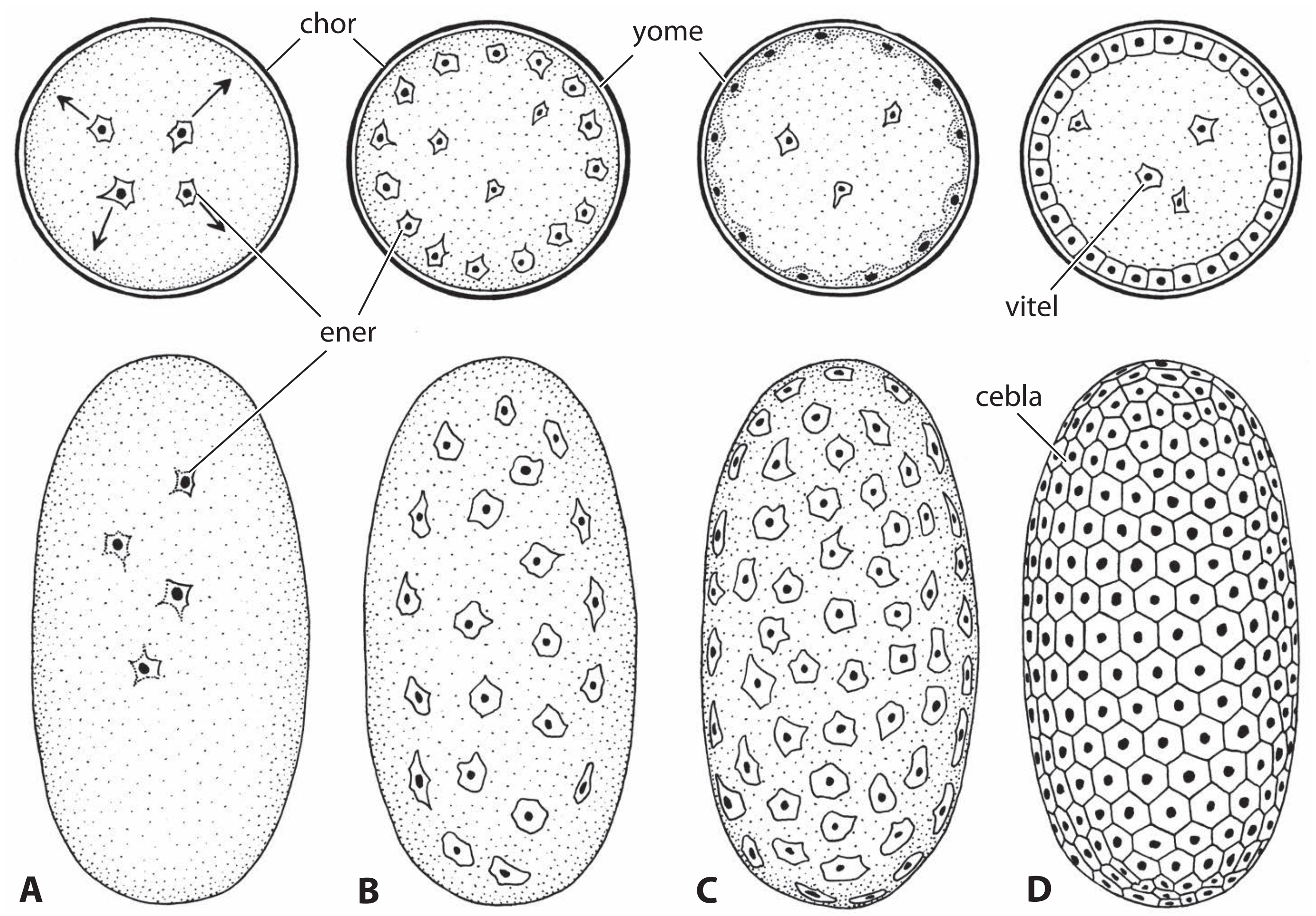
Fertilization and egg structure

External sperm transfer is a plesiomorphic groundplan feature of Hexapoda. This applies to all primarily wingless groups. A spermatophore (sperm package) is either deposited on a stalk formed of secretions (e.g., Collembola) or on silk threads (Archaeognatha, Zygentoma [partim]). Direct sperm transfer using an intromittent organ (penis, aedeagus) is an important evolutionary novelty of Pterygota, but it is unclear whether this is a groundplan feature of this lineage. The mechanism is completely different in Ephemeroptera and Neoptera on one hand, and Odonata on the other (secondary copulatory organ at the base of the abdomen). Females of many groups possess a bursa copulatrix (expansion of the vagina) which receives the aedeagus. Sperm is often stored in a receptaculum seminis or spermatheca, which can have a species specific shape and/or number. There the sperm cells can be kept in a functional condition for a longer period in some groups and then used for fertilization repeatedly (e.g., Hymenoptera). Males of most groups of Pterygota still produce spermatophores (groundplan of Hexapoda). However, more or less complex sperm pumps have evolved independently in several lineages (Strepsiptera, Mecoptera, Diptera, Siphonaptera). In these groups the males transmit fluid containing spermatozoa. A secondary external sperm transfer with a spermatophore attached to the female postabdomen occurs in one species of Zoraptera.

Parthenogenesis, i.e. the development of eggs without fertilization, occurs in some groups of hexapods as the normal mode of reproduction. It is usually found in phytophagous lineages (e.g., Sternorrhyncha, Chrysomelidae) where it enables populations to increase rapidly during favorable conditions. In groups with facultative arrhenotoky eggs may or may not be fertilized and haploid eggs produce males (Hymenoptera, Aleyrodidae, Thysanoptera, Micromalthidae). Thelytoky with extremely rare males and prevailing parthenogenesis is known from some species of Orthoptera and some other groups. Parthenogenetic and bisexual races co-occur in some cases (e.g., some species of Psychidae and Coccoidea). Facultative parthenogenesis as a result of lacking opportunity to mate is probably widespread in hexapods.

The eggs are formed in the follicles of the ovarioles. The primary oocyte usually undergoes the 1st and 2nd meiotic division shortly before, during or shortly after egg deposition. Eggs ready for deposition comprise the egg cell proper, the thin vitelline envelope, and the external chorion. They are usually large relative to body size and macrolethical, i.e. containing a large amount of yolk. Notable exceptions are the small and microlethical eggs of Collembola, Protura and a few other groups, notably many parasitoid Hymenoptera. The cytoplasm of the egg cell is divided into three components, a layer around the nucleus, a more or less thin peripherical periplasm beneath the oolemma, and the cytoplasmic reticulum, a fine meshwork which connects both and also suspends the nucleus in the yolk mass.

The ratio of cytoplasm and yolk mass varies considerably. Most groups of hemimetabolous insects have large eggs with lots of yolk, a thin periplasm and a poorly developed cytoplasmic reticulum, whereas the periplasm and cytoplasmic reticulum are usually well-developed in eggs of holometabolous insects. The shape of hexapod eggs is usually oval, ellipsoid or almost cylindrical and more or less elongated. They are often slightly curved, with a convex and a concave side. Rounded eggs occur in Heteroptera, Phasmatodea, and some basal lepidopteran lineages, and conical eggs in Pieris (Pieridae [Lepidoptera]). Eggs with long stalks are characteristic for some groups of Neuroptera (e.g., Chrysopidae). An anterior cap referred to as operculum occurs in different groups (e.g., Phasmatodea, Acercaria). It is pushed off by the hatching first instar nymph. In some species of Phasmatodea the operculum bears a knob-shaped or conical capitulum, which facilitates the transport of the eggs by ants. The chorion is produced by the follicle cells in the ovarioles. It is usually divided into an external exochorion, a trabecular endochorion, and an internal wax-layer. The exochorion forms a meshwork mainly involved in gas exchange. The wax layer is usually placed on the surface of the vitel- line membrane and reduces desiccation. In some groups the chorion it is very thin and more or less smooth (e.g., Psocodea, parasitic Hymenoptera, Strepsiptera, many groups of Coleoptera) but usually it is well-developed and distinctly sculptured (e.g., Orthoptera, Phasmatodea). A honey comb pattern occurs in many groups (e.g., Zoraptera, Gyrinidae, Archostemata). The surface structure of the chorion reflects the surface of the follicle cells which deposited it to a certain degree. One or more openings for passage of spermatozoa are often present. The position of these micropyles varies strongly. In several lineages they are arranged around the anterior pole of the egg. In Zoraptera a pair is present at the equator of the eggs, and a single micropyle is located near the posterior pole in phlaeothripid Thysanoptera. In most groups of Acercaria an operculum is present at the anterior pole with one or up to a dozen micropyles. There is little relation between the position of the micropyle and the site of fertilization. To unite, both pronuclei migrate over a considerable distance towards the cleavage center within the yolk mass, the female one from the maturation island, and its male counterpart from the micropyle. Additional perforations of the chorion are aeropyles for gas exchange and chorionic hydropyles for the uptake of water. Numerous of these small openings are usually present. The layer of air in the endochorion has direct access to the egg through pores or canals.



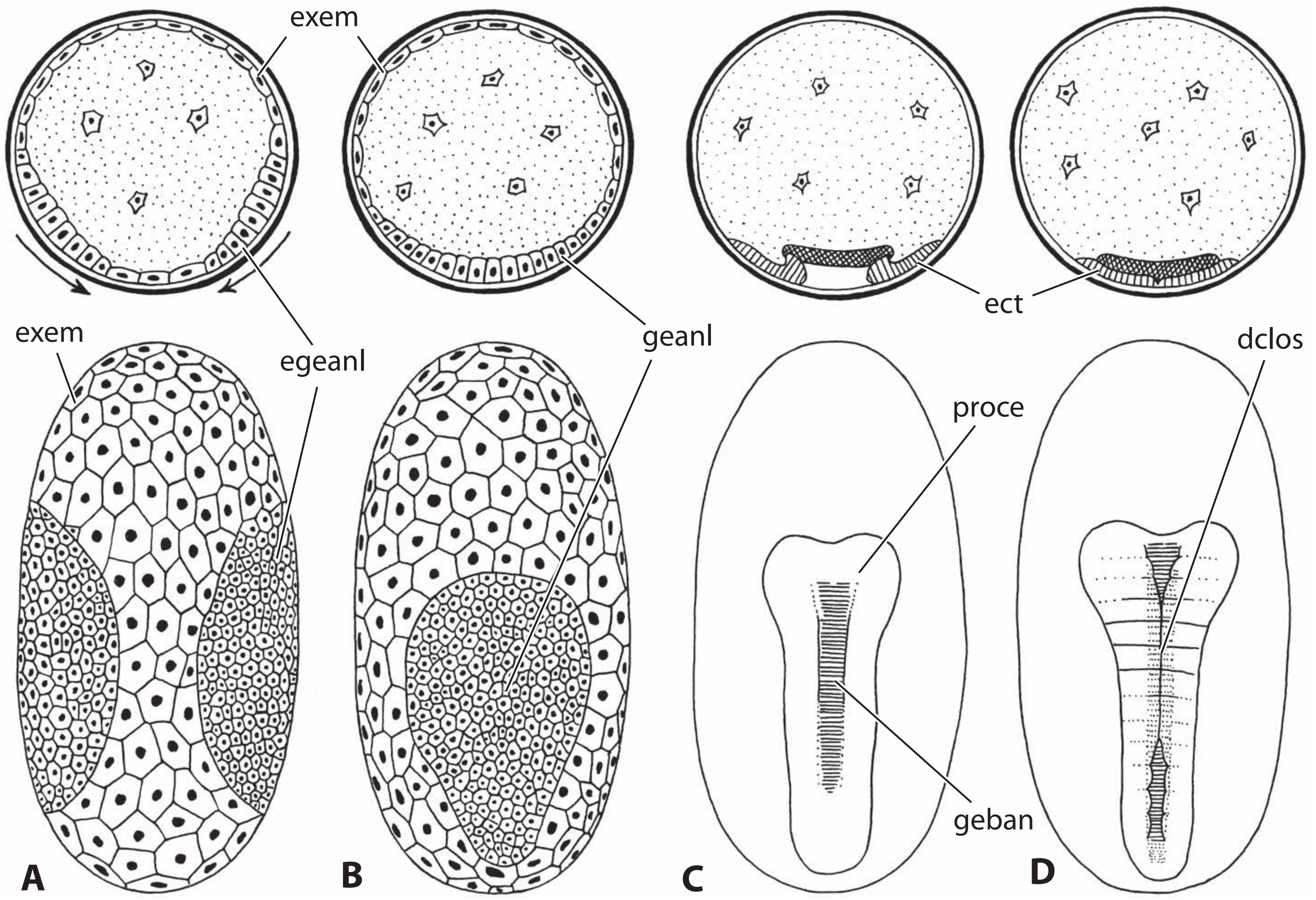
Early stages of superficial cleavage, cross sections (upper row) and ventral view. A, **B**, energid stages; **C**, syncytial preblastoderm, **D**, undifferentiated blastoderm. **cebla**: cellular blastoderm, **chor**: chorion, **ener**: energids, **vitel**: vitellophages, **yome**: yolk membrane.

Embryonic development: Cleavage and germ band formation

Cleavage is meroblastic and superficial in most groups of Hexapoda and in Arthropoda in general. However, within each major arthropod lineage the holoblastic type occurs, usually in basal groups. This suggests that superficial cleavage may have been acquired independently several times. The superficial cleavage pattern is apparently linked with the large size and specific configuration of the eggs, with a thin superficial periplasm covering a large central yolk mass. Cleavage is (secondarily?) holoblastic in some groups with small eggs containing limited amounts of yolk, such as Collembola. However, holoblastic cleavage also occurs in Archaeognatha, which produce normally sized eggs (ca. 1 mm).

In the typical superficial meroblastic (=partial) cleavage the diploid zygote nucleus divides several time mitotically but without cytokinesis. This takes place in the cleavage center, a species specific region in the egg cell. The nuclei lie within the central yolk mass after the first divisions . With a small body of ovoplasma enclosing them they form energids. After several division cycles most of the nuclei migrate towards the periphery and then enter the peripherical cytoplasm (periplasma), where they form the plasmodial preblastoderm (syncytial blastoderm). The cleavage divisions can be synchronous throughout the process or become desynchronized at a certain stage (parasynchrony or asynchrony). At the periphery, mitoses continue at a progressively slower rate. After the 256 cell stage (in Drosophila) is reached, external membrane grows inwards and separates the energids.

The lateral membranes form before the basal membranes, which separate the cells from the yolk mass. The external layer of cells is referred to as cellular blastoderm. Some nuclei remain in the central yolk mass and help to mobilize the nutrients (vitellophages or yolk cells). In many groups other nuclei migrate to the pole plasm at the posterior region of the egg, where they absorb granules containing RNA and differentiate as primordial germ cells. The single-layered blastoderm is thin and loosely arranged in the early stage of its formation. Regularly shaped cubic cells are formed after further mitoses, and in the following process the blastoderm differentiates into the embryonic and extraembryonic areas. The former proliferates resulting in relatively small cells crowding to form a thickened plate, the germ band or germ anlage. The larger cells of the extraembryonic region form the serosa and adjacent to the embryo the amnion.



Blastoderm stages, formation of the embryo, cross sections (upper row) and ventral view. A, **B**, later blastoderm stages, formation of the germ anlage; **C**, germ band, formation of the embryo, **D**, early stage of segment formation in the embryo. **dclos**: dorsal closure, **ect**: ectoderm, **egeanl**: early germ anlage, **exem**: extraembryonal area, **geanl**: germ anlage, **geban**: germ band, **proce**: procephalon.

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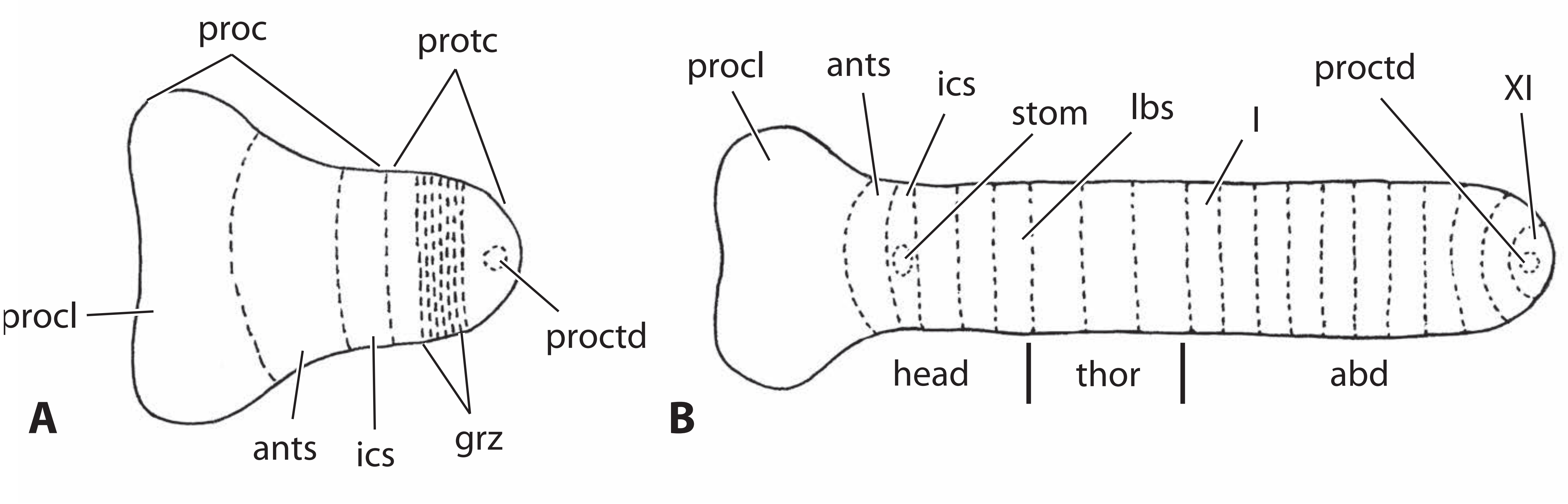
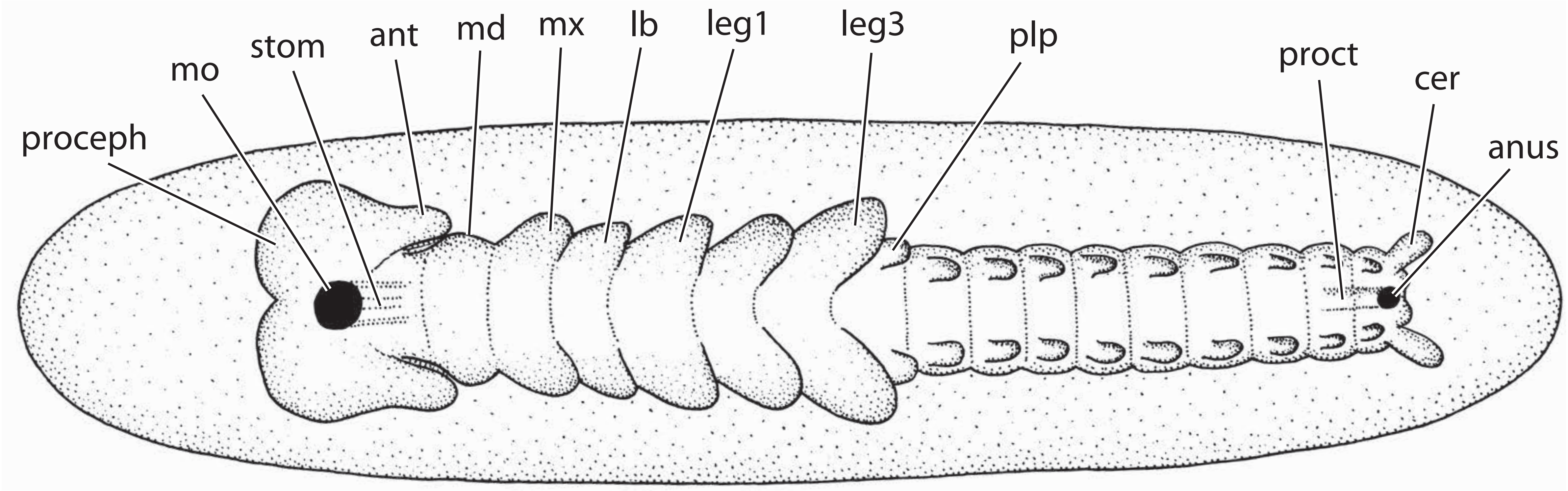


