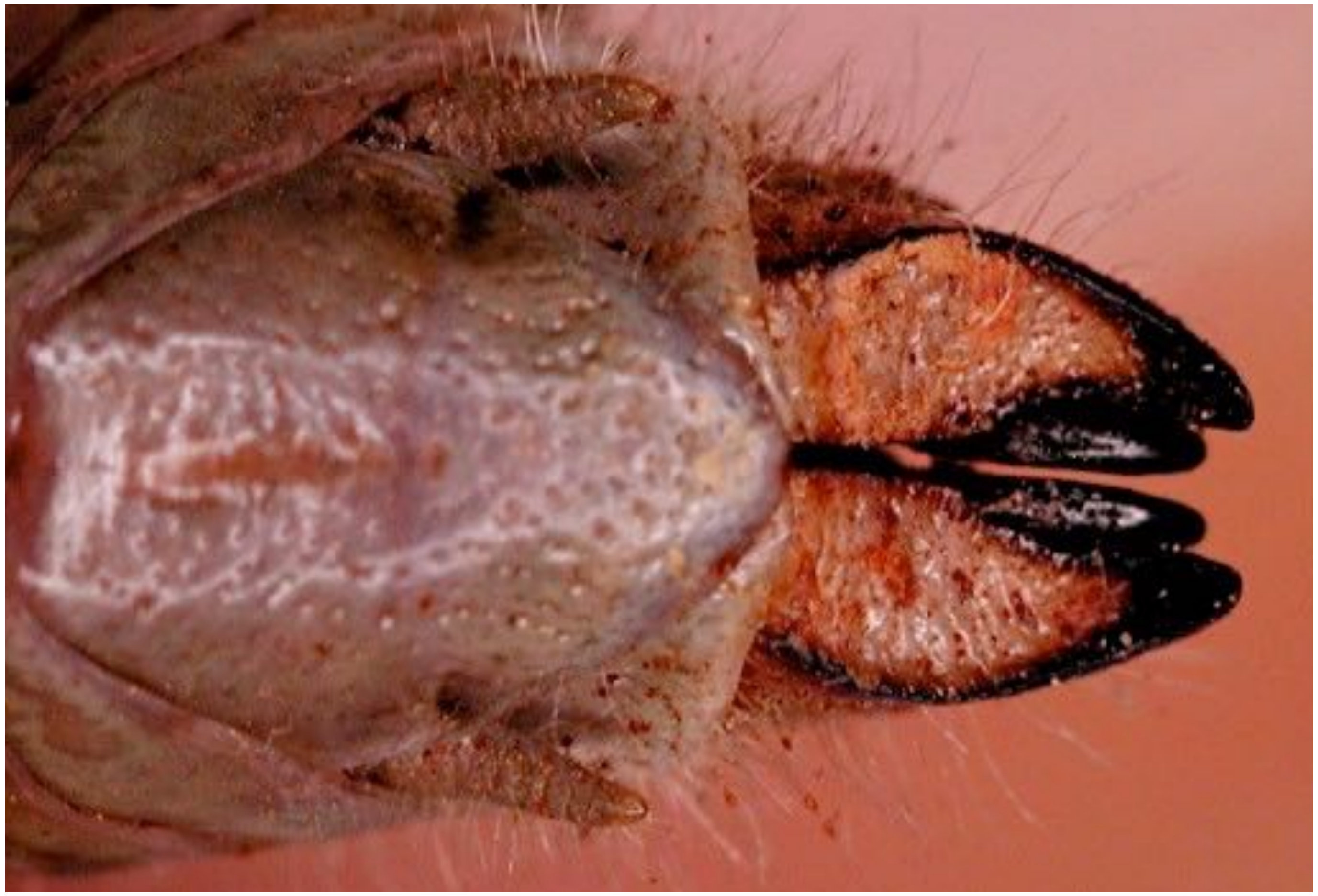

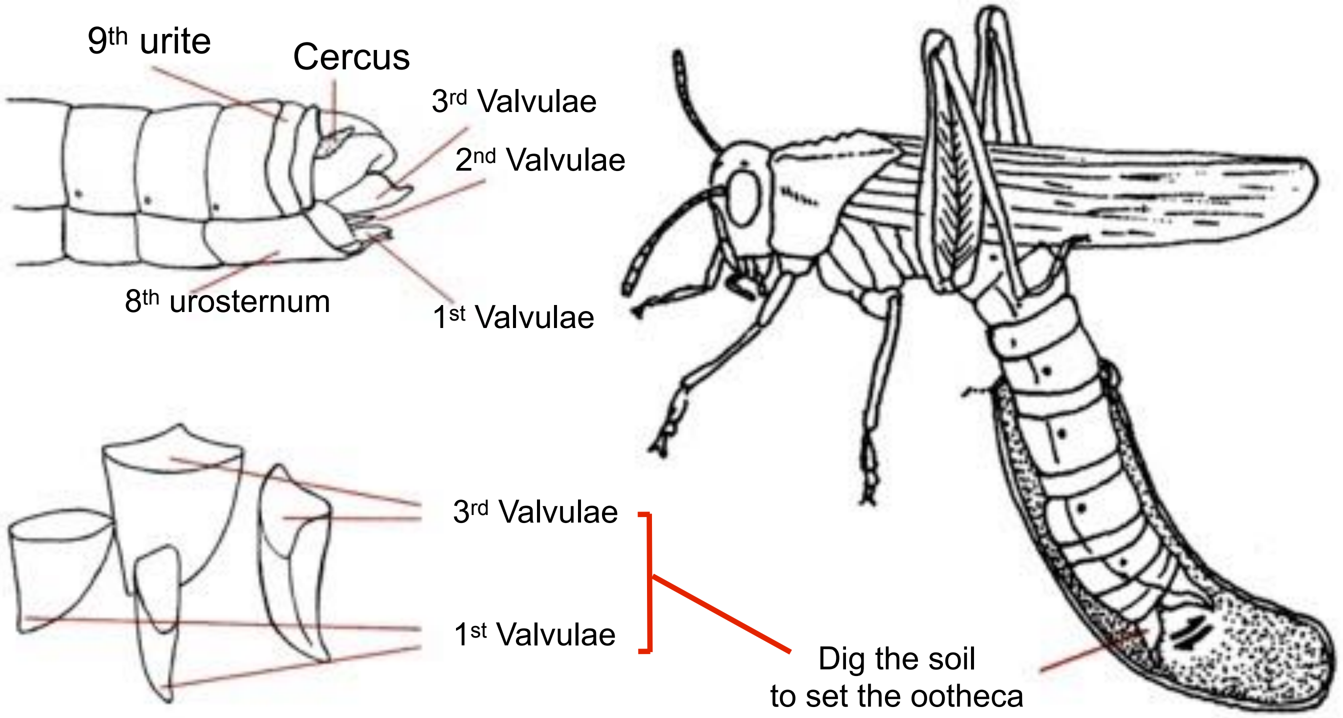
9th urite
Cercus
3rd Valvulae
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