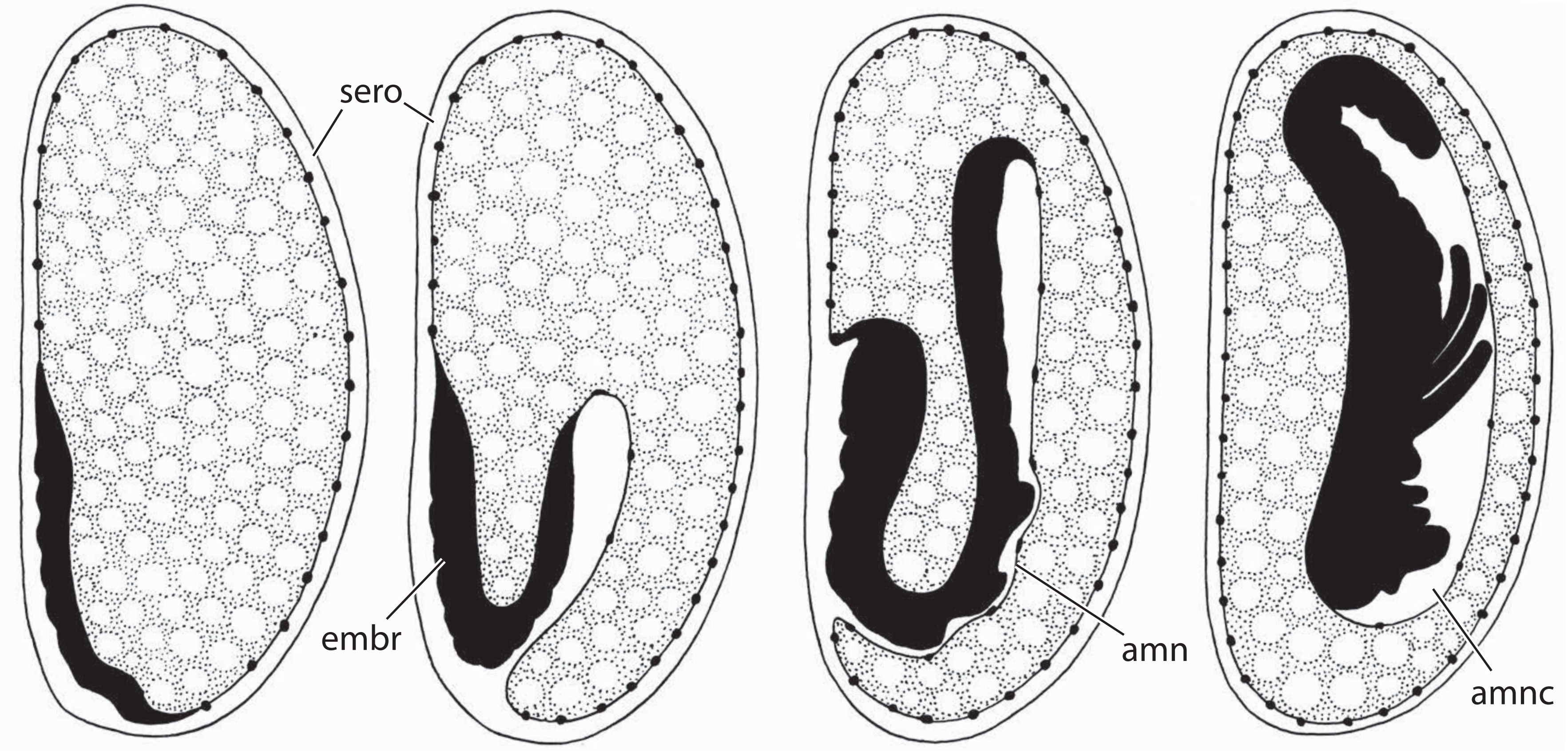
Different forms of embryos. **A**, short germ embryo; **B**, long germ embryo. **abd**: abdomen (I,XI), **ants**: antennal segment, **grz**: growth zone, **ics**: intercalary segment, **lbs**: labial segment, **proc**: proecephalon, **procl**: protocephalic lobes, **protc**: protocorm, **proctd**: proctodaeum, **stom**: stomodaeum, **thor**: horax.

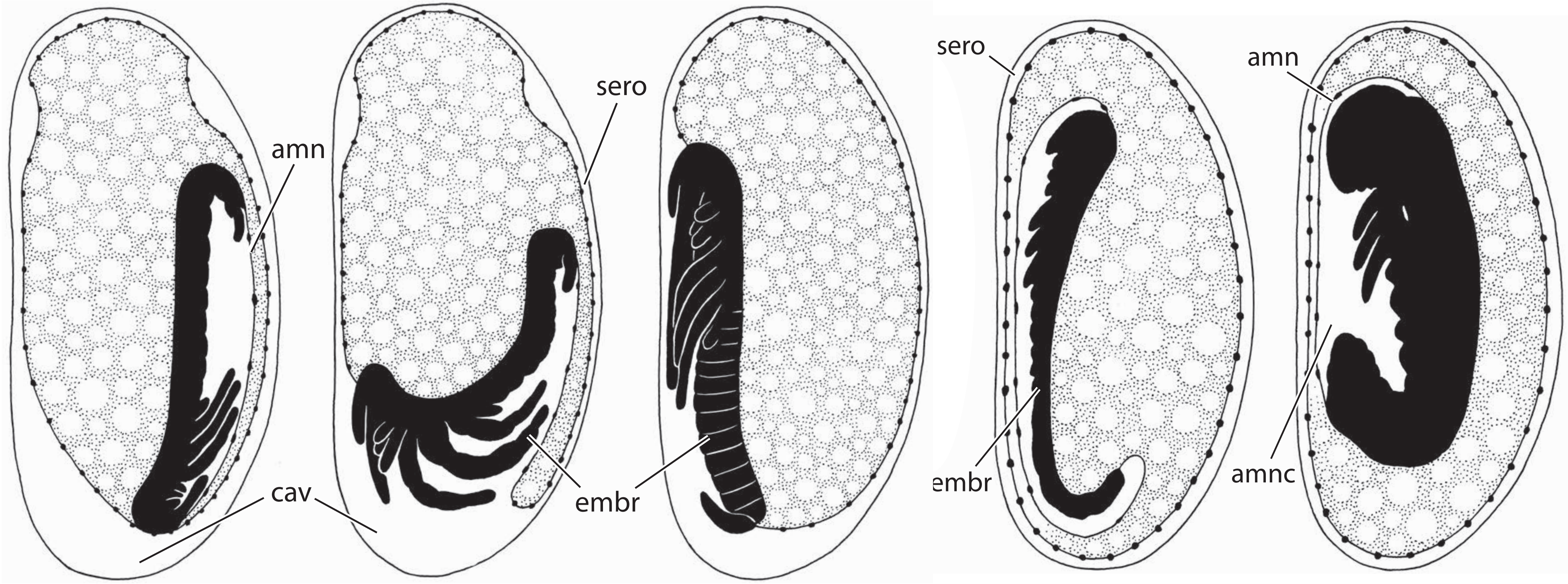


Short germ embryo at the polypod stage, after germ band elongation, gastrulation and segmentation. **ant**: antenna, **cer**: cerci, **lb**: labium, **leg1/3**: fore- / hindleg, **md**: mandible, **mx**: maxilla, **mo**: mouth opening, **plp**: abdominal pleuropodium, **proceph**: procephalon, **proct**: proctodaeum, **stom**: stomodaeum.

Blastokinesis, anatrepsis embryo shifted to the interior of the developing egg, formation of the amniotic cavity, groups with short or semi-long germ eggs.

Blastokinesis, katatrepsis, embryo shifted to the external surface of the developing egg, reversal of anatrapsis.





Blastokinesis, internalization of the embryo and formation of the amniotic cavity, groups with long germ eggs. **amn**: amnion, **amnc**: amniotic cavity, **embr**: embryo, **sero**: serosa, **cav**: coelomic cavity

Germ layer formation and blastokinesis

During the proliferation of cells of the germ anlage and the elongation of the embryo the formation of the three germ layers takes place. The ectoderm, mesoderm and entoderm are formed in a process which may be considered as a very atypical gastrulation. Longitudinally arranged midventral cells in the germ band move upward into a space between the embryo and the yolk, thus forming an inner layer of mesoderm. The ectoderm is formed by the remaining cells on the surface. The inner layers can be formed in three different ways: by formation of a midventral furrow that subsequently closes over (most orders), by lateral overgrowth of a midventral plate (Hymenoptera, e.g., Apis), or by ingression of individual ventral midline cells (Lepidoptera).

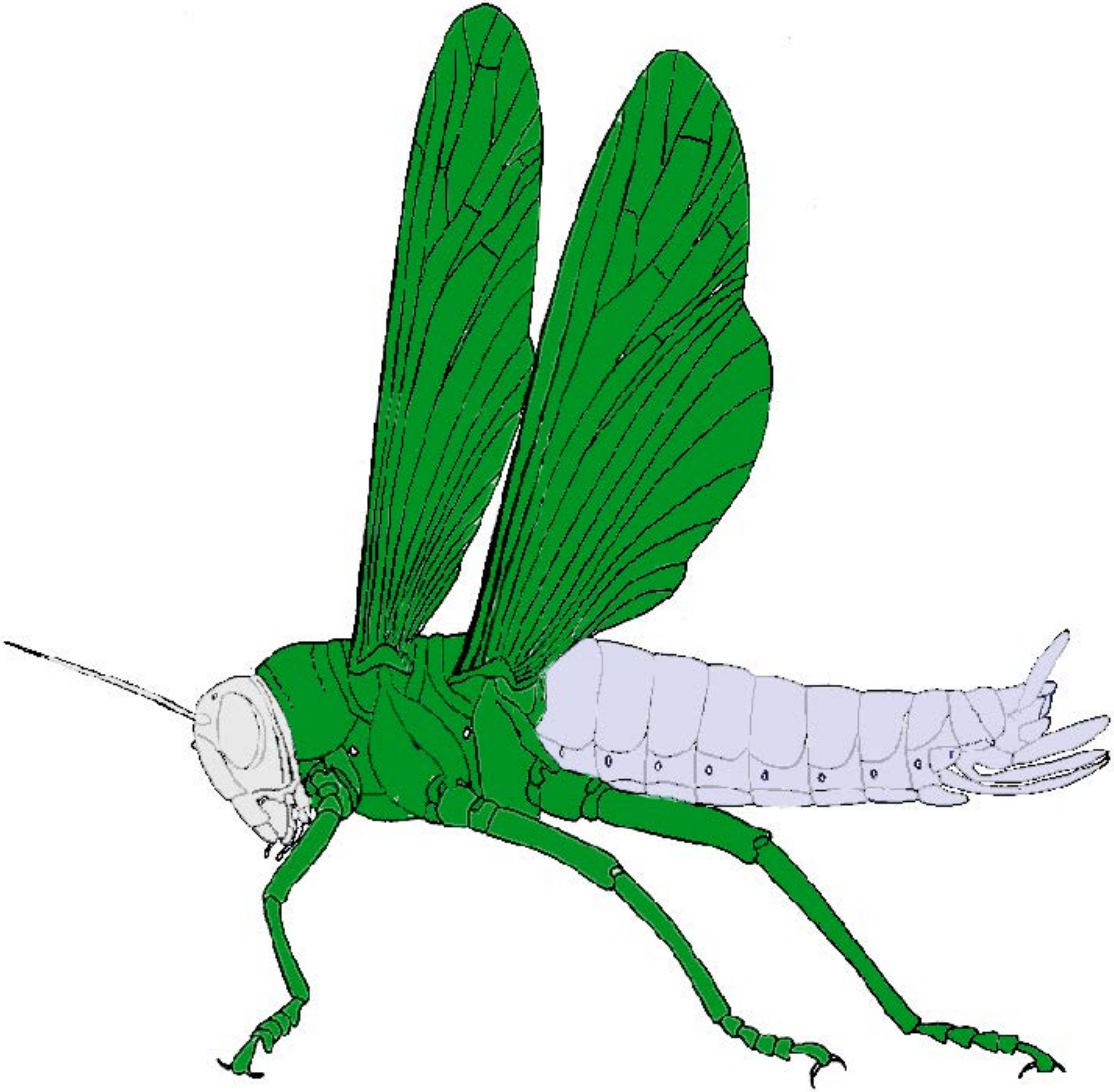
In groups with short or semi-long germ eggs the embryo is shifted to the central region containing the yolk mass by a rotation (anatrepsis). This results in the formation of the amniotic cavity. Later in development a reverse movement called katatrepsis results in return to the original external position of the embryo; both movements collectively being referred to as blastokinesis. The process differs in groups with a long germ egg. The embryo remains on the ventral side of the egg throughout embryogenesis. The amnion is formed by amnioserosal folds which arise at the margins of the embryo and extend inward and fuse midventrally, thus enclosing an amniotic cavity and the embryo. Formation of an amnionic cavity is a groundplan apomorphy of Insecta.

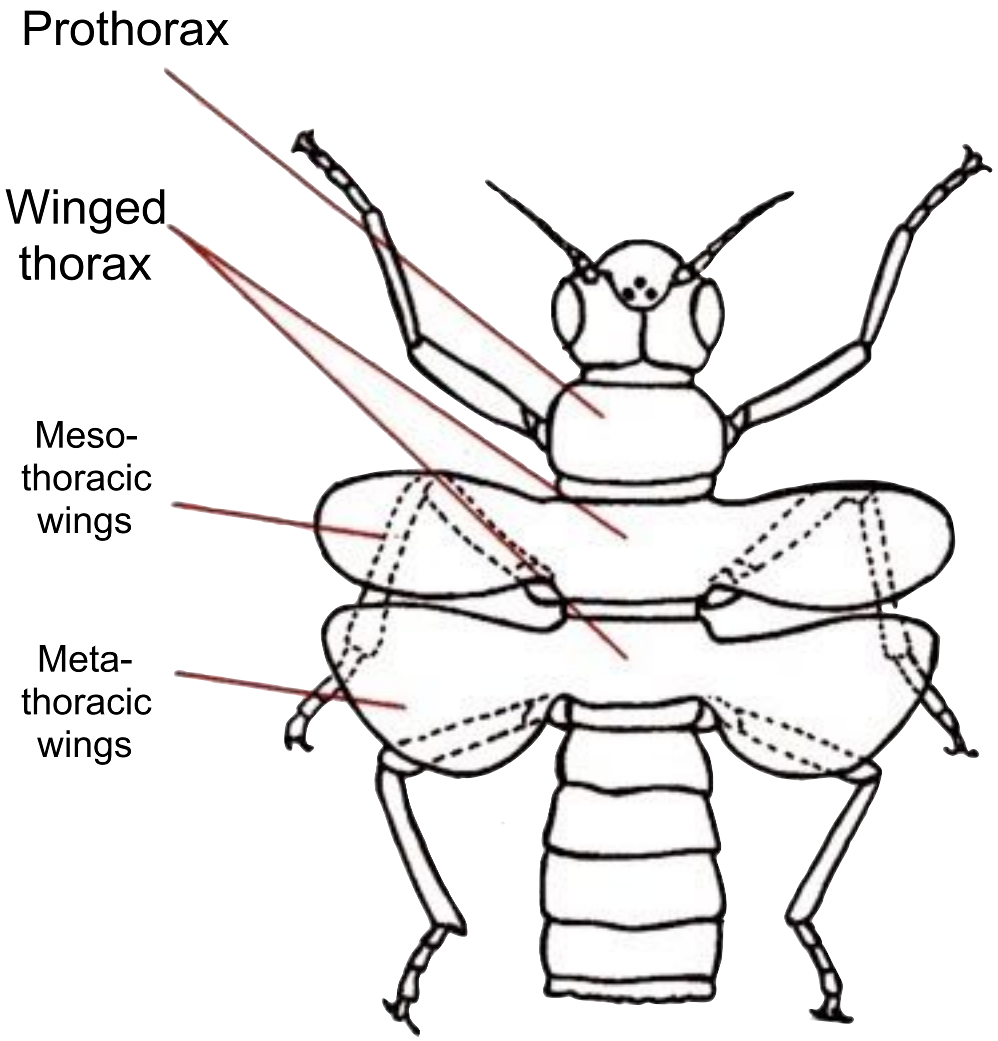
Segmentation

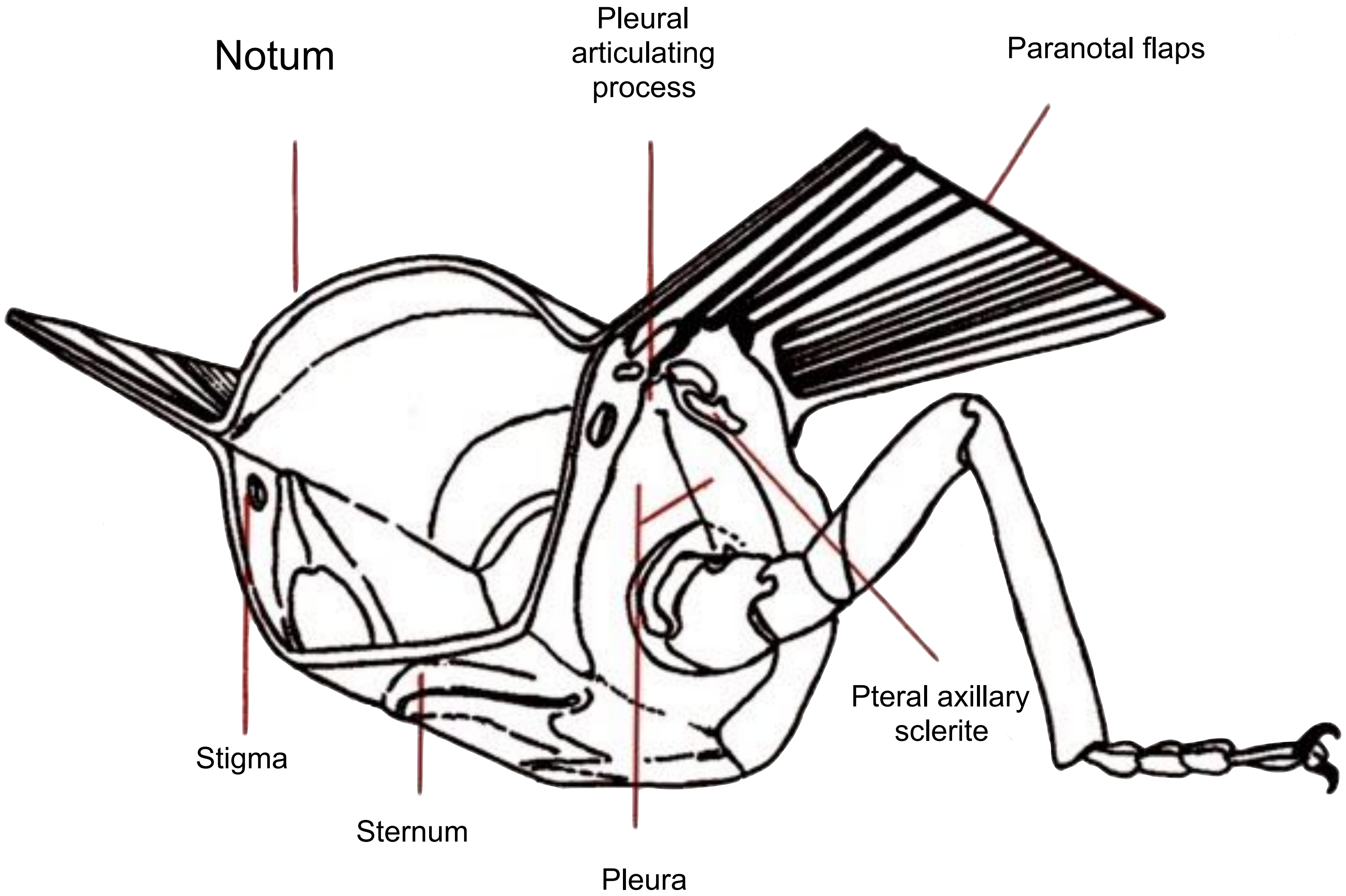
After the inner layer is formed the embryo is divided into segments by transverse furrows. In members of most orders each of the segments develops a pair of appendages, the antennae and three gnathal appendages (prospective mouthparts) in the cephalic region, three pairs of thoracic legs, ten pairs of abdominal appendages, and cerci on abdominal segment XI. Those of segment I develop into pleuropodia. Those of segments II—IX develop into simplified abdominal legs (coxites bearing styli and coxal vesicles) in apterygote lineages and into prolegs in some groups of Holometabola (symphytan larvae, lepidopteran caterpillars), but disappear before hatching in most hexapod orders.

Traditionally the protocephalon was considered as a unit composed of an acron and three pregnathal segments, the first of them bearing the labrum. A recent developmental study with a focus on the segment polarization gene engrailed has shown that it is in fact composed of an anterior ocular segment, an antennal segment, and an intercalary segment 3 with the labrum. The protocephalic lobes give rise to the protocerebrum including the optic lobes and lateral eyes. The ectodermal stomodaeum (prospective foregut) invaginates medially on the intercalary 3rd segment.

05 Torax







The thorax consists of three segments known as the pro-, meso- and meta-thoracic segments. In most insects all three segments bear a pair of legs, in addition, winged insects have a pair of wings on the meso- and meta-thoracic segments and these two segments are then collectively known as the pterothorax.

The tergum of the prothoracic segment is known as the pronotum. It is often small serving primarily for attachment of the muscles of the first pair of legs, but in Orthoptera, Blattodea and Coleoptera it forms a large plate affording some protection to the pterothoracic segments. The meso- and meta-nota are relatively small in wingless insects and larvae, but in winged insects they become modified for the attachment of the wings.

Various strengthening ridges develop on the tergum of a wing-bearing segment. These are local adaptations to the mechanical stresses imposed by the wings and their muscles. The ridges appear externally as sulci which divide the notum into areas. Often a transverse sulcus divides the notum into an anterior prescutum and a scutum, while a V-shaped sulcus posteriorly cuts off the scutellum. These areas are commonly demarcated, but, because of their origins as functional units, plates of the same name in different insects are not necessarily homologous.

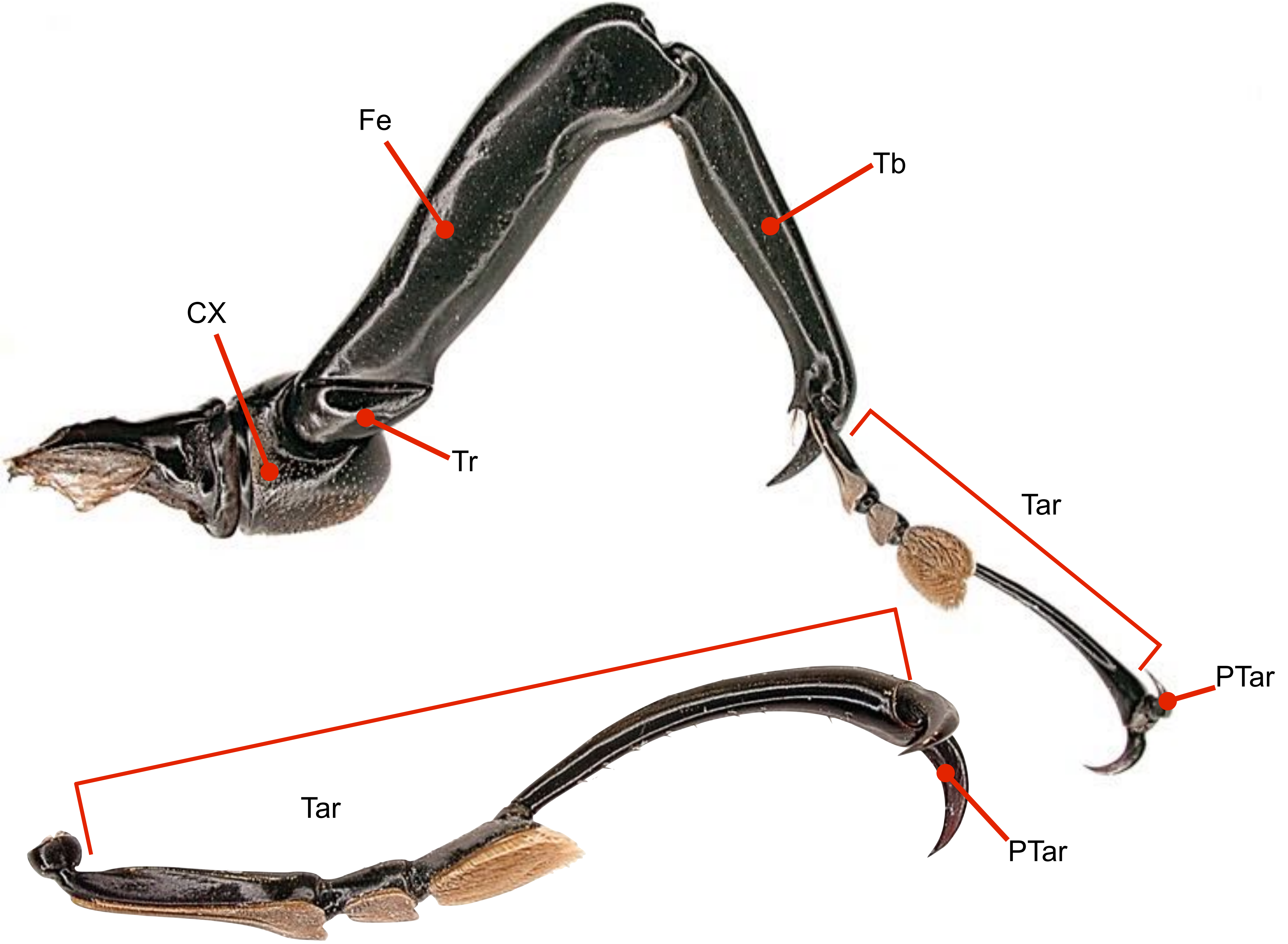
Sternum The primary sclerotizations on the ventral side are segmental and inter segmental plates which often remain separate in the thorax.

The sternum of the pterothoracic segments does not differ markedly from that of the prothorax, but usually the basisternum is bigger, providing for the attachment of the large dorsoventral flight muscles. Arising from the eusternum are a pair of apophyses, the so-called sternal apophyses. The origins of these on the sternum are marked externally by pits joined by a sulcus so that the eusternum is divided into a basisternum and sternellum, while in higher insects the two apophyses arise together in the midline and only separate internally, forming a Y-shaped furca. The sternal apophyses also serve for the attachment of the bulk of the ventral longitudinal muscles.

Pleuron The pleural regions are membranous in many larval insects, but typically become sclerotized in the adult. Basically there are probably three pleural sclerites, one ventral and two dorsal, which may originally have been derived from the coxa. The ventral sclerite, or sternopleurite, articulates with the coxa and becomes fused with the sternum so as to become an integral part of it. The dorsal sclerites, anapleurite and coxopleurite, are present as separate sclerites in Apterygota and in the prothorax of larval Plecoptera. In other insects they are fused to form the pleuron, but the coxopleurite, which articulates with the coxa, remains partially separate in the lower pterygote orders forming the trochantin and making a second, more ventral articulation with the coxa. Above the coxa the pleuron develops a nearly vertical strengthening ridge, the pleural ridge, marked by the pleural sulcus externally. This divides the pleuron into an anterior episternum and a posterior epimeron. The pleural ridge is particularly well developed in the wing-bearing segments, where it continues dorsally into the pleural wing process which articulates with the second axillary sclerite in the wing base.

In front of the pleural process in the membrane at the base of the wing and only indistinctly separated from the episternum are one or two basalar sclerites, while in a comparable position behind the pleural process is a well-defined subalar sclerite. Muscles concerned with the movement of the wings are inserted into these sclerites.

Typically there are two pairs of spiracles on the thorax. These are in the pleural regions and are associated with the mesothoracic and metathoracic segments. The mesothoracic spiracle often occupies a position on the posterior edge of the propleuron, while the smaller metathoracic spiracle may similarly move on to the mesothorax.



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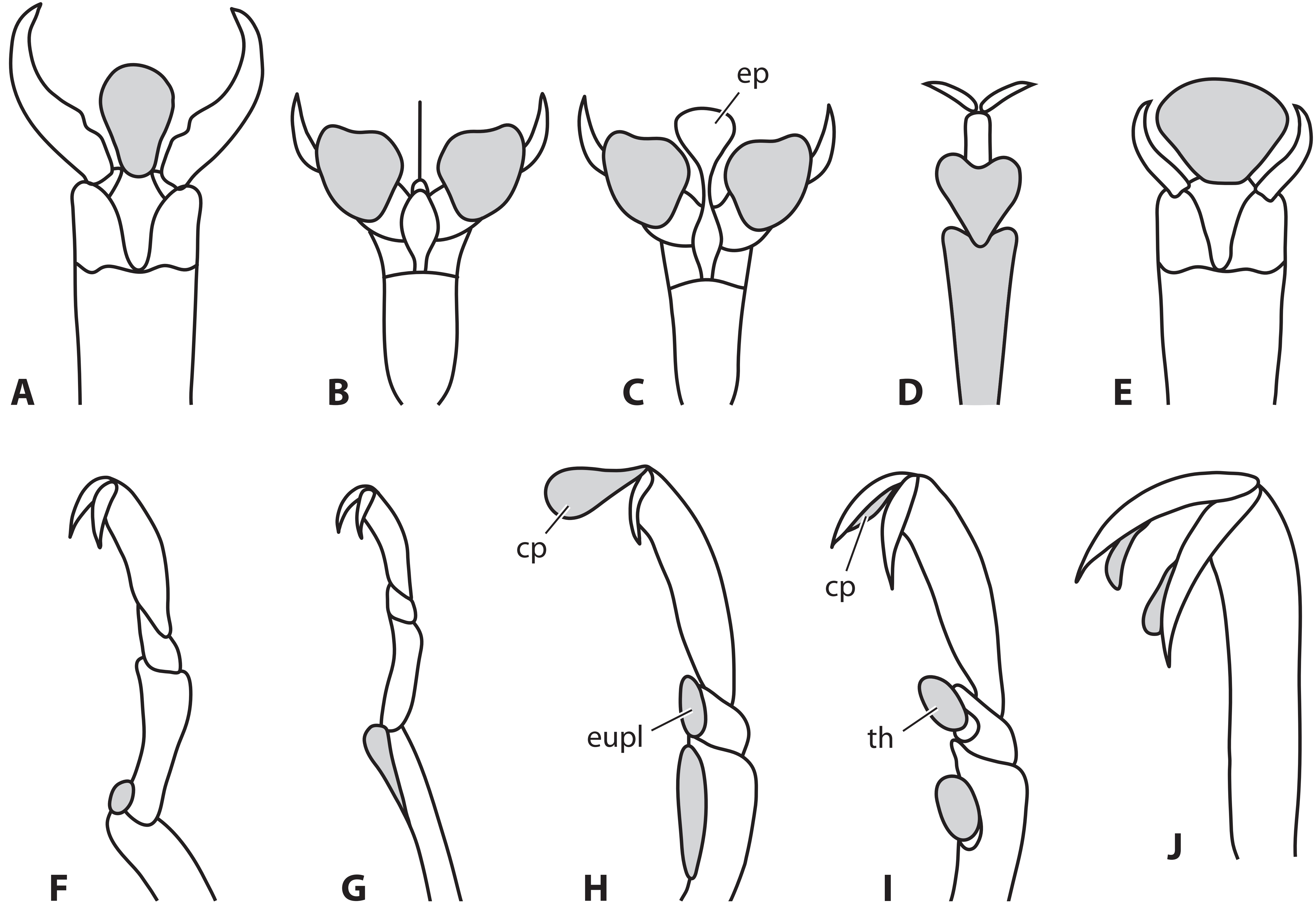
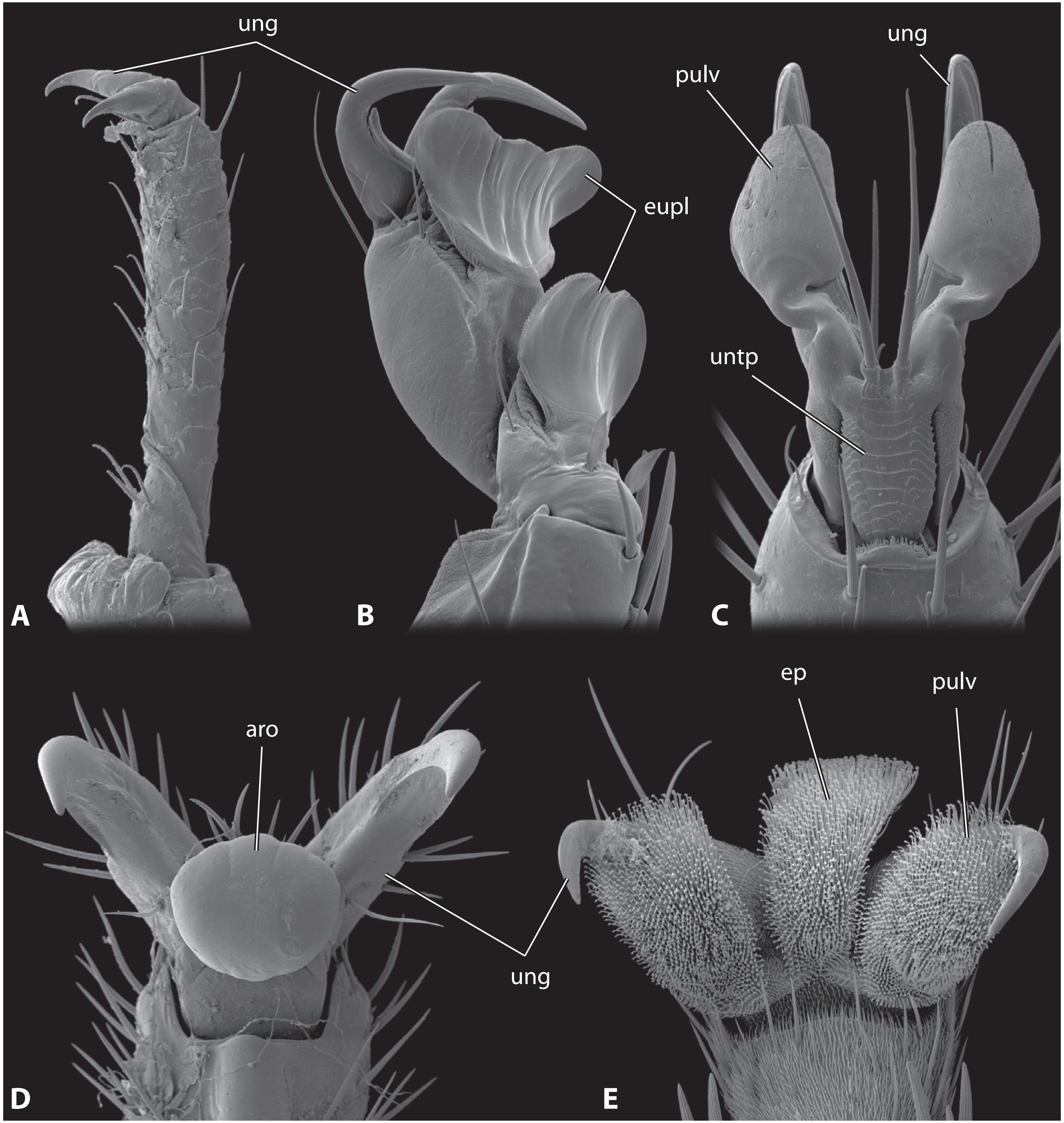
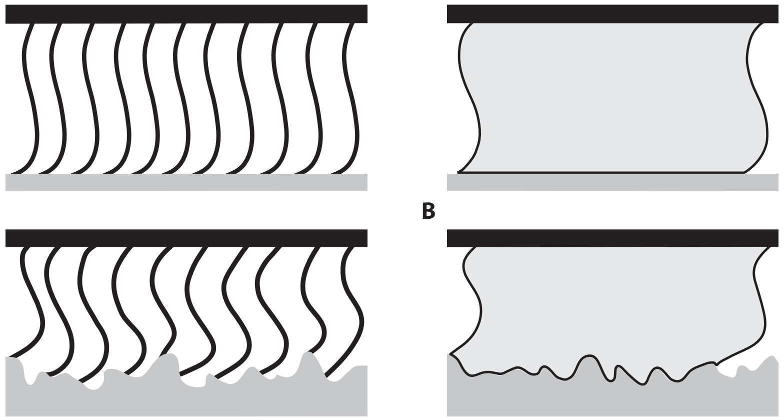


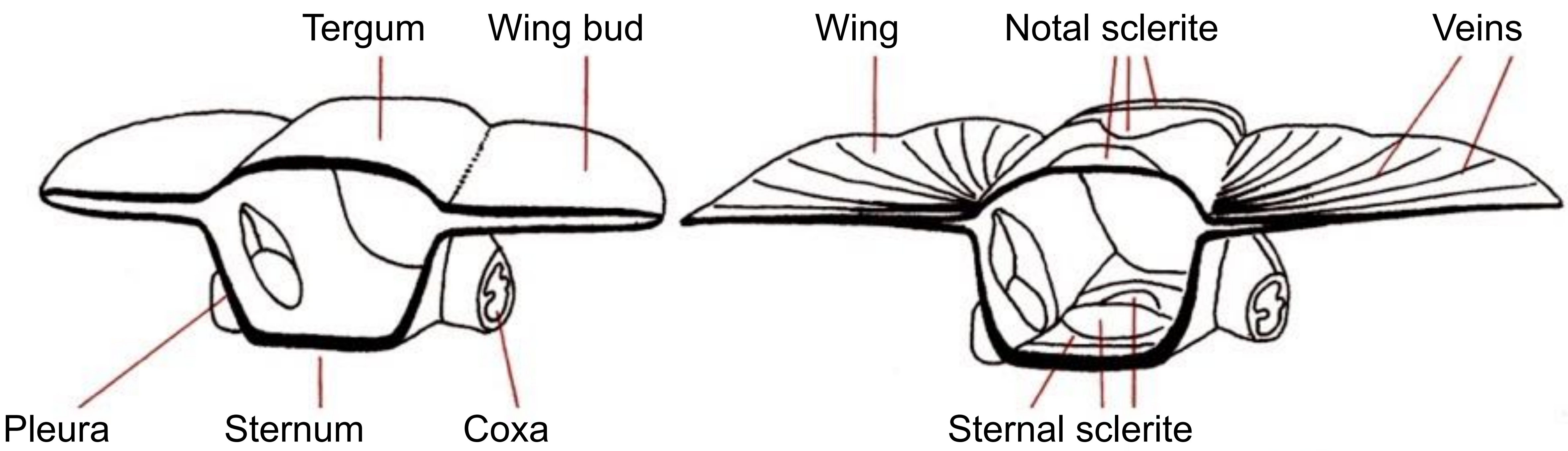
Attachment structures (grey) A: pretarsal arolium (almost always smooth); **B:** pretarsal pulvilli (smooth or hairy); **C:** widened empodium with adhesive microtrichia; **D:** hairy adhesive soles of tarsomeres; **E:** pretarsal protrusible vesicle (arolium); **F:** eversible adhesive structure between tibial apex and tarsus; **G:** hairy fossula spongiosa; **H:** tarsal euplantulae, almost always smooth; **I:** tarsal plantar lobes; **J:** adhesive claw setae. **ep:** empodium, **cp:** claw pad, **eupl:** euplantulae, **th:** tarsal horns.