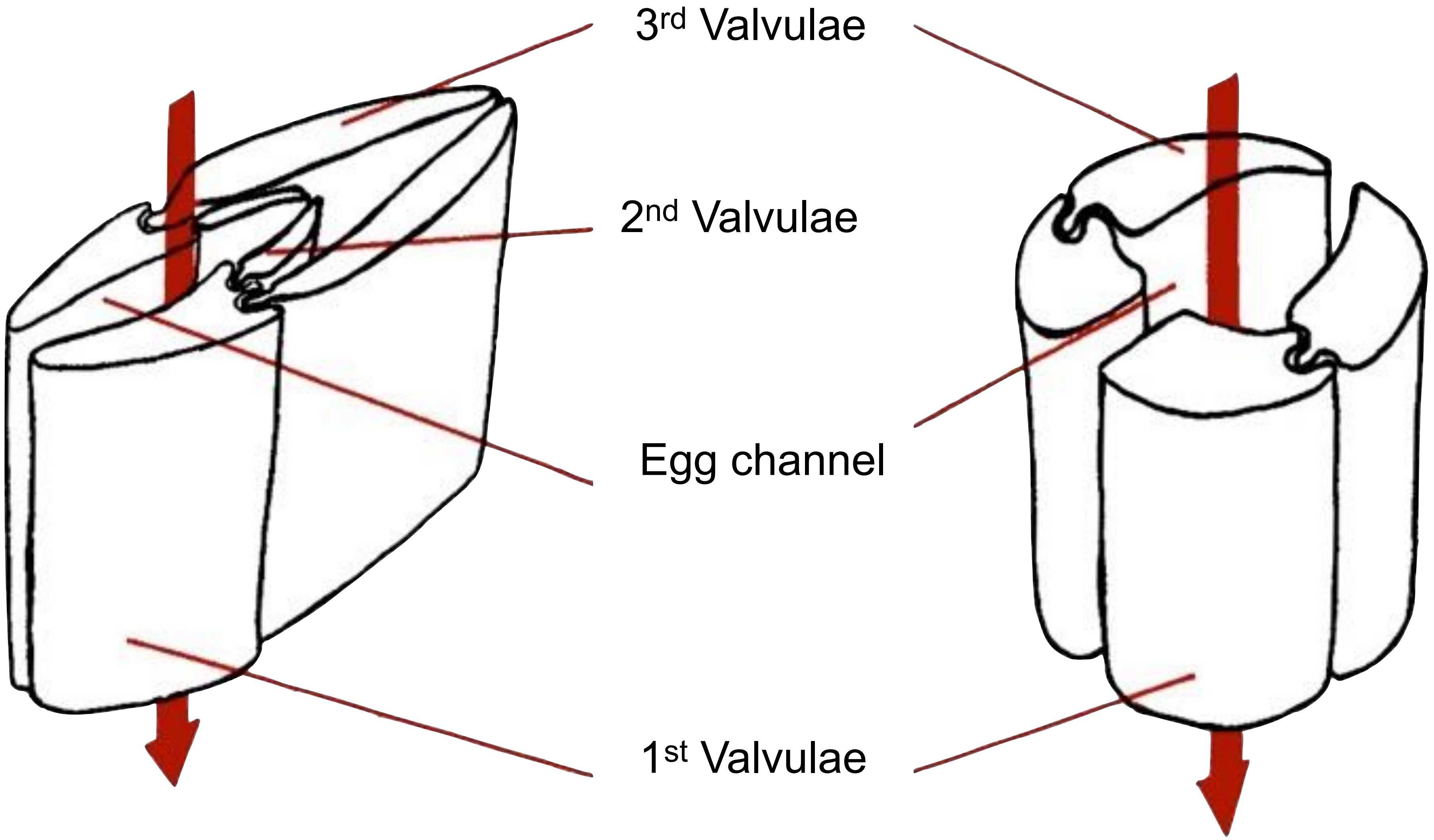
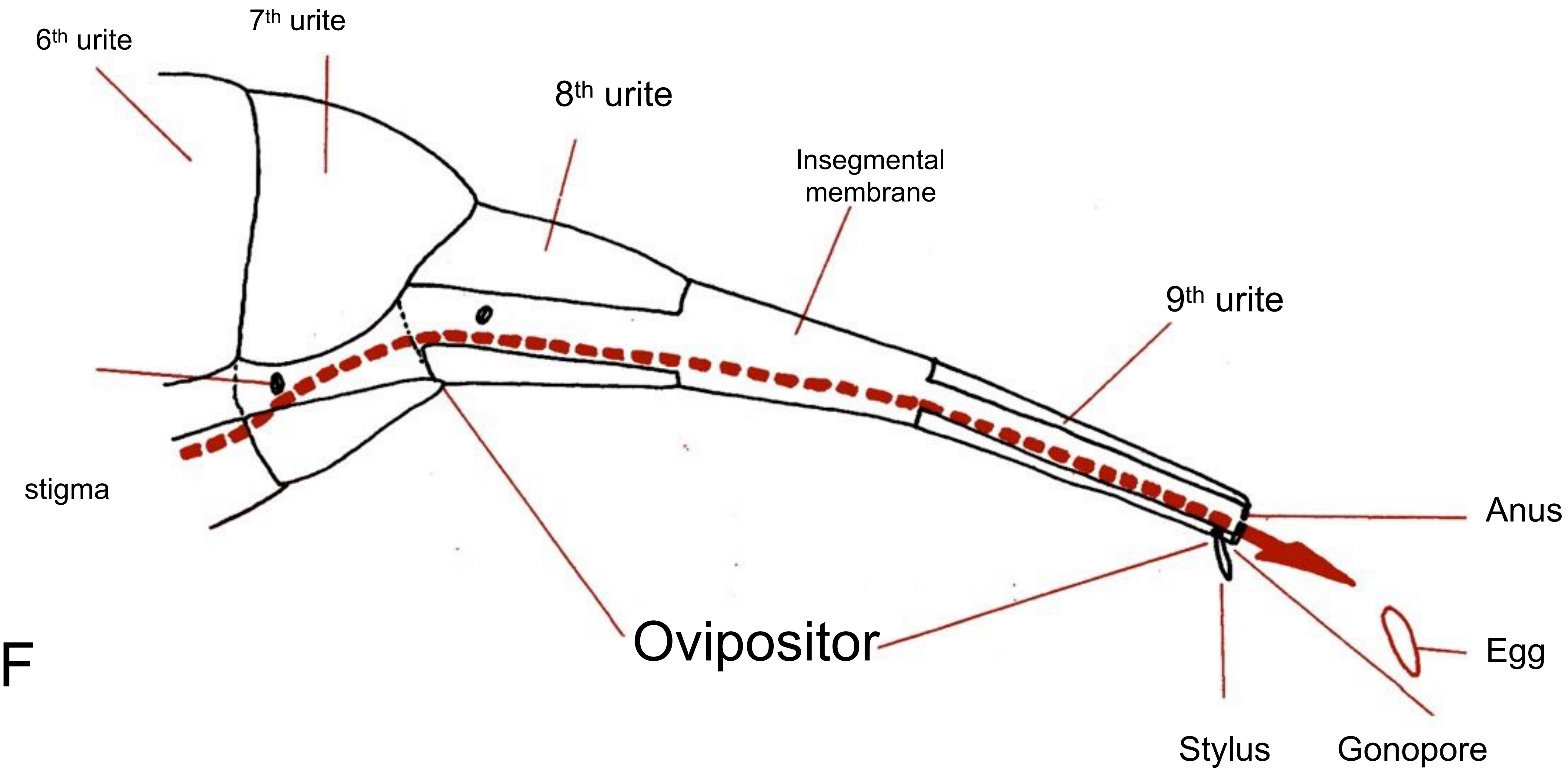
Dig the soil
to set the ootheca



Valvulae arragment to create the egg channel