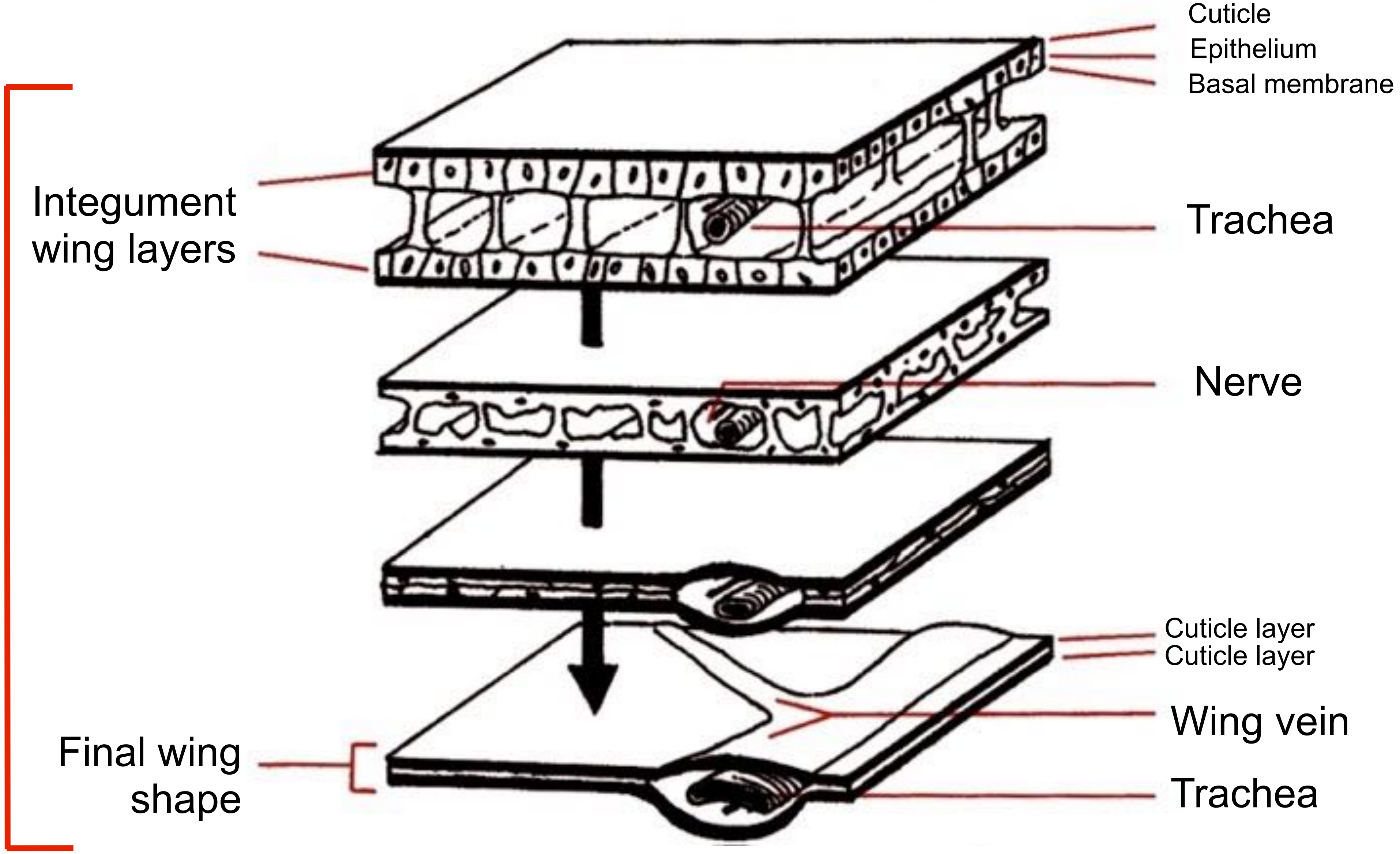


Function of different types of tarsal or pretarsal attachment structures. **A:** hairy type; **B:** smooth type.

Attachment structures SEM micrographs. **A:** *Aphis sambuci* (Sternorrhyncha, Aphididae); **B:** *Trinoton anserinum* (Amblycera, Menoponidae); **C:** *Graphosoma lineatum* (Heteroptera, Pentatomidae); **D:** *Locusta migratoria* (Orthoptera, Acrididae); **E:** *Tabanus* sp. (Diptera, Tabanidae). Abbr.: **aro:** arolium, **ep:** empodium, **eupl:** euplantulae, **pulv:** pulvilli, **ung:** ungues (claws), **untp:** unguitractor plate.



Wing growth during insect development



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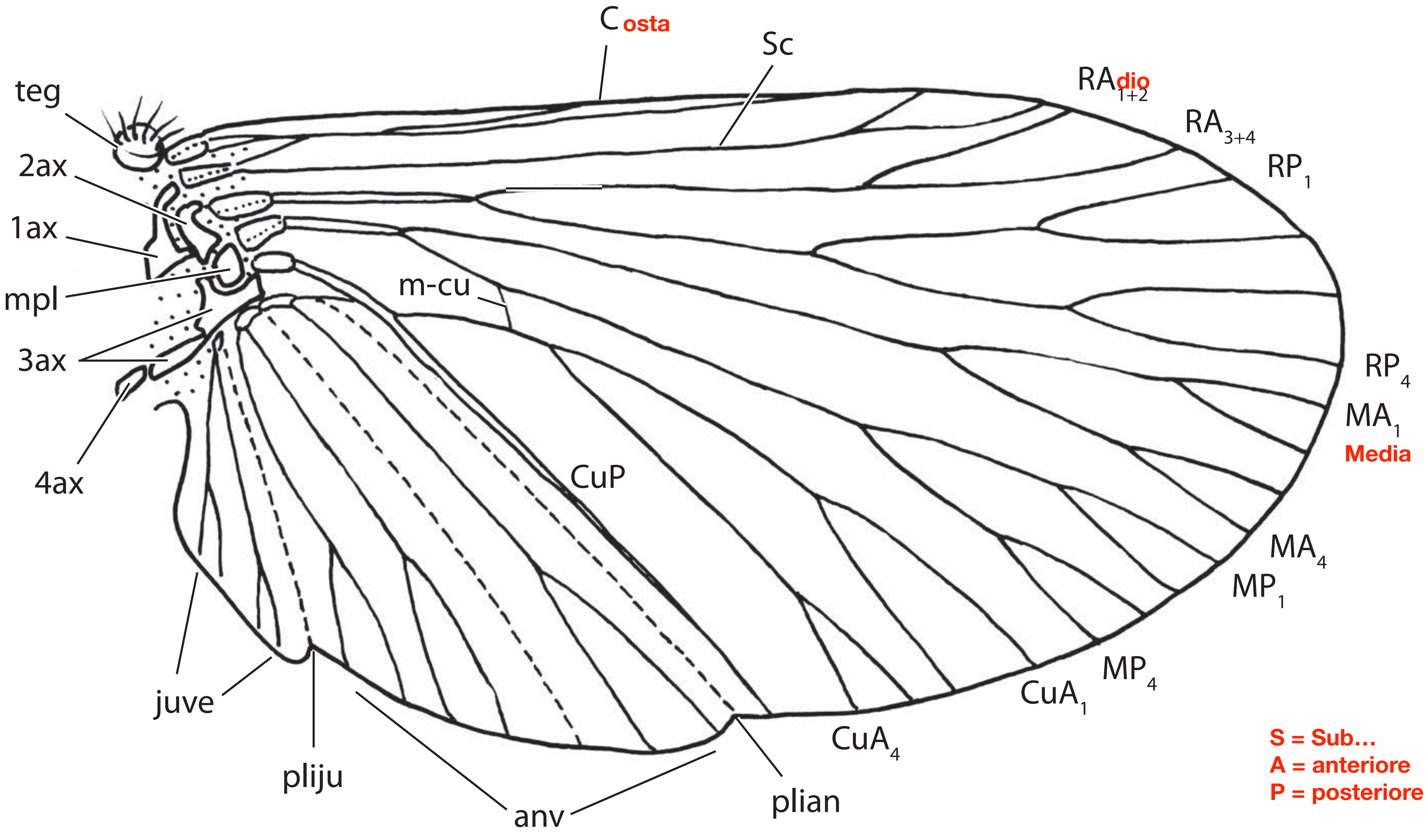
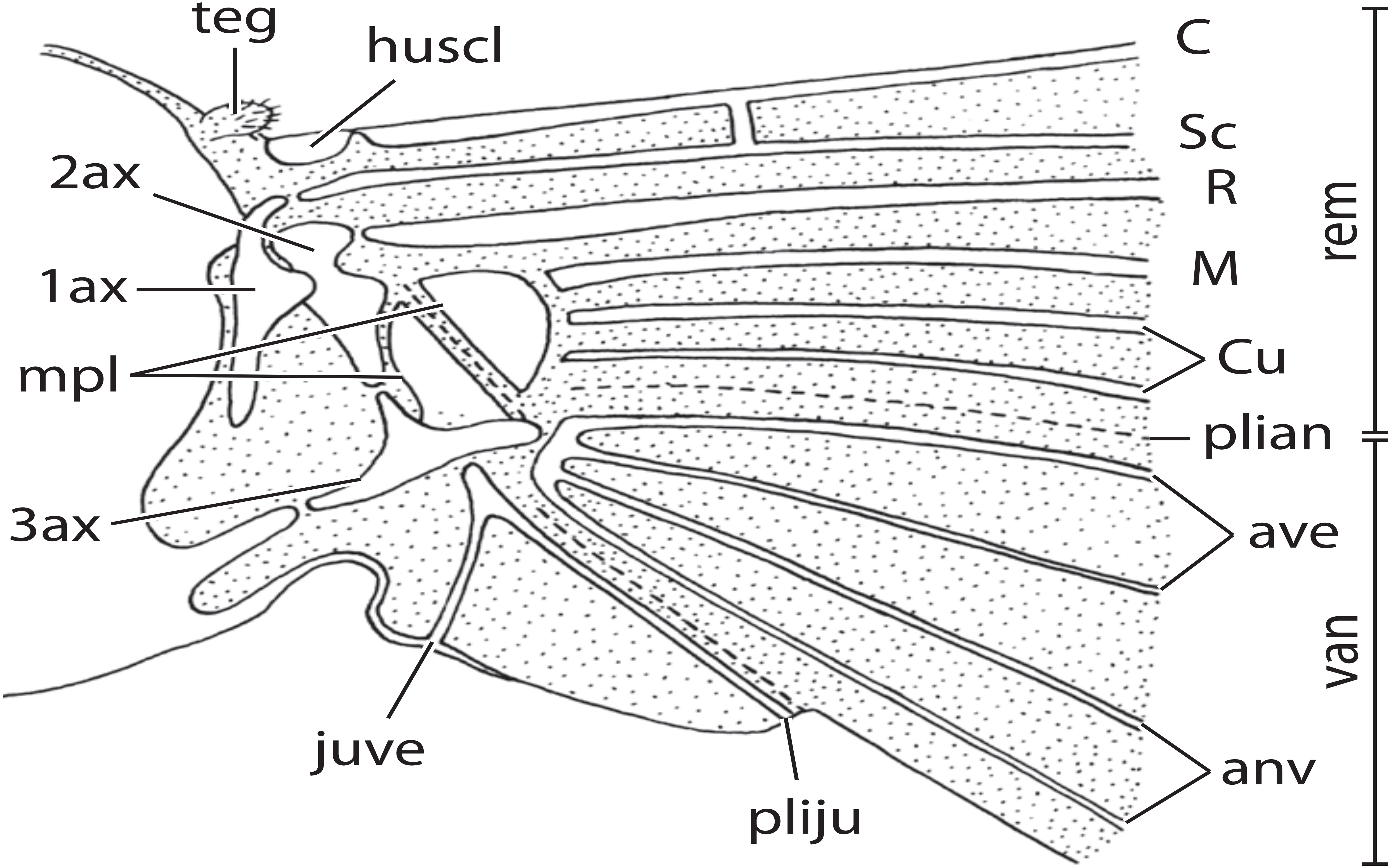


S = Sub…
A = anteriore
P = posteriore

Neopteran wing, generalized: 1–4ax: 1st – 4th axillary sclerite, **anv:** anal veins, **C:** costa, **CuA1/4:** branches of cubitus anterior, **CuP:** cubitus posterior, **juve:** jugal veins, **MA1/4:** branches of media anterior, **m-cu:** medio-cubital vein, **MP1/4:** branches of media posterior, **mpl:** median plate, **plian:** plica analis, **pliju:** plica jugalis, **RA1+ 2, 3+4:** branches of radius anterior, **RP1/4:** branches of radius anterior, **Sc:** subcosta, **teg:** tegula.



Neopteran wing base. **1–3ax:** 1st-3rd axillary sclerite (4th usually missing), **ave:** anal veins, **C:** costa, **Cu:** cubitus, **huscl:** humeral sclerite, **juve:** jugal veins, **M:** media, **mpl:** median plates, **plian:** plica analis, **pliju:** plica jugalis, **R:** radius, **rem:** remigium (costal field), **Sc:** subcosta, **teg:** tegula, **van:** vannus (anal field).

Wings

The wings are doubtlessly an autapomorphy of Pterygota but their evolutionary origin is disputed. The traditional hypothesis suggests that they originated from meso- and metathoracic paranota. The alternative exite or gill theory hypothesizes an origin from basal leg appendages (exites), which are considered as serial homologues of abdominal gills as they occur in aquatic larvae of some extant groups (e.g., Ephemeroptera, Megaloptera). In any case, the highly complex structure of the wings clearly indicates a single origin in the evolution of Hexapoda. Different modifications occur but the ancestral pattern is almost always still recognizable.

Fully developed wings occur only in mature insects, with the notable exception of the subimago of Ephemeroptera. They are connected to the lateral edge of the scutum (alinotum) and the upper margin of the pleuron, involving three axillary sclerites of the wing base in most groups of Pterygota. An atypical condition is found in Odonata, which like Ephemeroptera are unable to fold back their wings (Palaeoptera). They possess only two large plates (**humeral** and **axillary plate**) hinged to the scutum and supported by two arms of the pleural wing process. Three **axillary sclerites** are present in Ephemeroptera and most groups of Neoptera, but four in Orthoptera, Hymenoptera and Diptera. They are embedded in the double membrane at the wing base and form a complicated 3-dimensional functional complex. Axillary 1 is a part of the dorsal membrane and articulates mesally with the anterior notal wing process, anterolaterally with the subcostal vein, and laterally with axillary 2. Axillary 2 is a sclerotisation of both, the dorsal and the ventral membrane (at least in some groups). Mesally it articulates with axillary 1, ventrally with the pleural wing process, and posteriorly with axillary 3. Anterolaterally it is connected with the third major longitudinal vein, the **radius** (R), and laterally it is adjacent with the **median plates** (see below). Axillary 3 is usually Y-shaped. Its posterolateral margin is adjacent with the bases of the **anal** (A) and **jugal veins** (J; if present) and its posterior edge articulates with the posterior notal wing process. In Neoptera a muscle attached to axillary 3 triggers the rotation of this sclerite. As a consequence the wings can be folded back over the abdomen (autapomorphy of Neoptera).

A structure at the posterior wing base is the **axillary cord**. It connects the posterolateral edge of the alinotum with the posterior wing base. The **tegula** is a characteristic small lobe at the anterior wing margin. It is unsclerotized and covered with short sensilla trichodea. It is closely connected with the **humeral plate**, a small sclerotisation at the anterior wing base, which is laterally connected with the anteriormost longitudinal vein, the **costa** (C).

A simple criterion to distinguish between the wing base and the wing plate is that both membranes are completely fused in the latter, without epidermal cells between them. A proximal structure of the wing interacting with the axillaries 2 and 3 is the **median plate**. In the typical case it is diagonally subdivided into a proximal and a distal subunit (proximal and distal plate) and is in contact with the bases of three major longitudinal veins laterally, the **media** (M), the **cubitus** (Cu) and the **postcubitus** (PCu).

The very thin sheath formed by the connected two wing membranes is reinforced by a system of longitudinal and transverse veins. Only the longitudinal veins contain haemolymph, tracheae and nerves. Their arrangement on alternating levels (costa convex, subcosta concave etc.) results in a structure resembling corrugated iron, which also increases the mechanical stability of the thin wing foil. The transverse veins are solid structures. They form a dense reticular network in some basal neopteran lineages, the **archedictyon** (probably a groundplan feature of Pterygota). This condition is preserved in the extant Ephemeroptera, Odonata (Palaeoptera) and Orthoptera, and also in the extinct †Palaeodictyoptera, which have also preserved prothoracic winglets with such a veinous pattern. In most extant groups the number of transverse veins is strongly reduced. They are completely absent in extant Strepsiptera and some other lineages.

The wing is subdivided into three main regions. The anterior **remigium** or **costal field** is the most extensive part and plays a dominant role in flight. The posteriorly adjacent **anal field** or **vannus** usually displays a fan-shaped pattern of veins. The **jugal field** at the posterior wing margin is small and completely absent in many groups. The remigium is usually subdivided by the median flexion line, which originates close to the media (M) and runs behind the radial sector (RP) (see below). The **plica vannalis** runs close to the postcubitus and separates the costal and anal fields. Additionally, a **plica jugalis** separating the anal and jugal fields can be present.

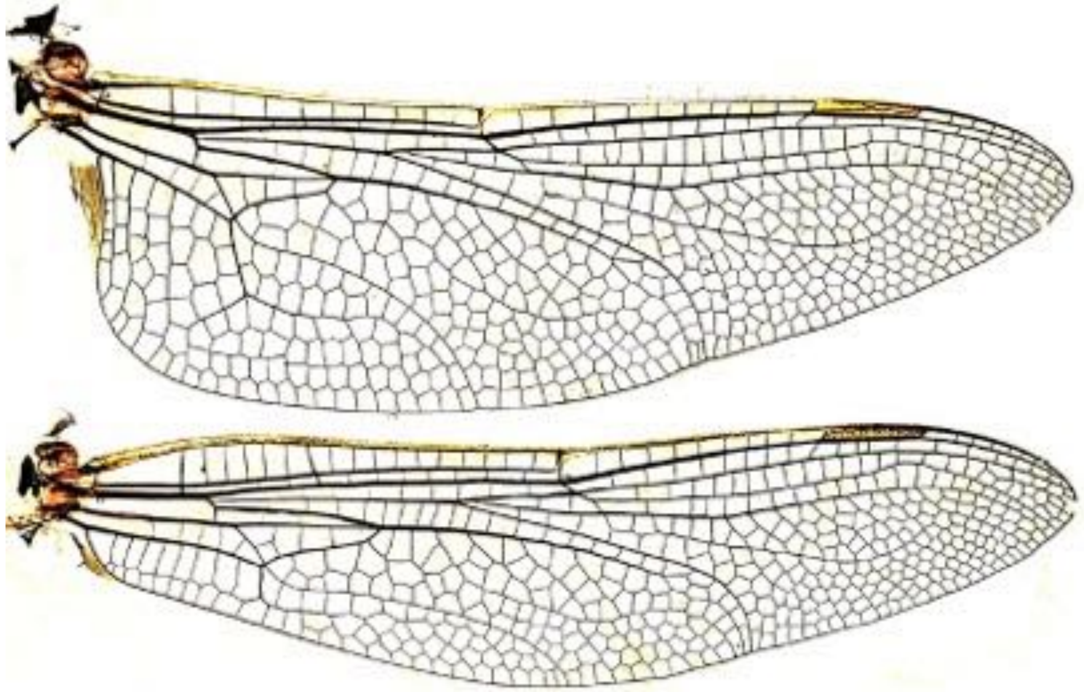
The first and strongest vein of the remigium is the unbranched **costa** (C). The following vein, the **subcosta** (Sc), often branches once. The **radius** (R) usually divides several times. Its anterior primary branch is referred to as **radius anterior** (RA) and the posterior one as **radial sector** or **radius posterior** (RP). The secondary branches are usually designated by subscripts (e.g., RA_1, RA_2). Connections by transverse veins resulting in closed radial cells occur frequently. The next vein, the **media** (M), also divides several times. The primary branches are the media anterior (MA) and the media posterior (MP). Similarly, the following **cubitus** (C) branches into the cubitus anterior (CuA) and cubitus posterior (CuP), both again dividing into further secondary and tertiary branches. The posteriormost longitudinal vein of the remigium is the **postcubitus** (PCu). The anal field is usually subdivided by several **anal veins** (1A, 2A, etc.). The small jugal field occasionally bears one or two short veins in some groups, but is often devoid of veins or reduced (see above).

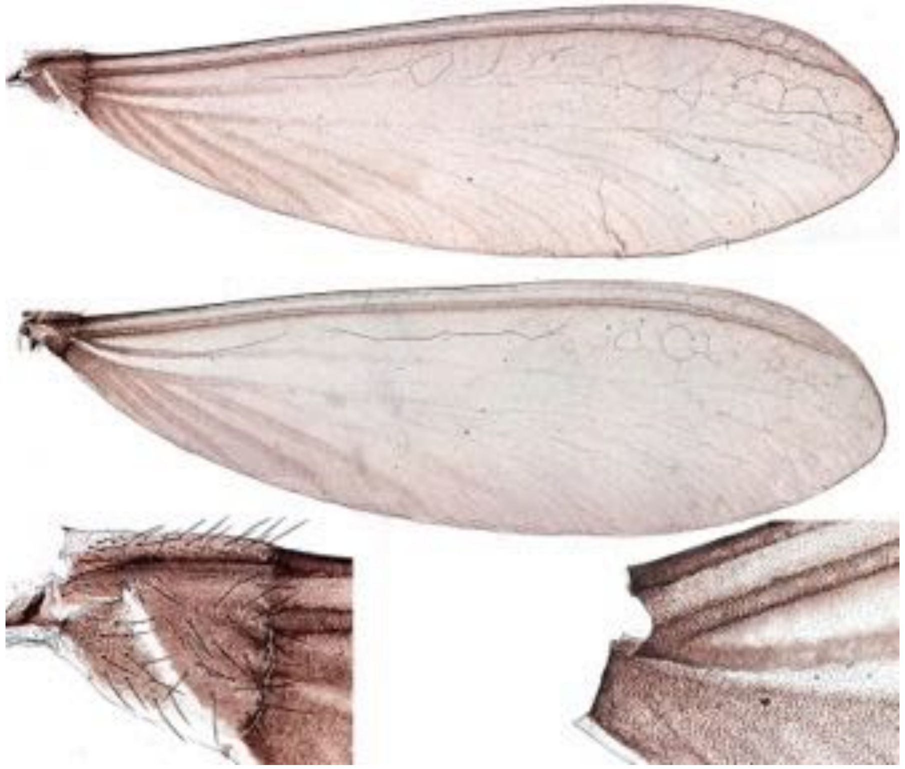
The surface of the wing is usually more or less densely covered with very short microtrichia. The wing membrane can be partly or entirely transparent (e.g., Hymenoptera) but color patterns occur frequently, most conspicuously in Lepidoptera. A specialized structure of the anterior margin is the **pterostigma**, a pigmented spot occurring in Odonata and some other groups (e.g., Psocoptera, Megaloptera).

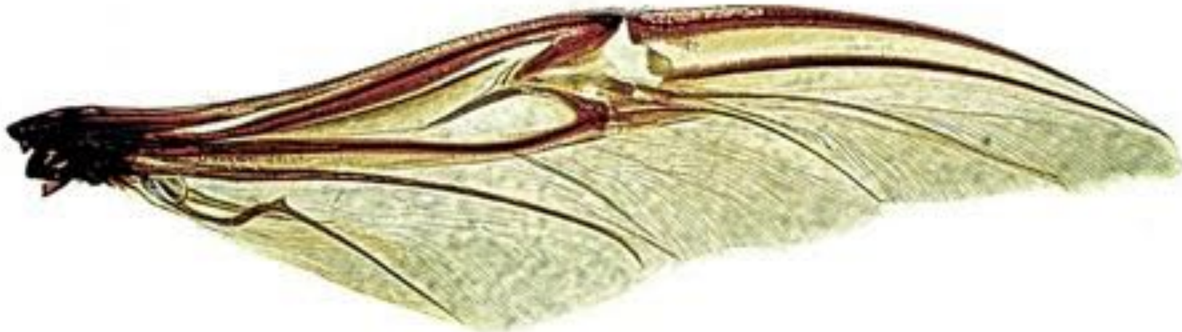
Different modifications and reductions of wings occur in pterygote insects. They are completely absent in all known species of Grylloblattodea, Mantophasmatodea and Siphonaptera and also in subordinate lineages of other groups (e.g., Phasmatodea). Alate and wingless morphs occur in Zoraptera and some subordinate lineages (e.g., Isoptera, Formicidae). Females of Embioptera are always wingless, whereas males have simplified wings which are shed after a short mating flight. The forewings are moderately sclerotized **tegmina** in different groups of Polyneoptera (e.g., Orthoptera, Blattodea). The anterior part of the forewings is sclerotized in Heteroptera (**hemielytra**) and the entire forewings in Coleoptera (**elytra**). The anal field of the hindwings of different polyneopteran lineages is enlarged, with a fan-like folding pattern (Plecoptera [partim], Orthoptera, Dictyoptera [excl. Isoptera], Dermaptera).

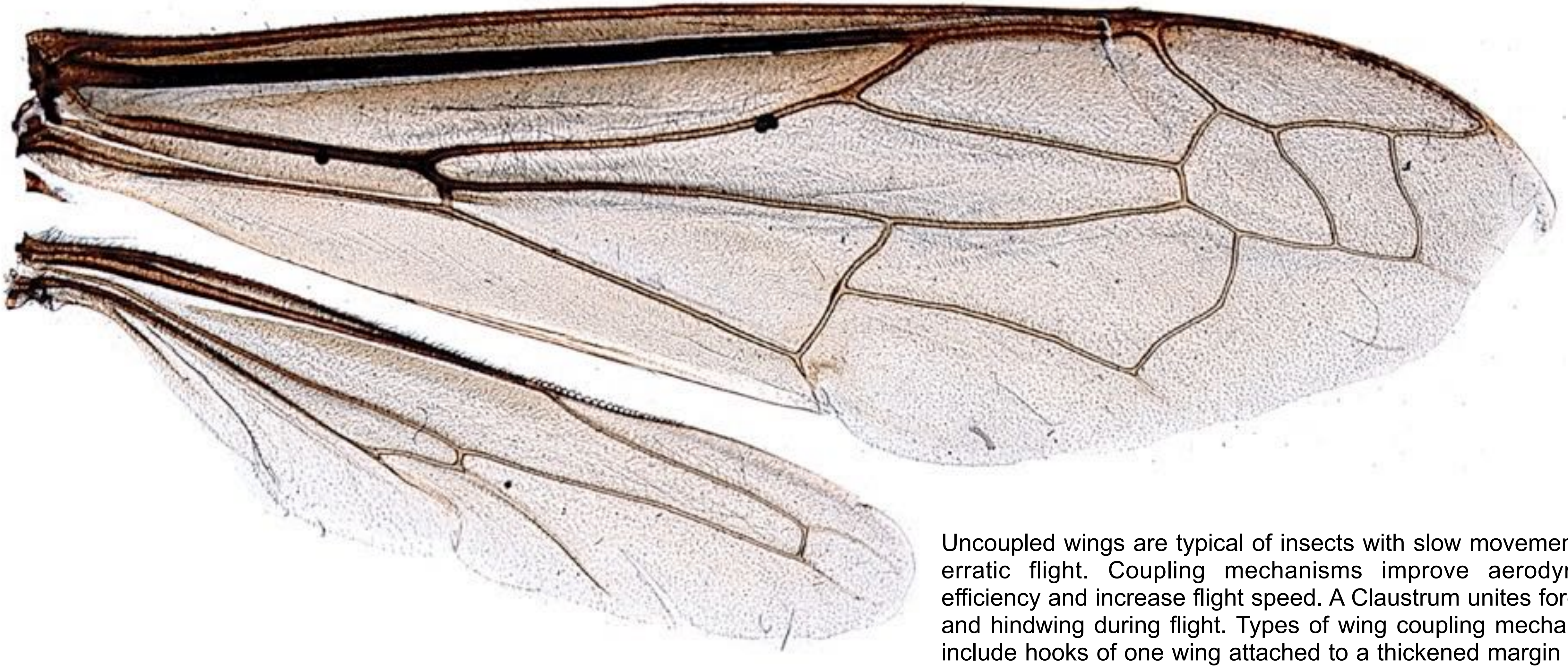
Aside from the ability to fold back the wings (autapomorphy of Neoptera) different transverse or longitudinal folding patterns occur. This is always linked with modifications of veins such as articulations (Scarabaeoidea) or bending zones (e.g., other groups of Coleoptera). A complicated mechanism of folding the greatly enlarged anal field has evolved in Dermaptera, which store the modified hindwings under the strongly shortened and sclerotized forewings. The hindwings of Diptera are modified as **halteres**, which are highly specialized gyroscopic sense organs and stabilize the flight by their rotating movements. A very similar condition has evolved independently in Strepsiptera, where the forewings are transformed into halteres. A typical modification of wings of very small insect is the reduction of the wing membrane to narrow straps with only one or two longitudinal veins, and fringes of long bristles along the margin. The air has an increased viscosity for these minute insects (low Reynolds number). Their modified wings enable them to “swim” through this medium. This condition has independently evolved in Thysanoptera and in some groups of Coleoptera.

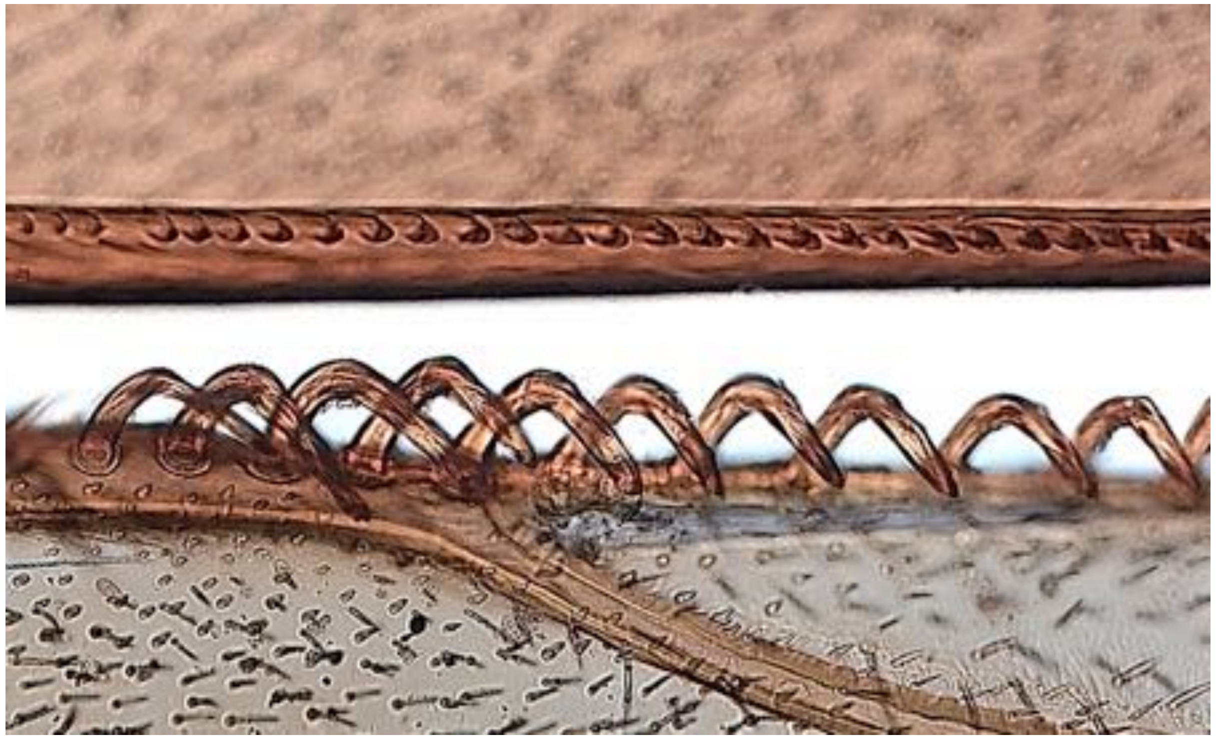
Insect wings are paired, often membranous and reticulated cuticular expansion of dorsolateral portion of Mesothorax and Metathorax. Wings are appendages derived from Integument and consist of a dorsal and ventral lamina. Forewings (primaries) are attached to Mesothorax; hindwings are attached to Metathorax. Wings are specifically adapted as organs of flight in insects, or modified to protect the pair of wings involved in flapping flight. Wings first appear in fossils during the Carboniferous. and were present in most Species collected from that Period. Insect groups that do not bear wings show many modifications to the Thorax. Environmental factors can promote or maintain flightlessness. Parasitism is a lifestyle in which wings may be a liability, particularly when living on a vertebrate host. Wingless parasitic insects comprise entire Orders (e.g. Mallophaga, Anoplura and Siphonaptera).



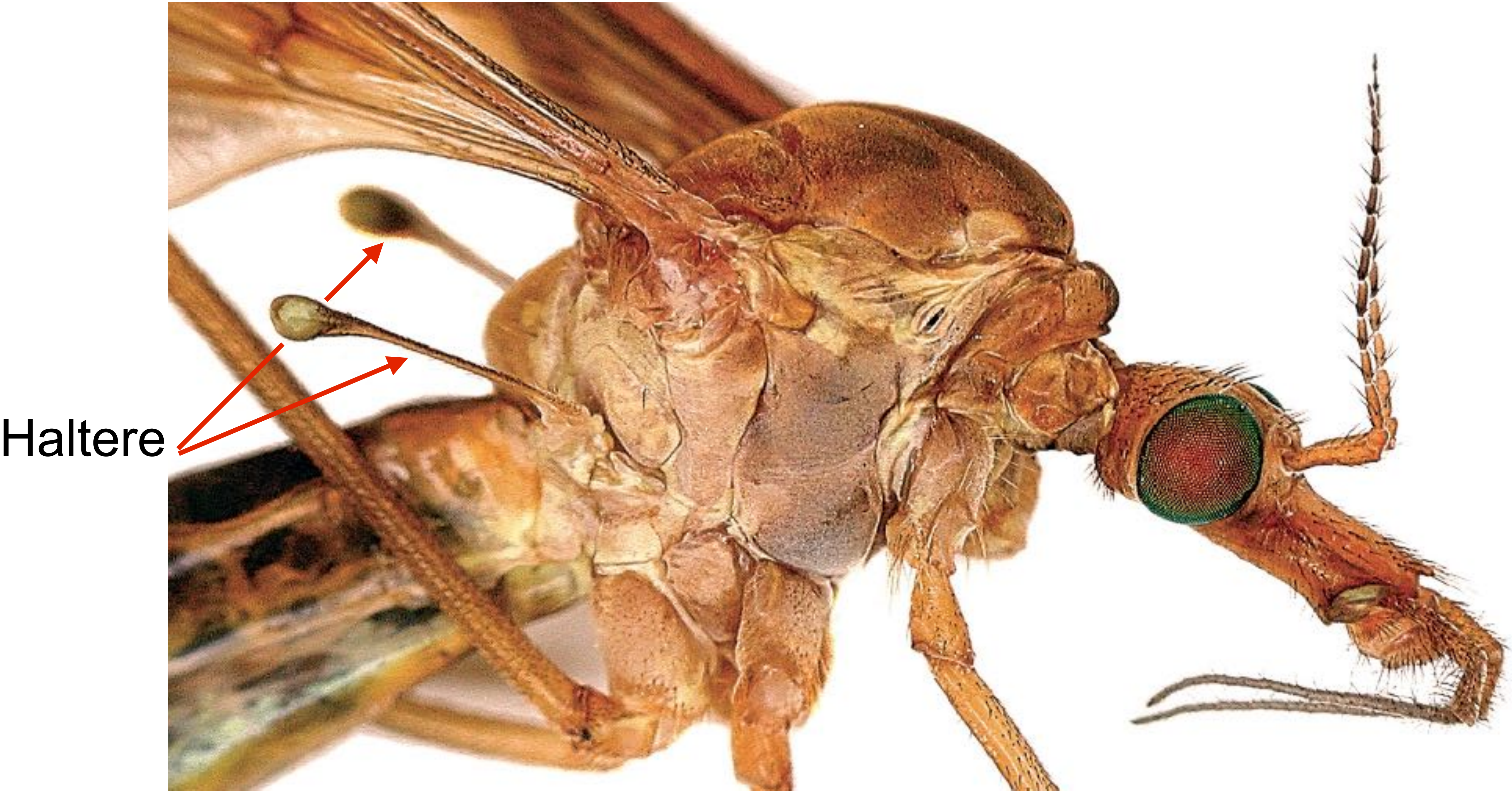




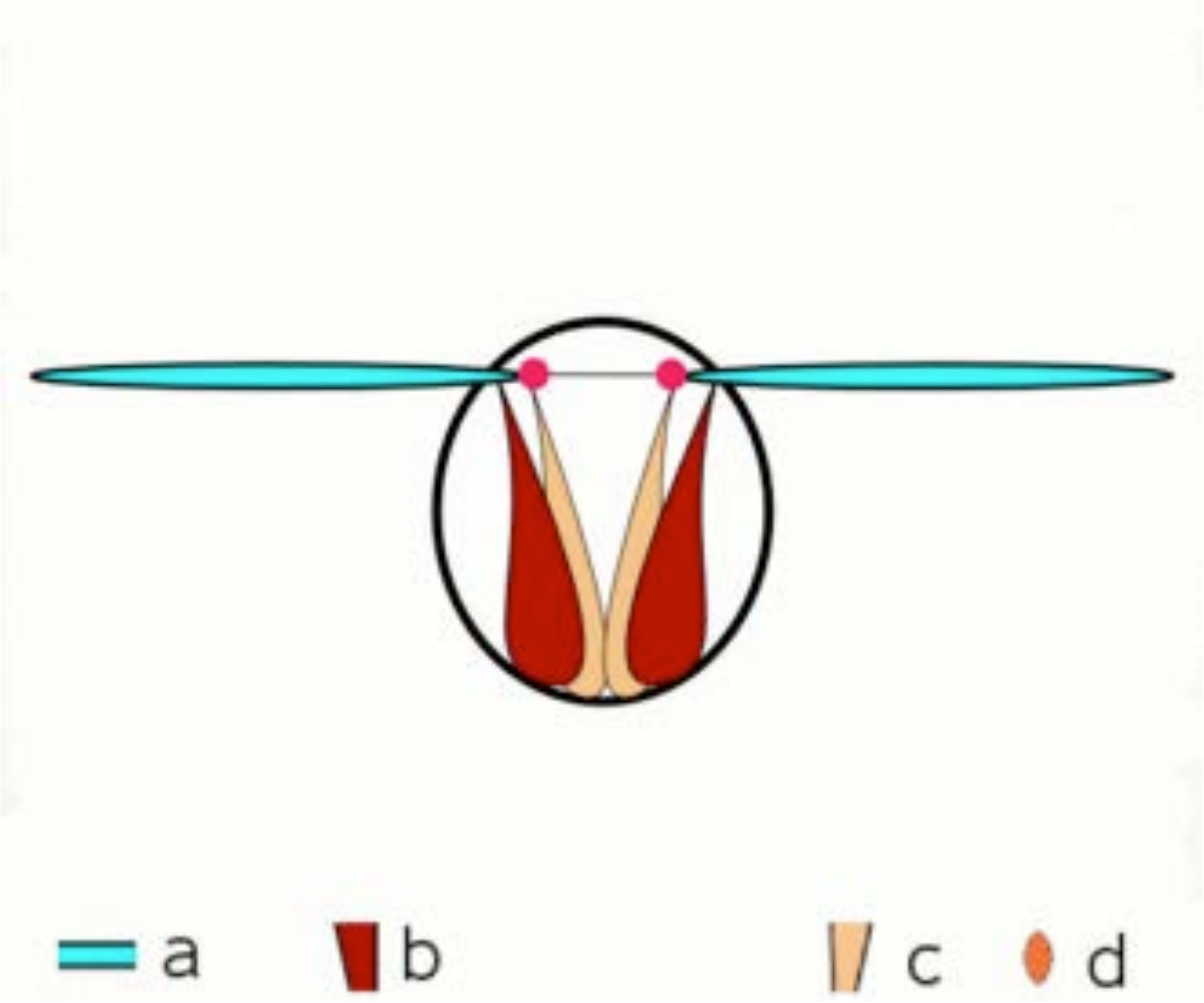




Uncoupled wings are typical of insects with slow movement and erratic flight. Coupling mechanisms improve aerodynamic efficiency and increase flight speed. A Claustrum unites forewing and hindwing during flight. Types of wing coupling mechanisms include hooks of one wing attached to a thickened margin of the other wing. A Hamulus consists of curved spines along the costal margin of the hindwing that engage a Retinaculum of the forewing (Hymenoptera). Jugale Coupling occurs in Trichoptera and primitive moths. Amplexiform Jugale Coupling involves a forewing overlapping a developed Humeral Lobe of the hindwing. More advanced Jugale Coupling involves a slit in the forewing Jugum and either side of the slit covers the dorsal and ventral surfaces of the hindwing's costal margin. Primitive Frenate Coupling occurs in some Mecoptera. Frenular bristles of the hindwing 's Humerus overlap the forewing Jugal Lobe to keep the hindwing in phase with the forewing. Frenate Coupling is common in Lepidoptera. External forces applied when squeezing into 'light places' may cause wings to move or separate. Some Coleoptera (e.g. ground beetles) have developed mechanisms for locking the wings together or to the body while moving on the ground.The forewing Jugal Lobe is thicker and more sclerotized than the wing membrane.