Schematic side view of female terminalia without gonapophysis



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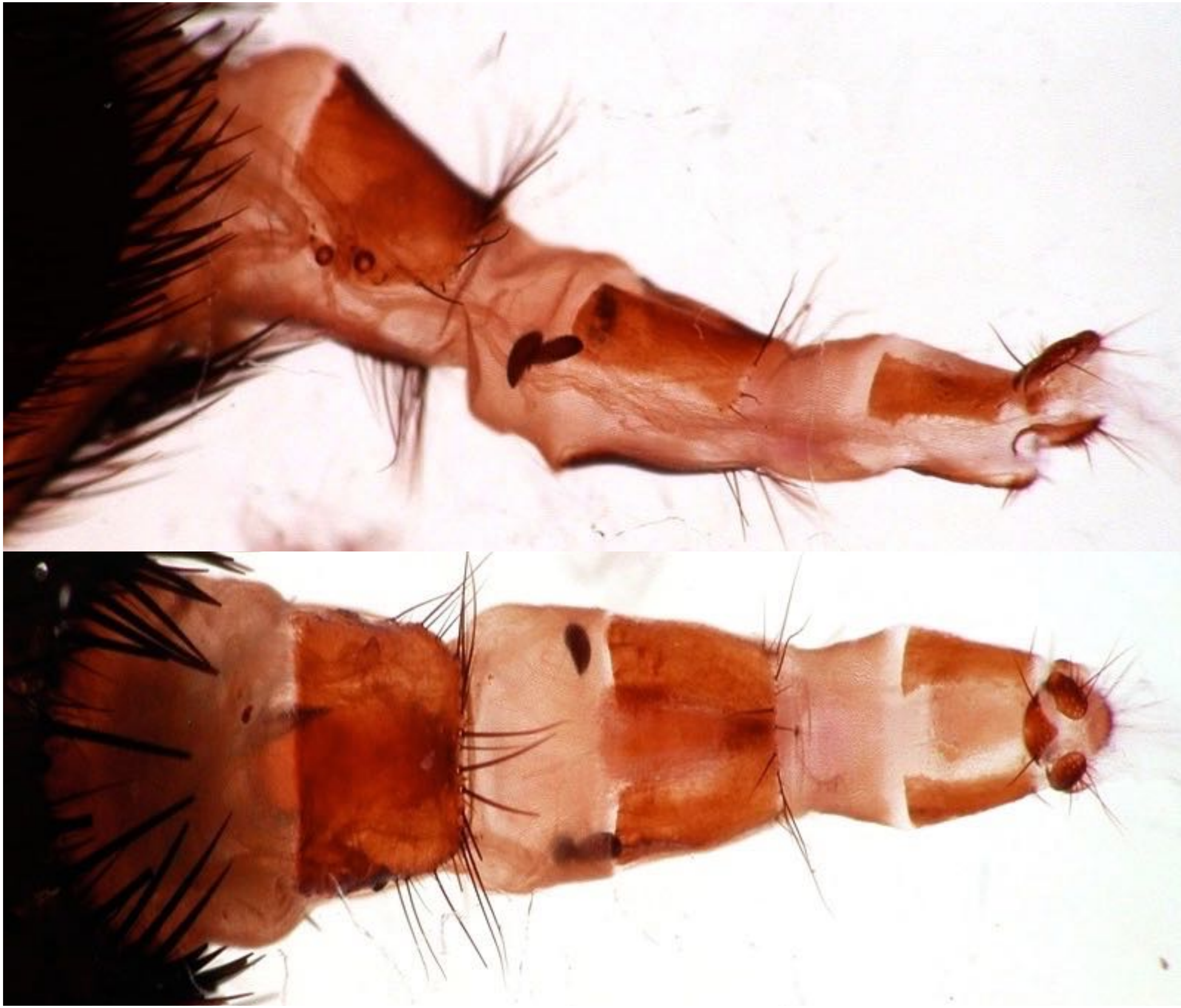


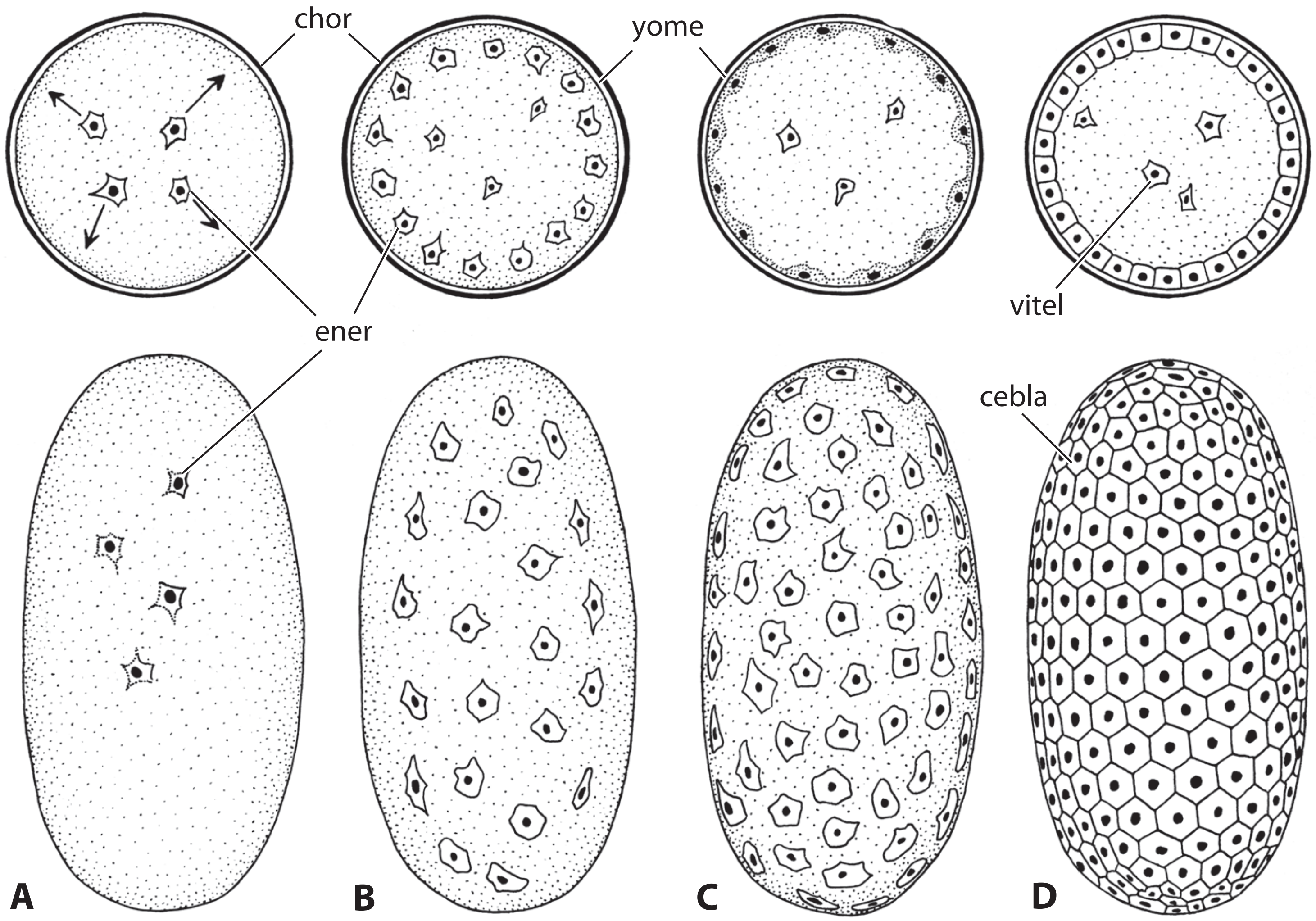
Fertilization and egg structure

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.