The Haltere forms a complex orientation device. Anatomically, the Haltere consist of a base (Scabellum), an elongate pedicel and an apically enlarged knob (Capitulum). The base of the Haltere is invested with campaniform Sensilla, Hicks' Papillae and chordotonal organs. The Haltere is a balancing organ used to maintain stability during flight. Halteres vibrate at the same frequency as the forewings but at antiphase. Halteres vibrate in vertical motion, not 8-shaped as the forewings. The Halteres' centre-of-gravity is located near the knob. Campaniform Sensilla on the Haltere respond to changes in stress developed from changes in the inertia of harmonic motion of the oscillating Haltere. Dipterists speculate that the Haltere originated as an adaptation for aerial swarming.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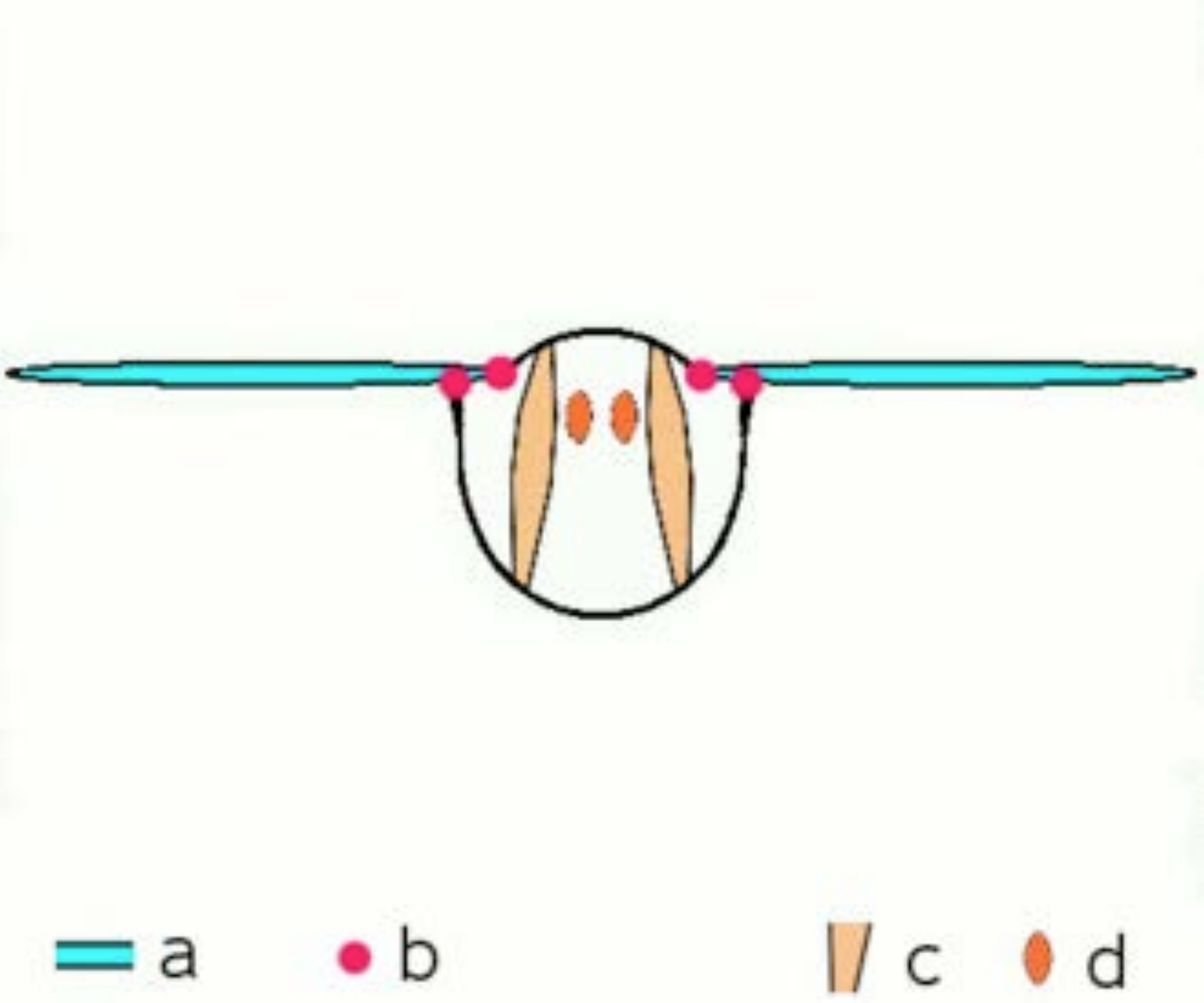
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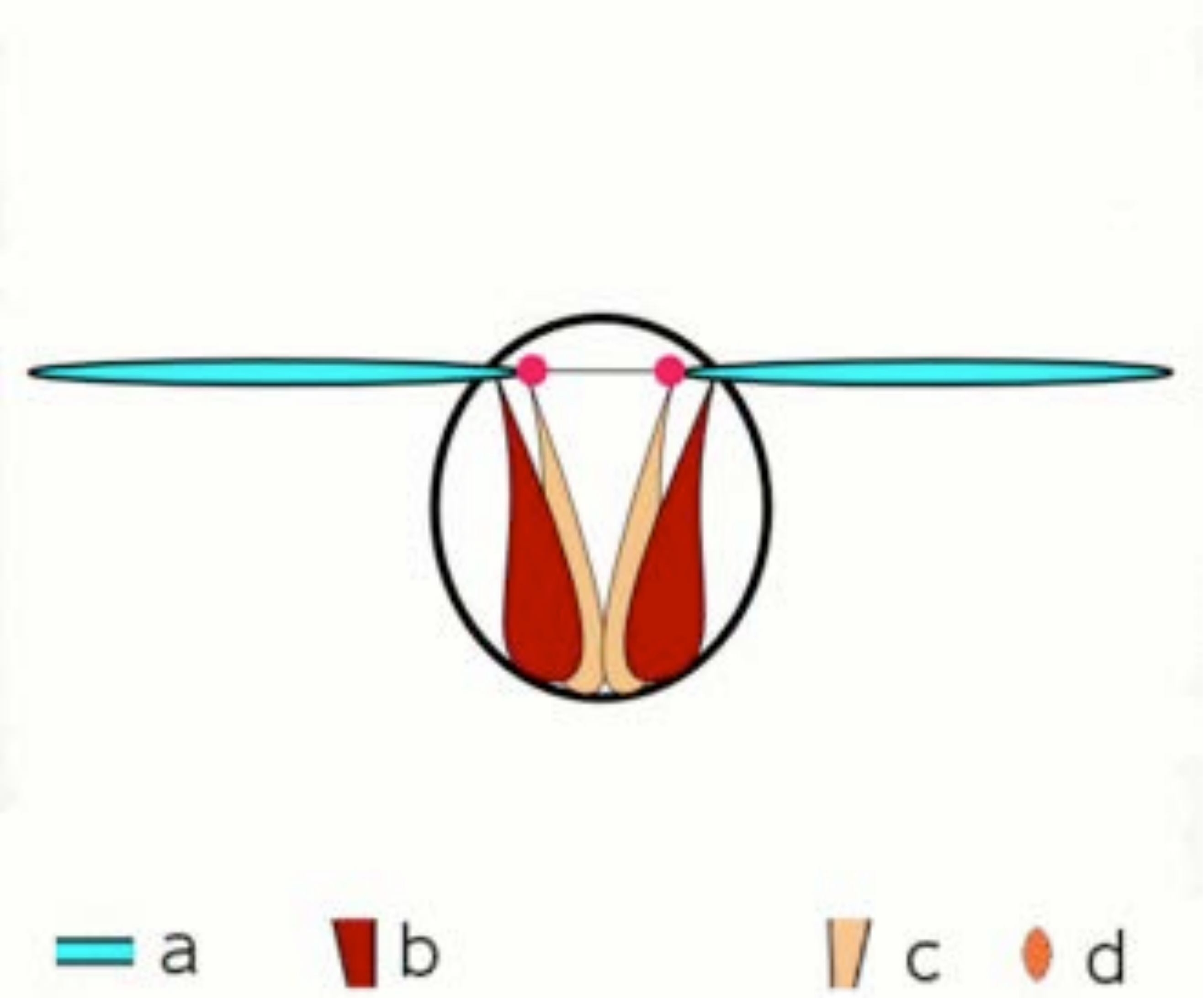
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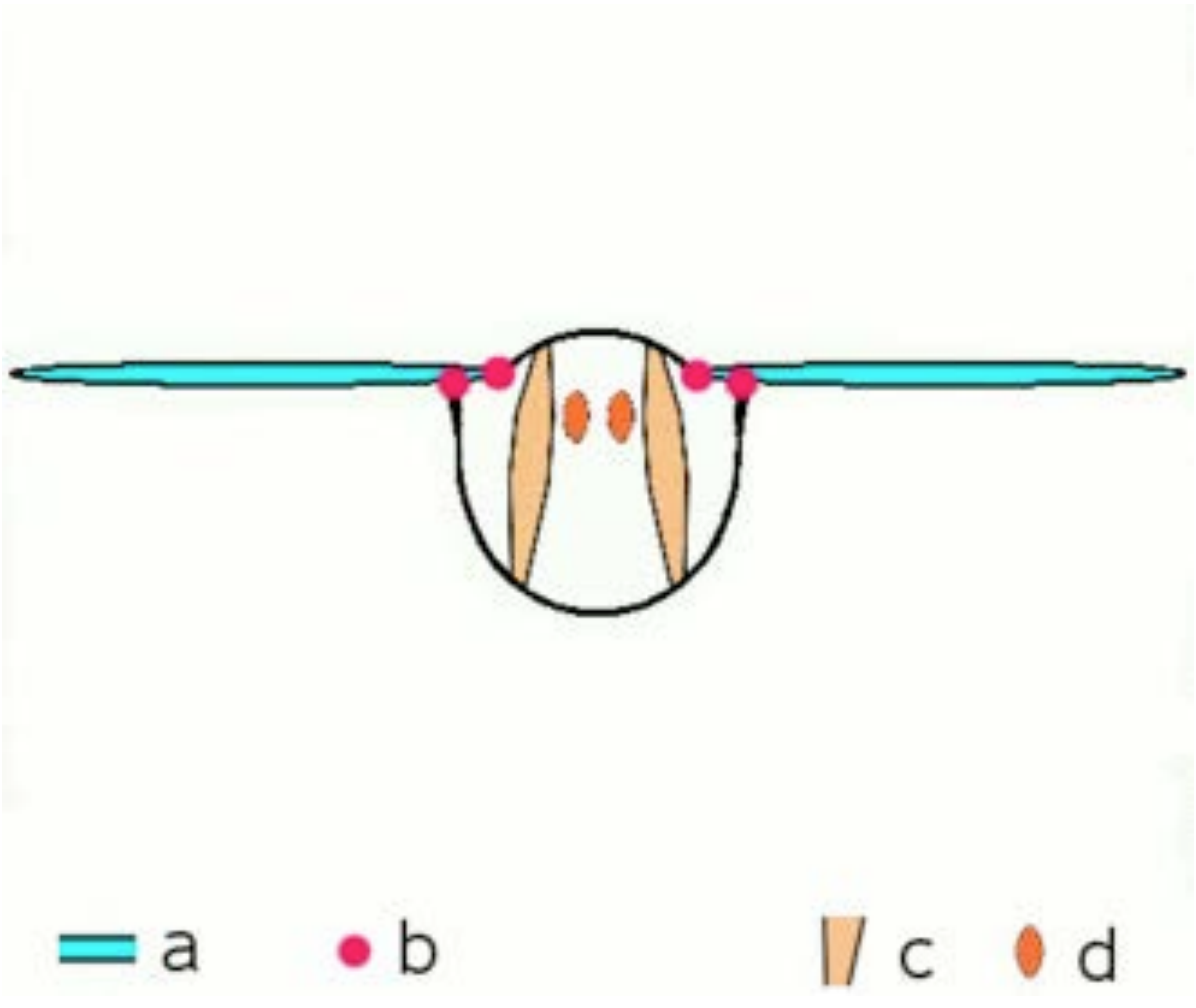
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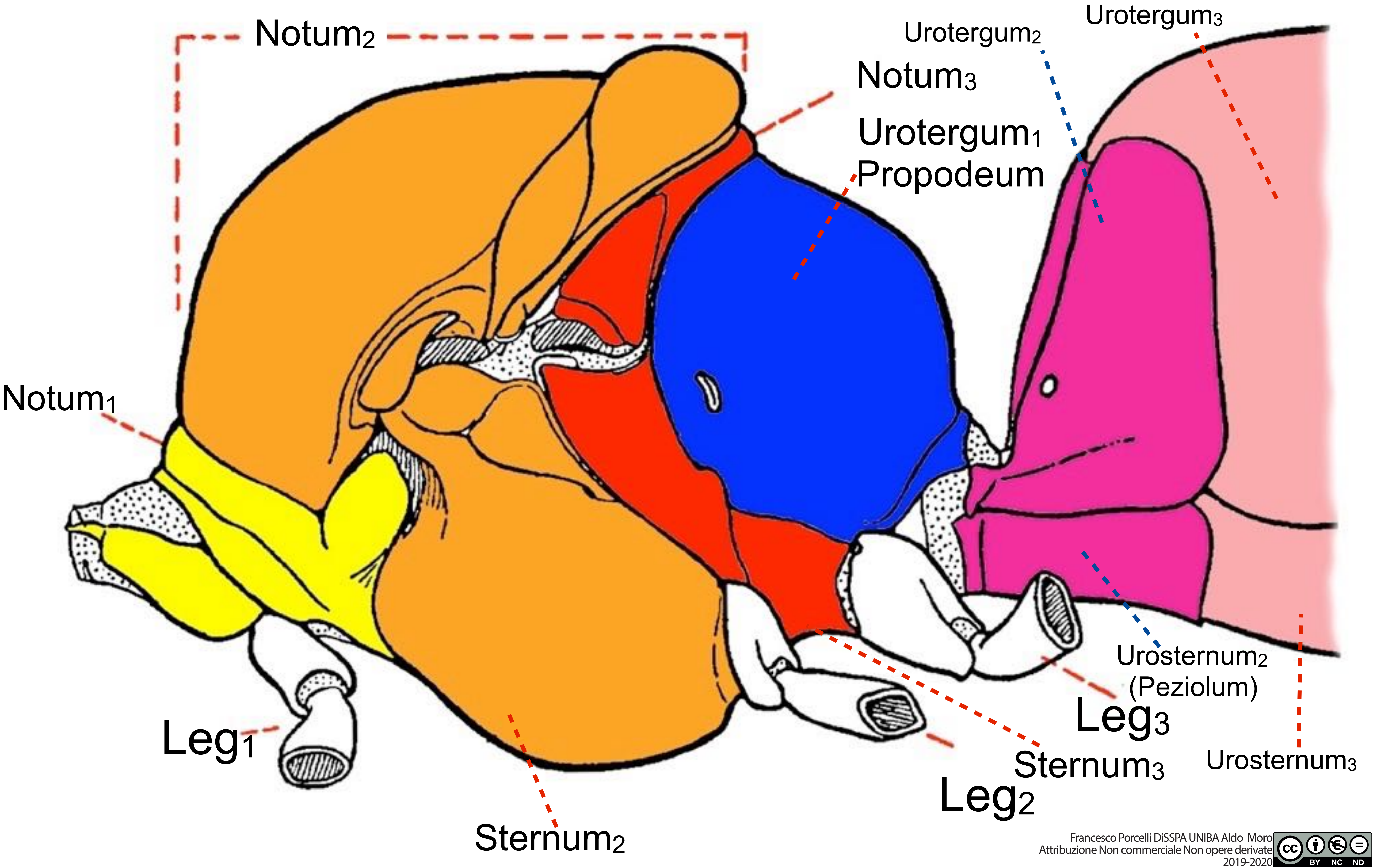
Apocrita is a numerically large, holophyletic, cosmopolitan Suborder of Hymenoptera, including ants, bees and wasps. Morphologically characterized by adult without closed Anal Cells in the wings and first abdominal segment (Propodeum) functionally incorporated with Thorax and separated from remainder of Abdomen by a constriction formed through reduction of second abdominal segment, Petiole, that appears like a slender or narrow tubular segment between the Thorax and Abdomen. The Propodeum is the first abdominal tergum which has through evolution disassociated from the Abdomen and becomes incorporated into the thoracic region. In Parasitica and Aculeata, the Propodeum is characterized by anterolateral spiracles, a broad attachment to the Metanotum anteriorly and posteriorly separated from the remainder of the Abdomen by a narrow constriction (Petiole). This anatomical reorganization has resulted in problems with terminology. Some specialists use the term Mesosoma when referring to the combined Propodeum and Thorax. The term Metasoma is used when referring to the remaining abdominal segments.



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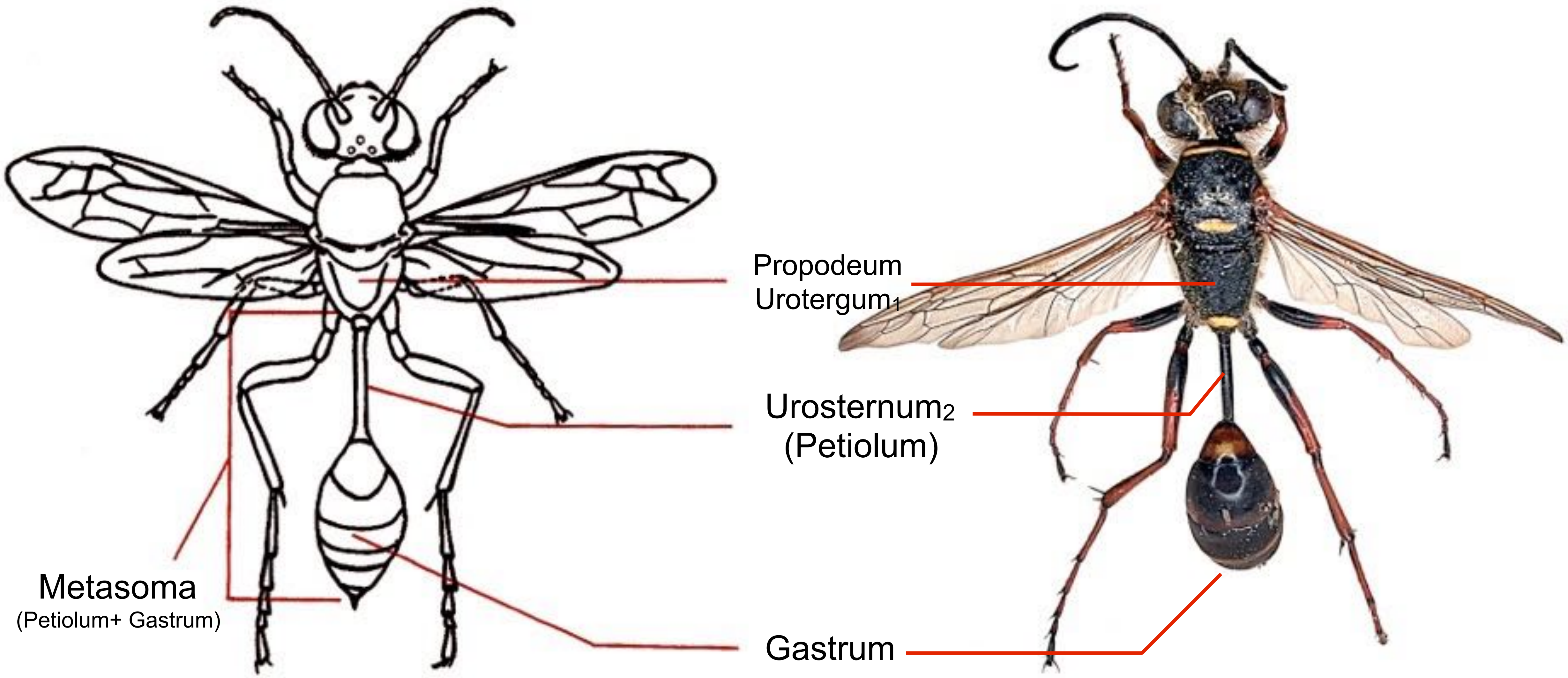

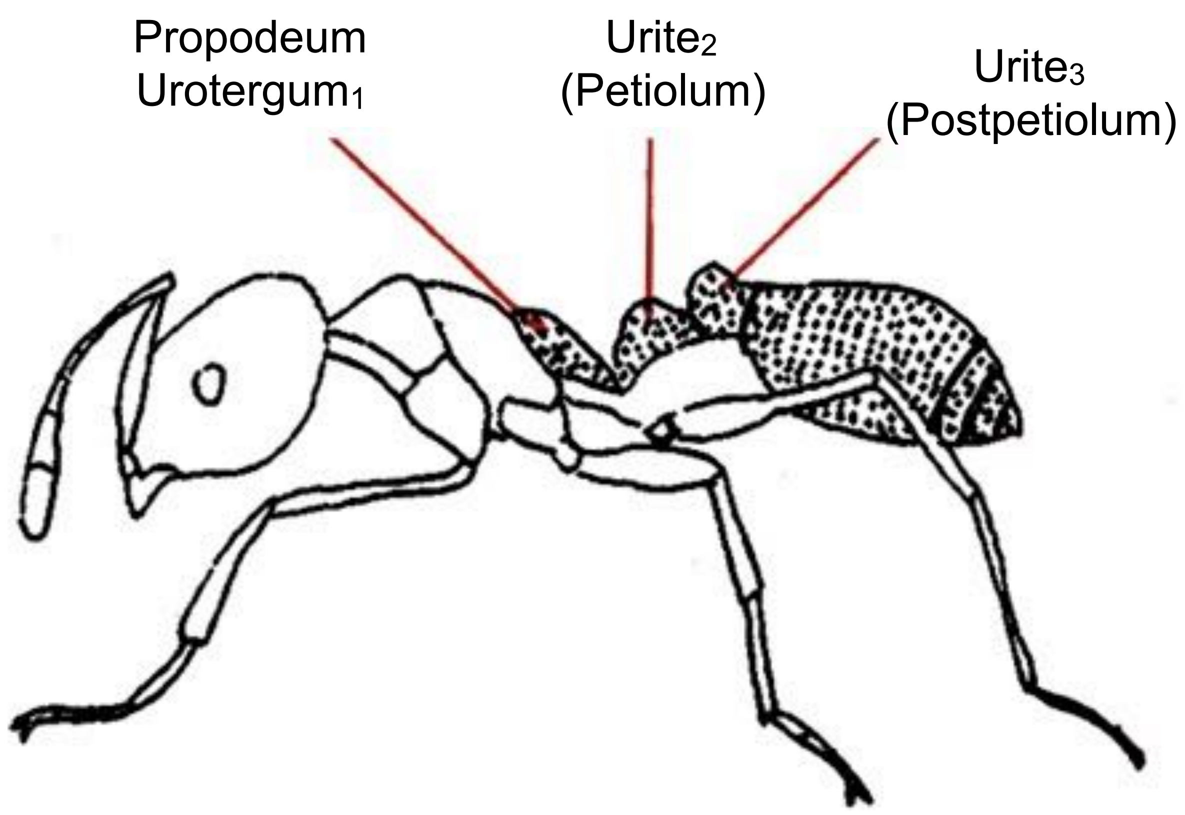

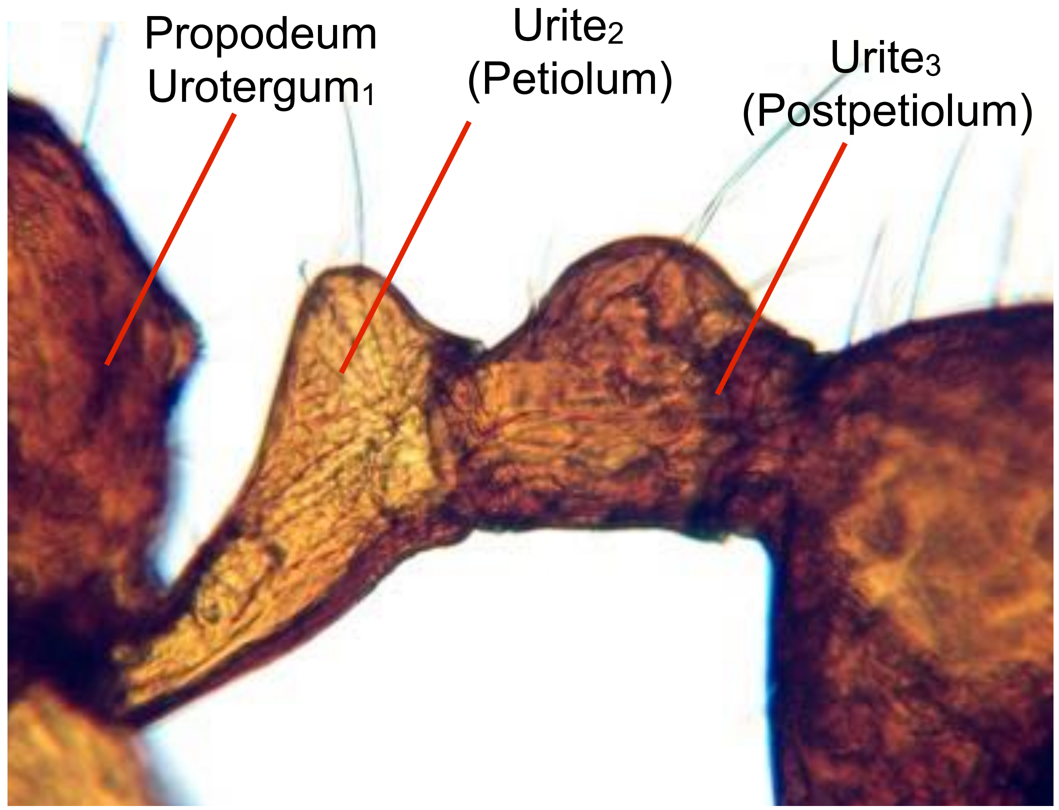

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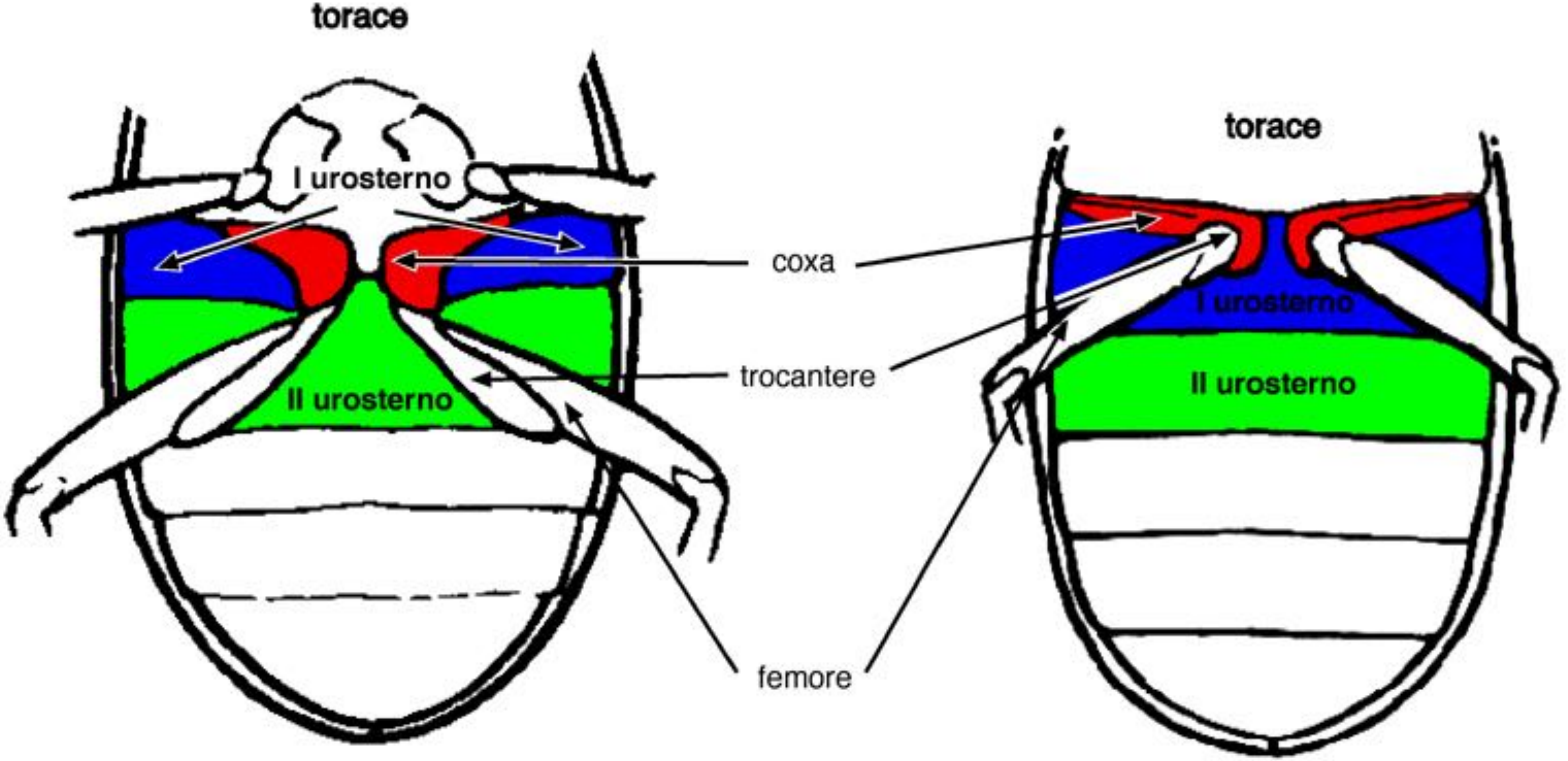
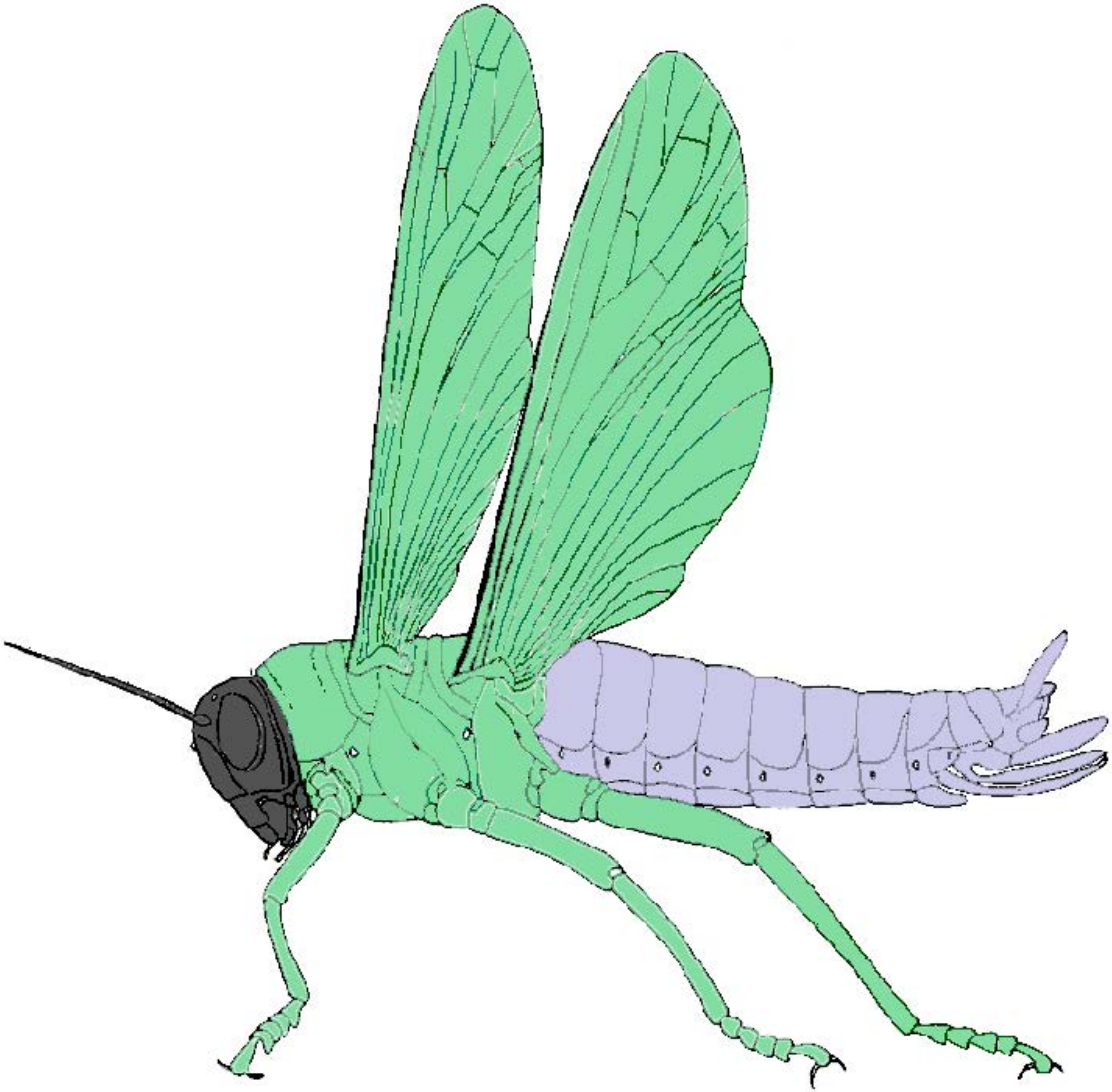
Coleoptera