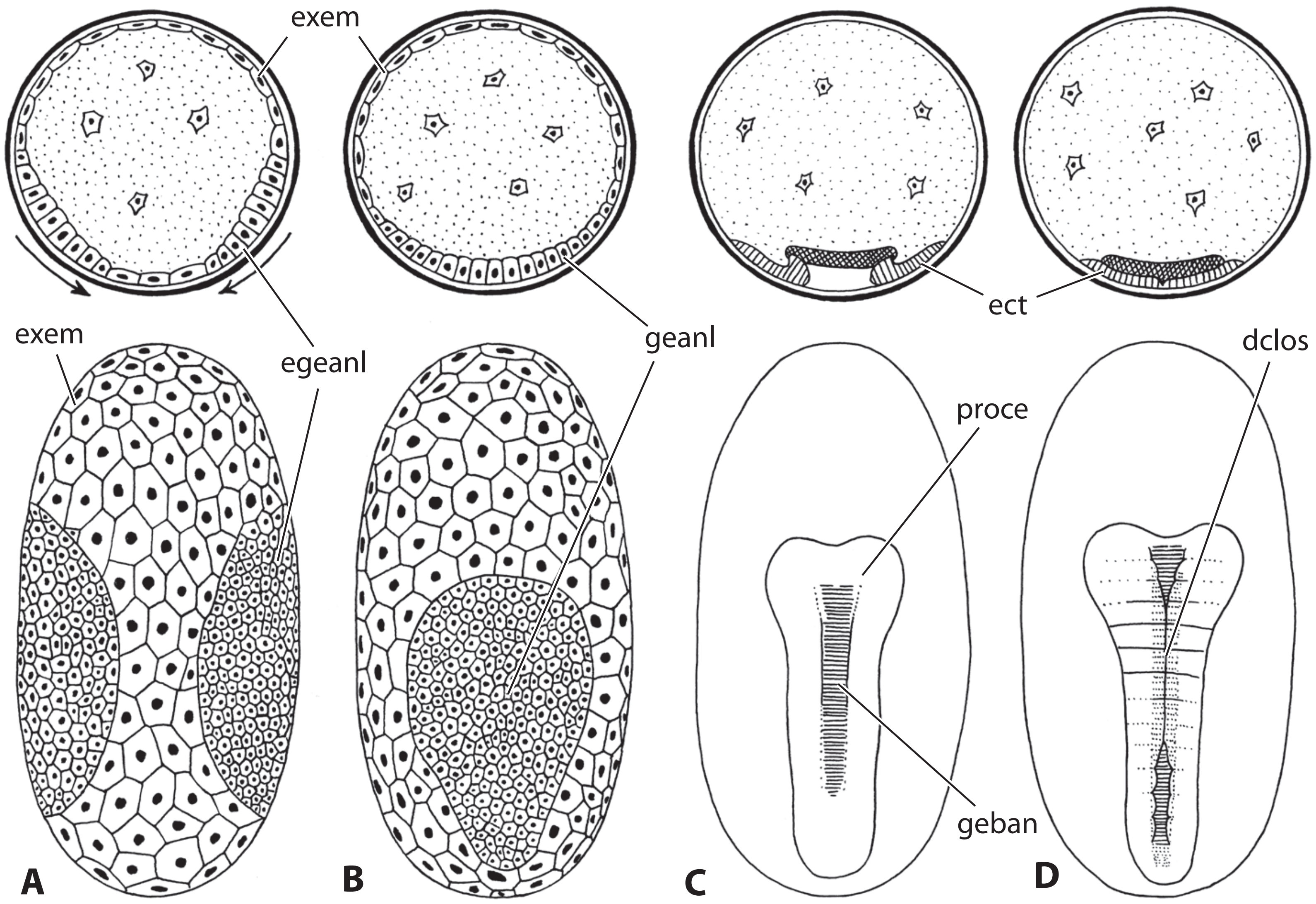
Embryonic development: Cleavage and germ band formation

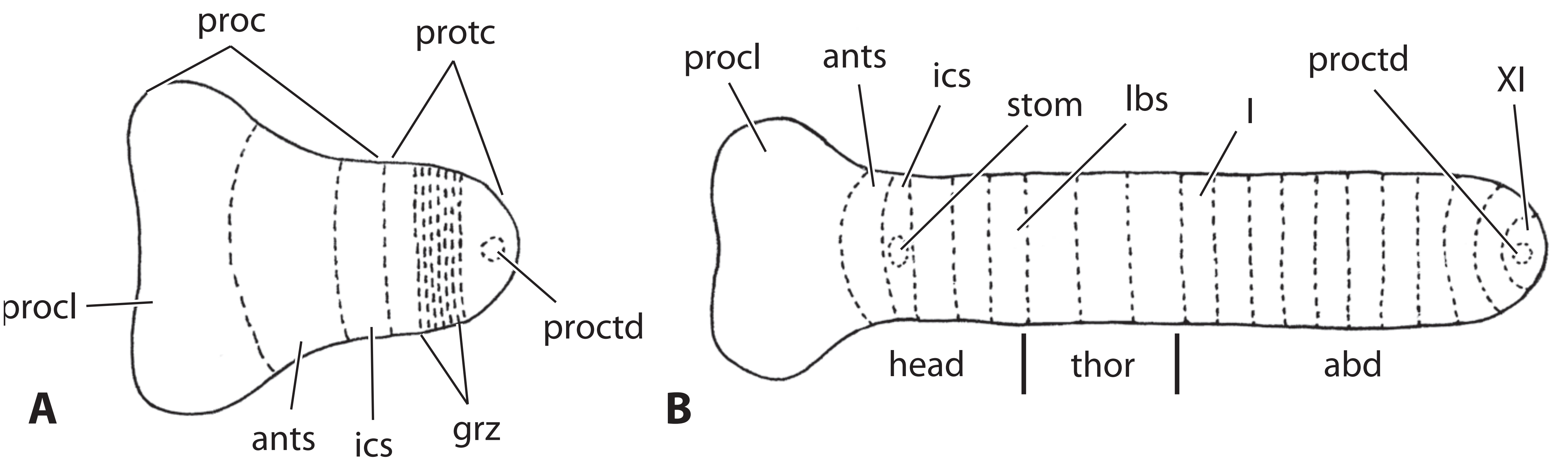
Cleavage is meroblastic and superficial in most groups of Hexapoda and in Arthropoda in general. However, within each major arthropod lineage the holoblastic type occurs, usually in basal groups. This suggests that superficial cleavage may have been acquired independently several times. The superficial 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.

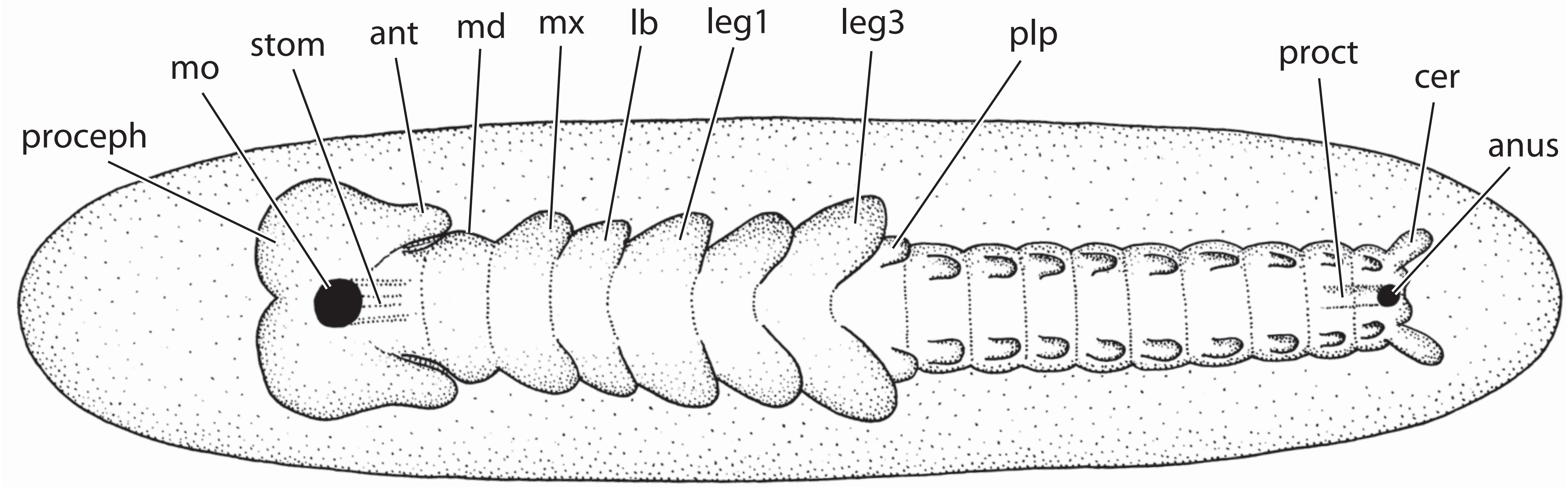
The lateral membranes form before the basal membranes, which separate the cells from the yolk mass. The external layer of cells is referred to as cellular blastoderm. Some nuclei remain in the central yolk mass and help to mobilize the nutrients (vitellophages or yolk cells). In many groups other nuclei 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.



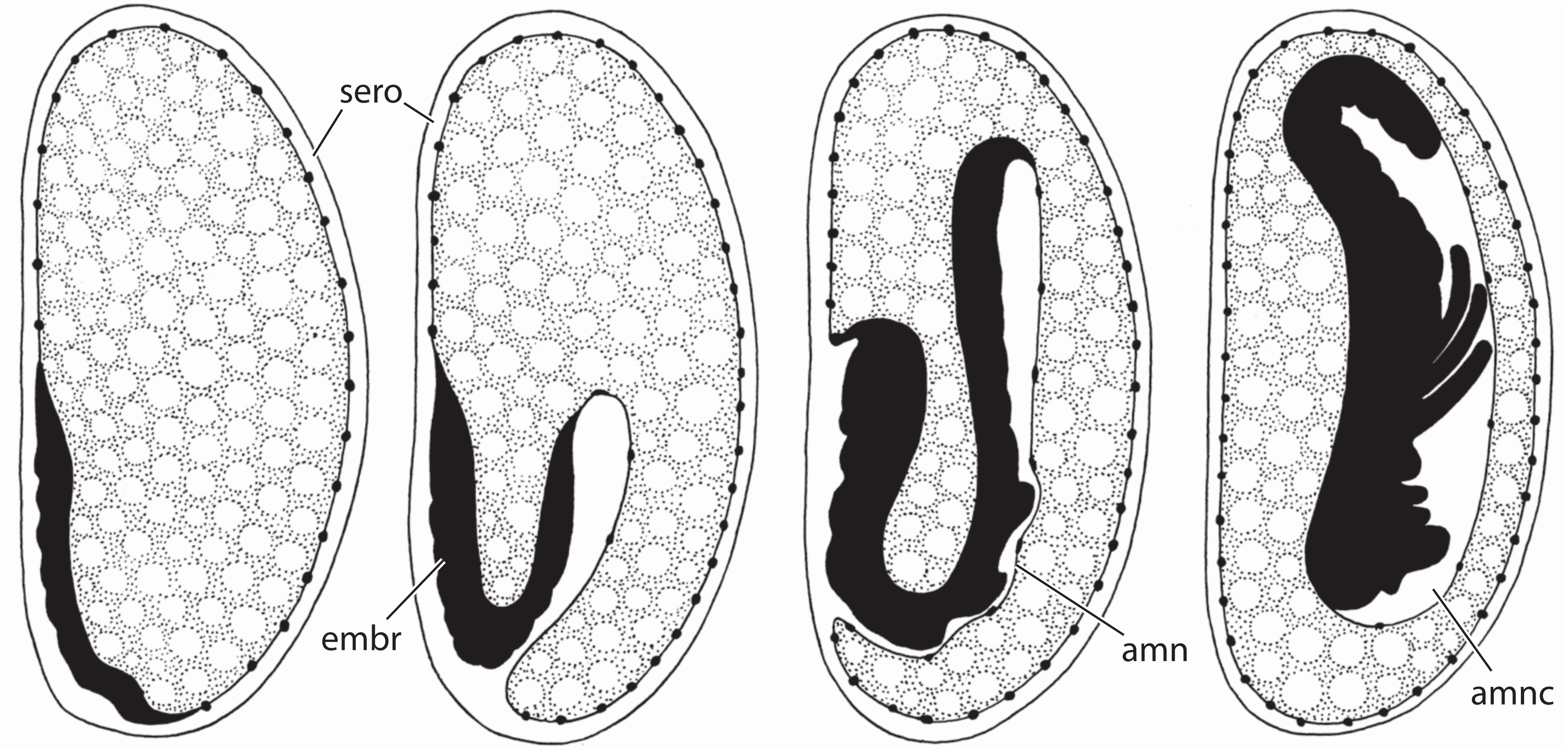