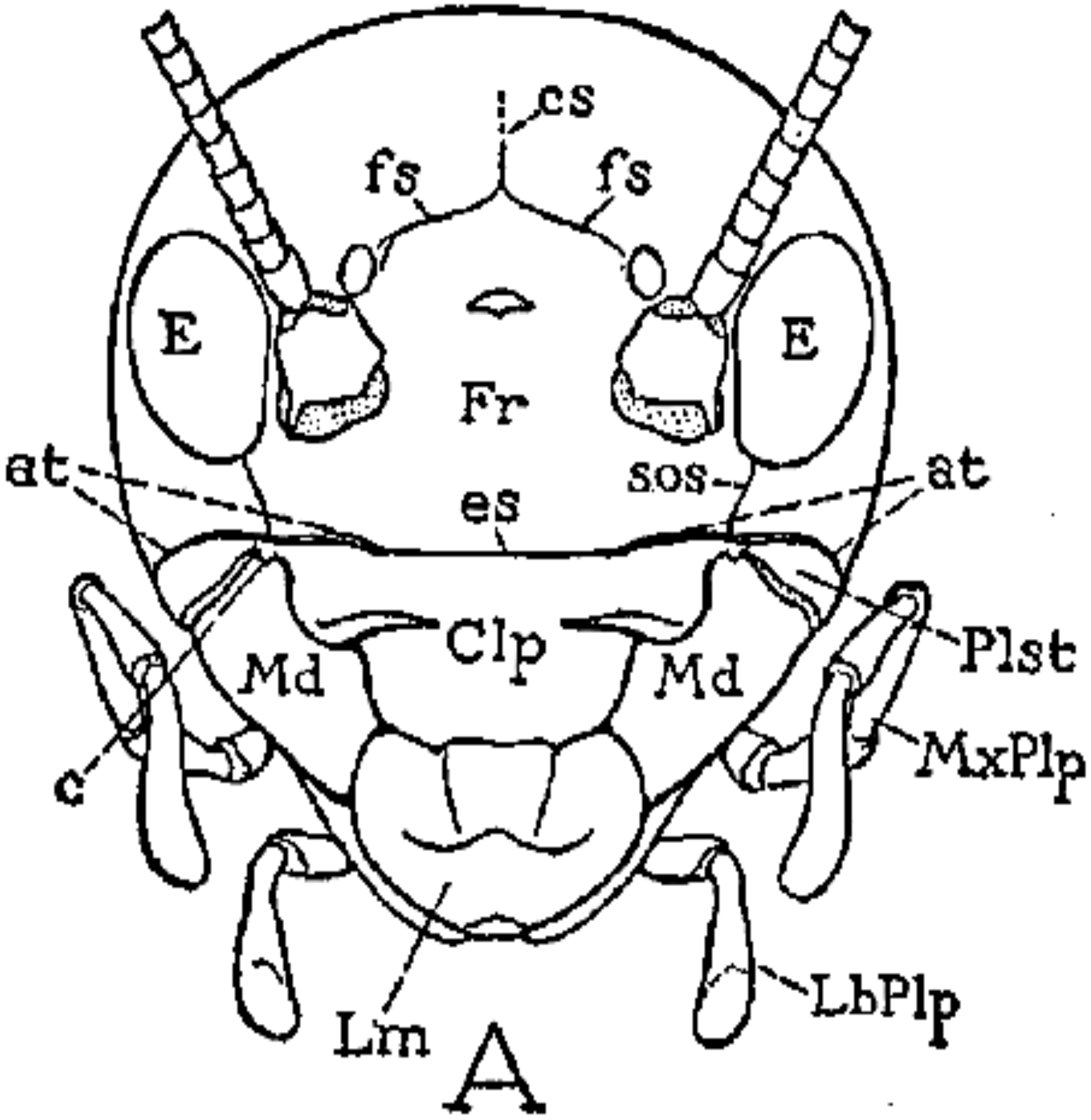


Adephaga

Polyphaga

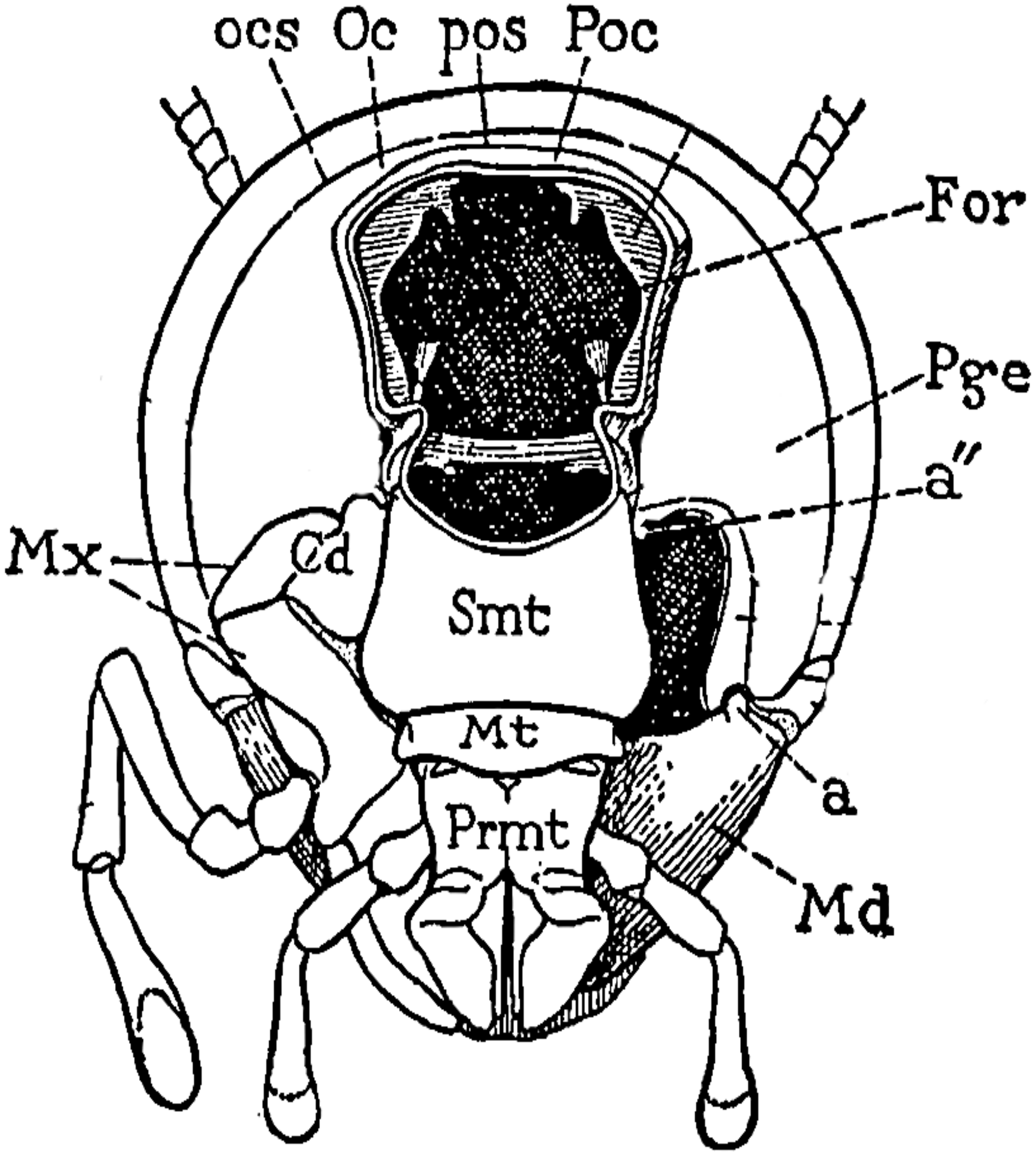
06 Head



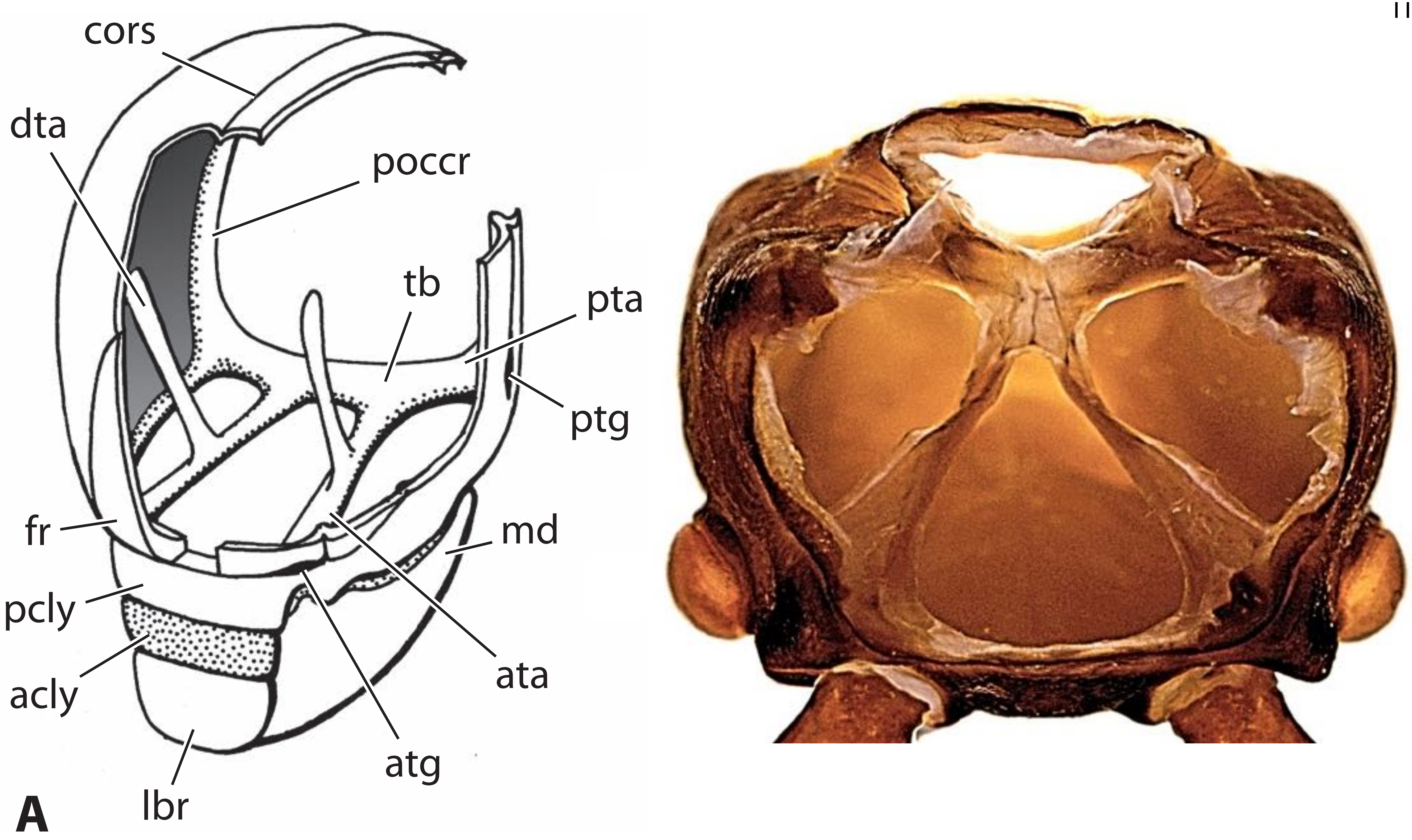


Mouthparts are cranial appendages specifically adapted for the acquisition and processing of food. Principal mouth parts include Mandible, Maxilla and Labium; Each appendage is subdivided into component parts of varing complexity and functional interaction among different groups of insects. The Labrum and Antenna sometimes act as accessory feeding structures. Insects have modified their mouthparts in many ways as adaptation for biting, chewing, piercing and sucking. In the context of evolution, these modifications are viewed as strategies for processing food items of different physical complexity and chemical properties. Food is utilized by insects as a liquid, a solid, or a solid suspended in a liquid.

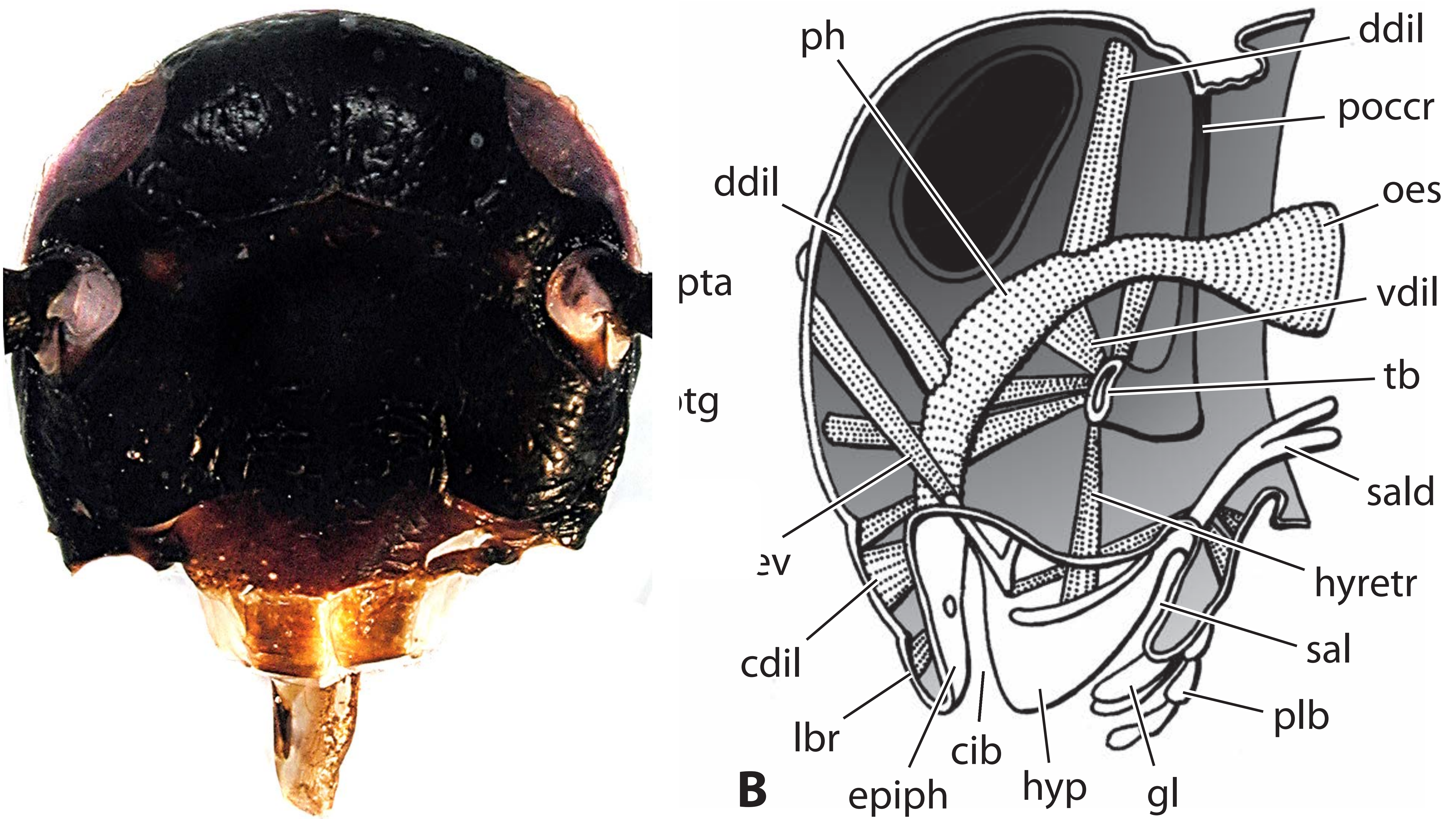
Labrum is the 'upper lip' of the insect head which covers the base of the Mandible and forms the roof of the mouth. Labrum traditionally has been viewed as a preoral feature that is not homologous with segmental appendages. Labrum articulates with the cranial capsule via membrane (Ciypeolabral 'Suture') or is fused to the cranial capsule and immobile. Apical margin of Labrum of some insects is unusually shaped or invested with Setae. For instance, digitate Labrum of parasitic Hymenoptera Eucharitidae and Perilampidae. Digits of Labrum mesh with Setae on labiomaxillary complex and form a sieve-like apparatus. Functionally, this apparatus may exclude pollen when nectar feeding.



The Mandibles are the anterior-most pair of oral appendages on the insect head. Mandibles are lateral appendages, immediately behind Labrum and may represent segmental appendages of fourth segment of head groundplan. Early in their evolutionary history, insects perfected Mandible as an appendage for processing food and it represents one of the hardest parts of insect's Integument (ea 3.0 on Mohs Scale). Mandibles vary considerably in size, shape and apical geometry. Mandibles are stout and highly modified in form, but not showing signs of segmentation. Mandible shape is strongly influenced by function: tooth-like in chewing insects and needle-like or sword-shaped in piercing-sucking insects. Mandibles are not always used for feeding. Some Holometabola use their Mandibles to exit Puparium or area of pupal confinement (e.g. exodont Mandible of alysiine braconid wasps). Some bees and wasps use Mandibles to construct nests in soil, wood and other hard material (e.g. bee). Mandible is useful for processing matrices of varying structural complexity, chemical composition and physical hardness. Complex plant fibres of differing degrees of hardness require a Mandible that is harder than fibres under process and a Mandible with complex surface features.



Generalized hexapod head, internal structures. **A: anterolateral view, frontal side of head capsule opened; B, sagittal section, brain and suboesophageal complex removed**. **ata:** anterior tentorial arm, **acly:** anteclypeus, **atg:** anterior tentorial groove, **cib:** cibarium, **cdil:** cibarial dilator (M. clypeobuccalis), **cors:** coronal suture, **ddil:** dorsal pharyngeal dilator (M. fronto-/verticopharyngalis), **dta:** dorsal tentorial arm, **epiph:** epipharynx, **fr:** frons, **gl:** glossa, **hyp:** hypopharynx, **hyretr:** hypopharyngeal retractor, **lbr:** labrum, **lbrlev:** external labral levator (M. frontohypopharyngalis), **md:** mandible, **oes:** oesophagus, **pcly:** postclypeus, **ph:** pharynx, **plb:** palpus labialis, **poccr:** postoccipital ridge, **pta:** posterior tentorial arms, **ptg:** posterior tentorial groove, **sal:** salivarium, **sald:** salivary duct, **tb:** tentorial bridge, **vdil:** ventral pharyngeal dilator (M. tentoriopharyngalis).



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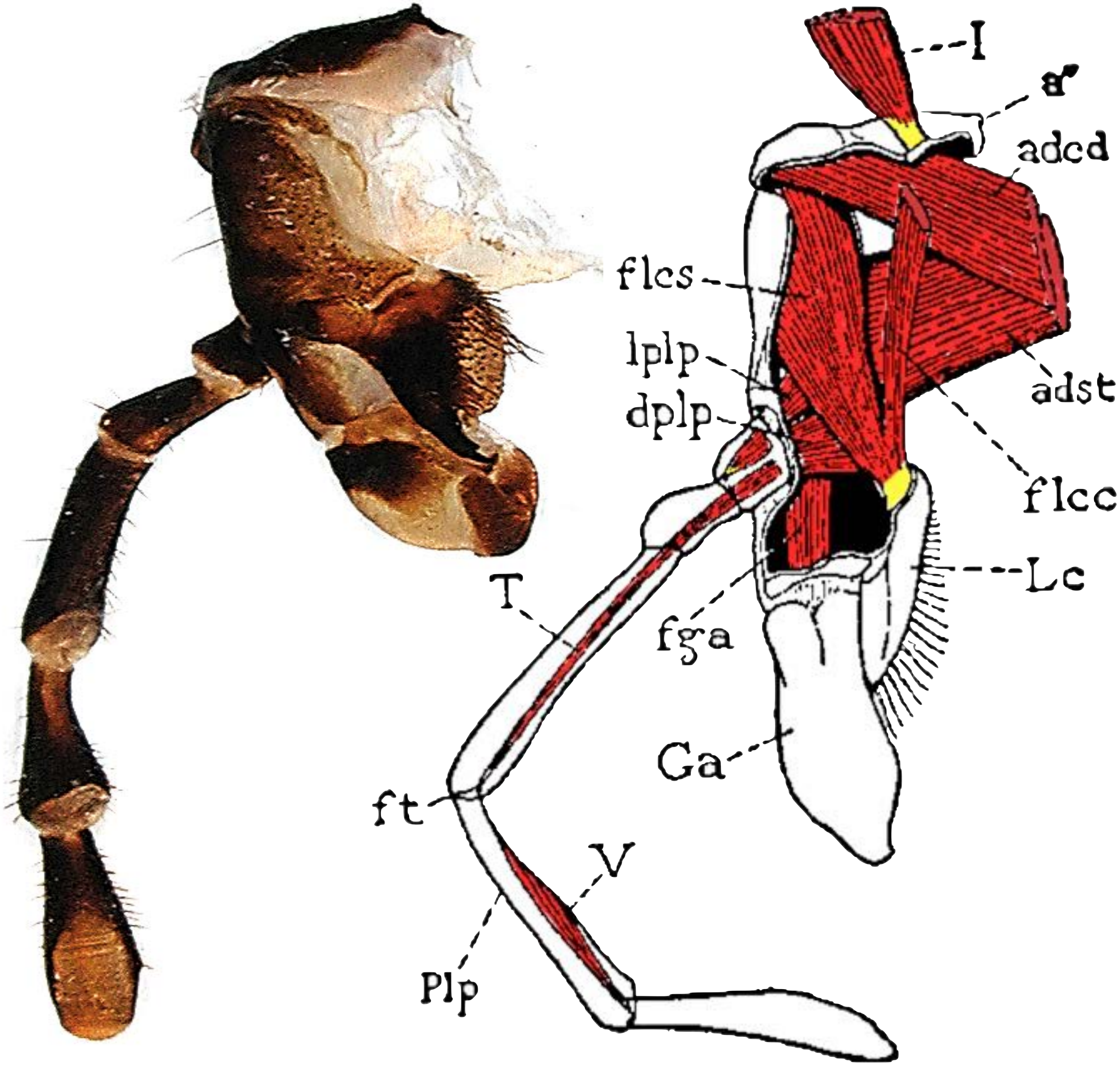
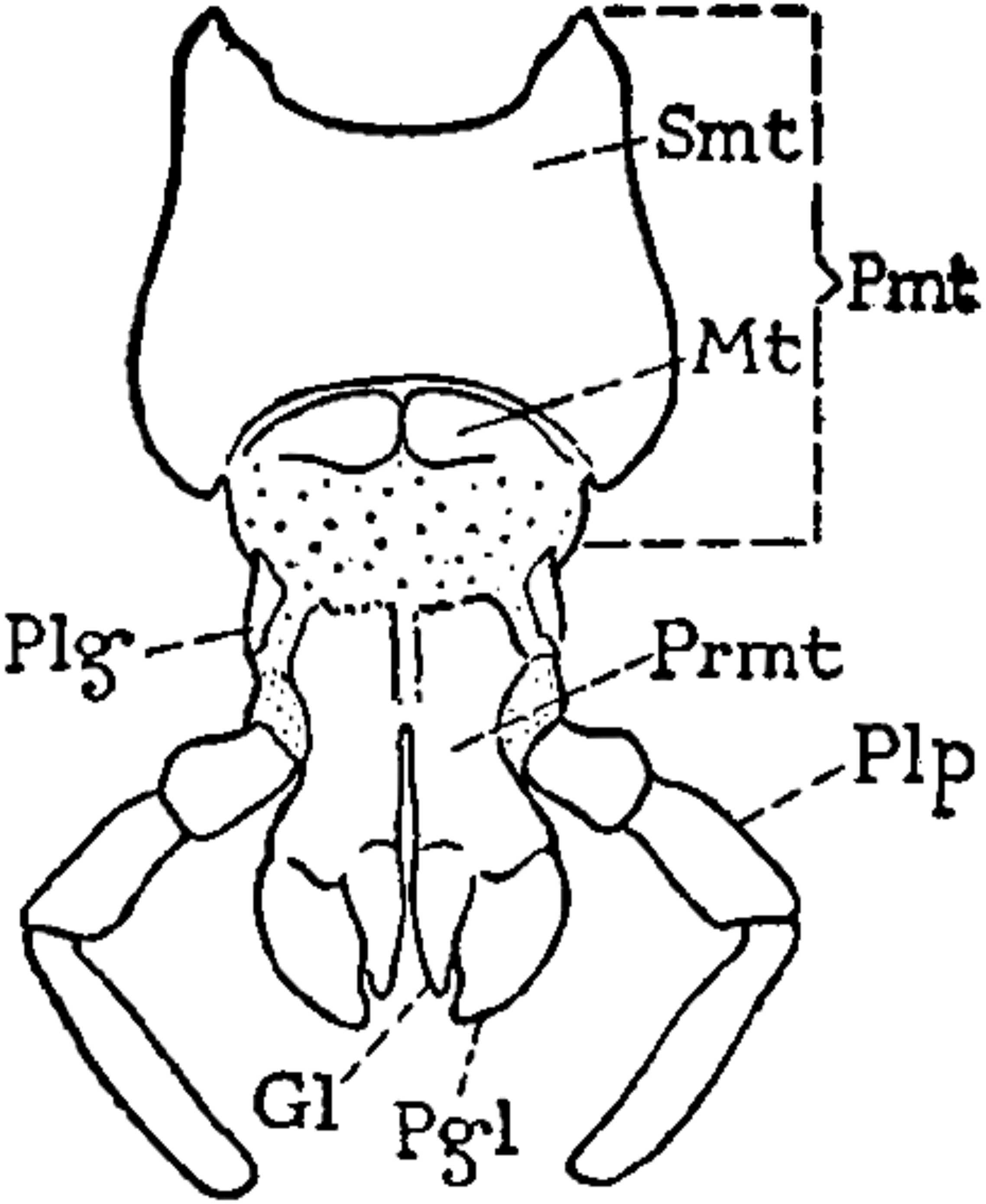


The Maxillae are paired, lateral Accessory 'jaws' located immediately posterior of the Mandibles. Maxilla is structurally more complex than Mandible. (Mandible is not an apparently segmented structure in insects and not obviously derived from a segmented appendage). Maxilla demonstrates more clearly a condition of generalized Homology with an appendage. Maxillary appendage components include: Coxopodite (Cardo and Stipes) and Telopodite (Maxillary Palpus). Maxilla typically is elongate with one point of articulation on Cranium. Cardo (basal segment that articulates with Cranium) is attached to Stipes. Cardo is variable in size and shape. Stipes forms second segment of Maxilla. Stipes is broadly attached to Cardo basally , bears a movable Palpus laterally, and is attached to Galea and Lacinea distally. Stipes is modified into a piercing device in some Diptera and into a lever for flexing Proboscis in Diptera.



The Labium is a compound, bilaterally-symmetrical sclerite that forms the 'lower lip' or floor of the mouth in mandibulate insects, and sometimes called the 'tongue'. Labium is positioned behind the first Maxilla and opposed to the Labrum. Labium is regarded as the 'second Maxilla' and seems serially homologous with second Maxillary Sclerites of crustacean mouthparts. The insect Labium consists of laterally paired structures in the embryonic insect which become sclerotized and fuse in postembryonic life. Labium exhibits considerable variation in development among mandibulate insects. In lower pterygotes Labium consists of a Postmentum (attached to Cranium) and a more distal Prementum (attached to apical margin of Postmentum). In Hemiptera, Labrum is represented by a short flap opening at the base of Rostrum. The Labrum is usually shorter than the Labium and not segmented. Three types of Labrum in Hemiptera: Transverse, flap-like without epipharyngeal projections, elon- gate without epipharyngeal projections and transverse with epipharyngeal projections. Controverse prevails over naming labial parts. In some insects, Postmentum is divided into a proximal sclerite called Submentum and a distal sclerite called Mentum. The Mentum is frequently lost. Prementum (Prelabium, Ligula) forms the distal (moveable) part of Labium and is homologous with Stipes of Maxilla. Palpiger contains musculature attached to the base of Prementum. Labial Palpus is usually shorter than the Maxillary Palpus and typically displays fewer segments.