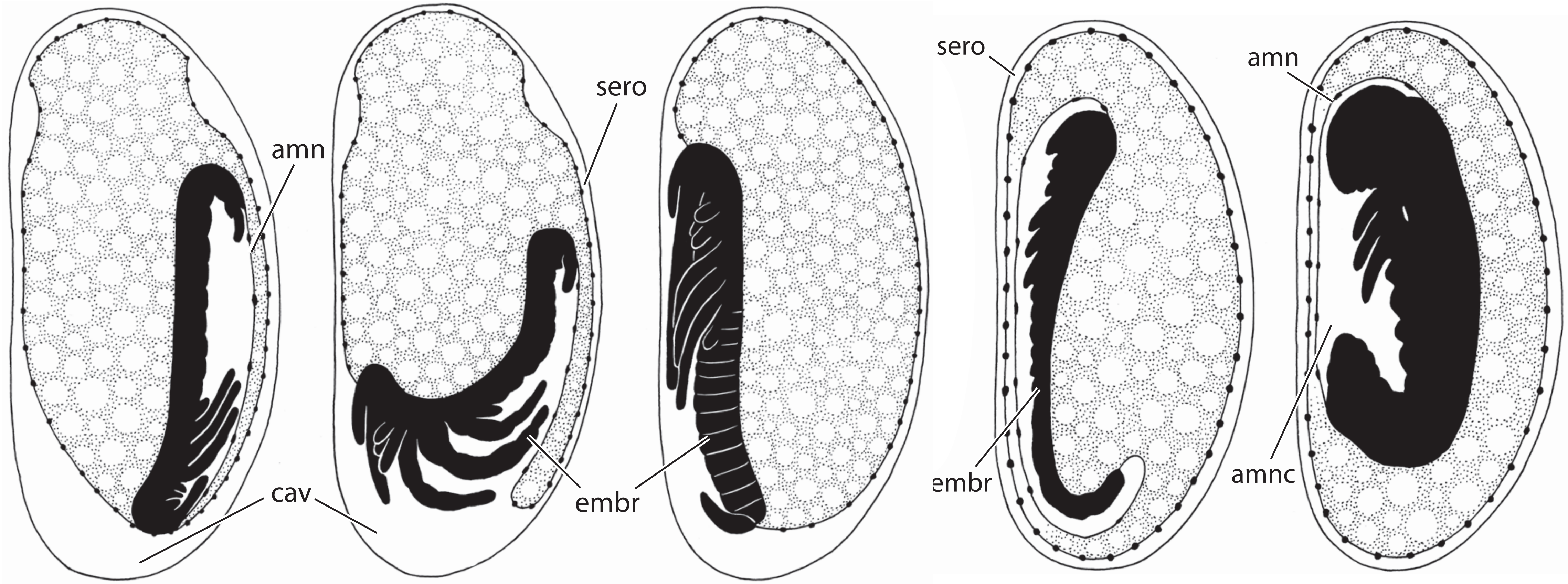
Different forms of embryos. **A**, short germ embryo; **B**, long germ embryo. **abd**: abdomen (I,XI), **ants**: antennal segment, **grz**: growth zone, **ics**: intercalary segment, **lbs**: labial segment, **proc**: proecephalon, **procl**: protocephalic lobes, **protc**: protocorm, **proctd**: proctodaeum,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

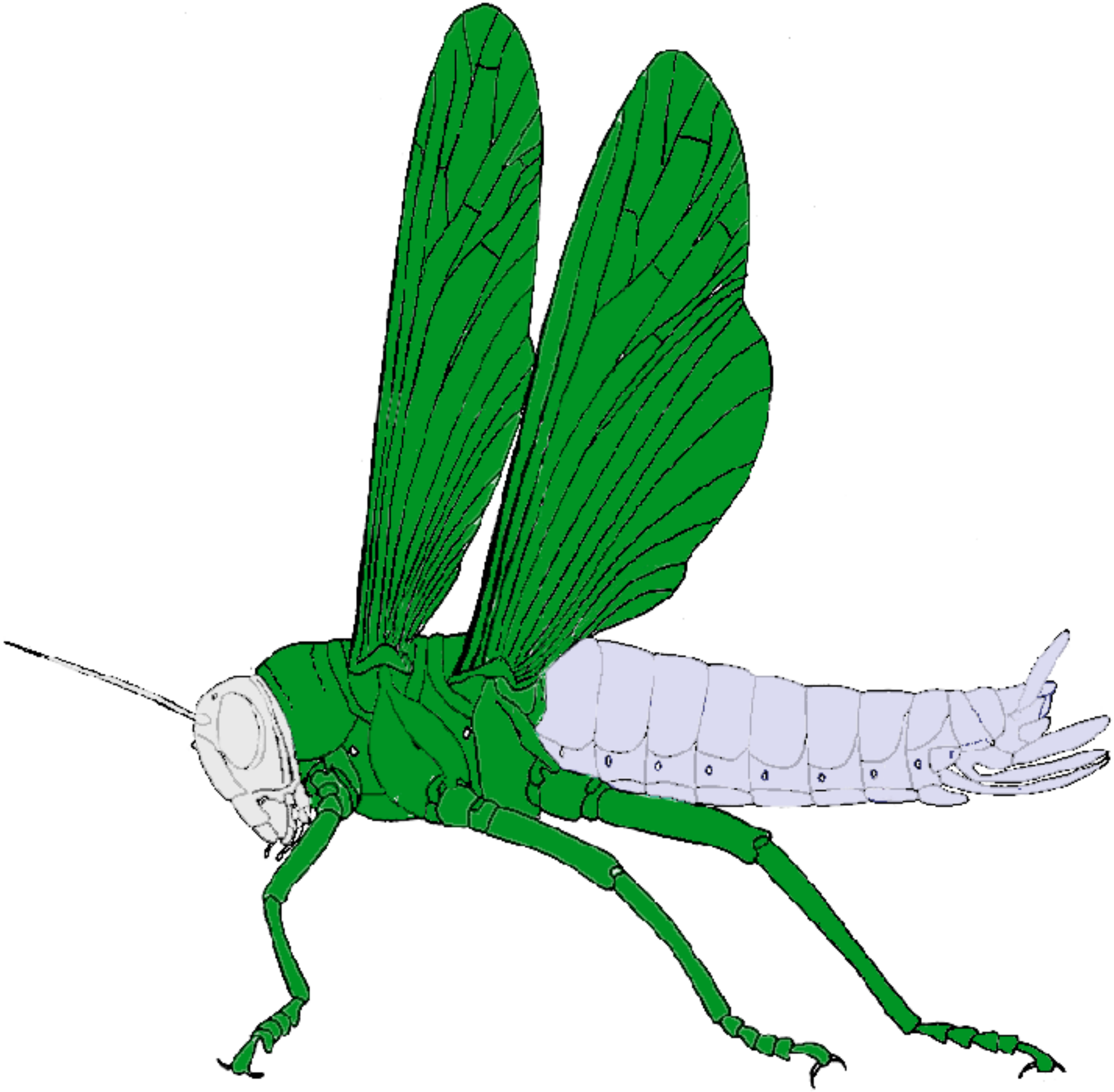
In groups with short or semi-long germ eggs the embryo is shifted to the central region containing the yolk mass by a rotation (anatrepsis). This results in the formation of the amniotic cavity. Later in development a reverse movement called katatrepsis results in return to the original external position 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.

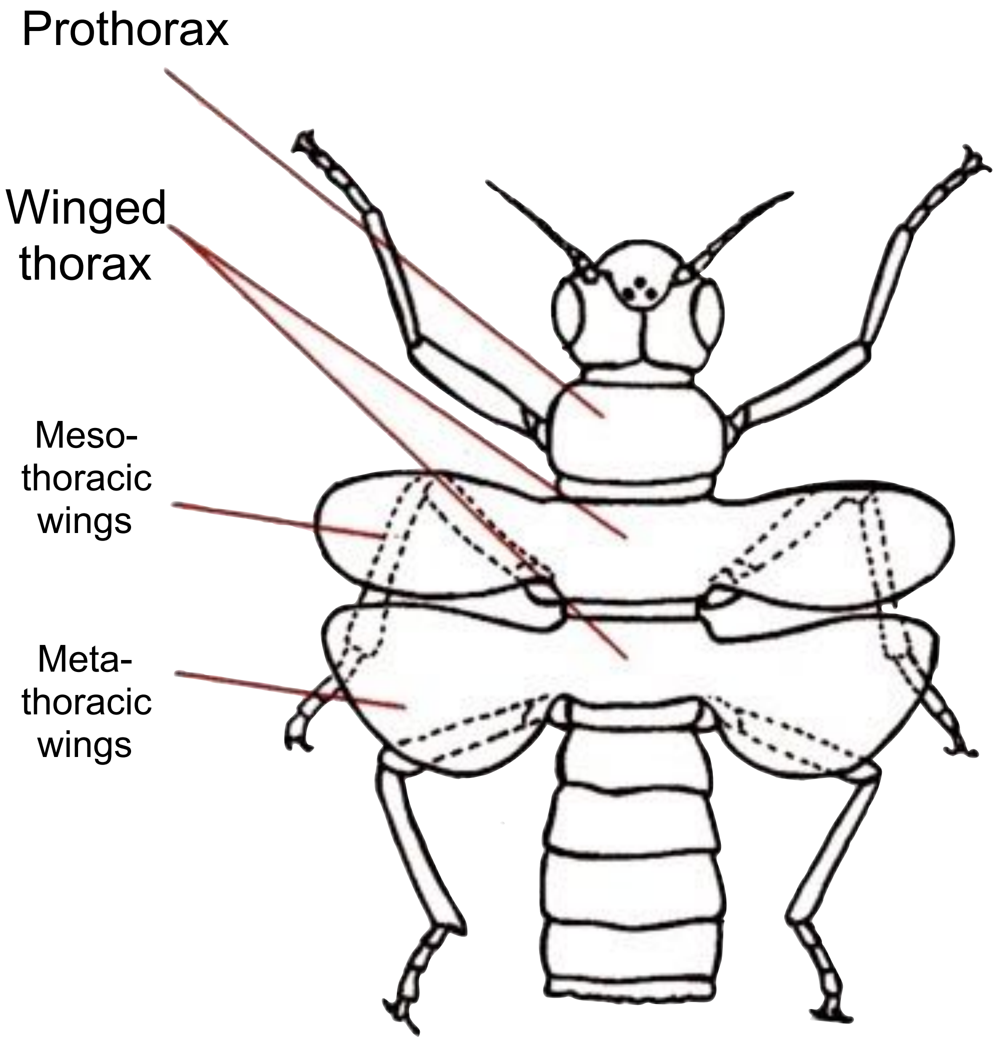
Segmentation

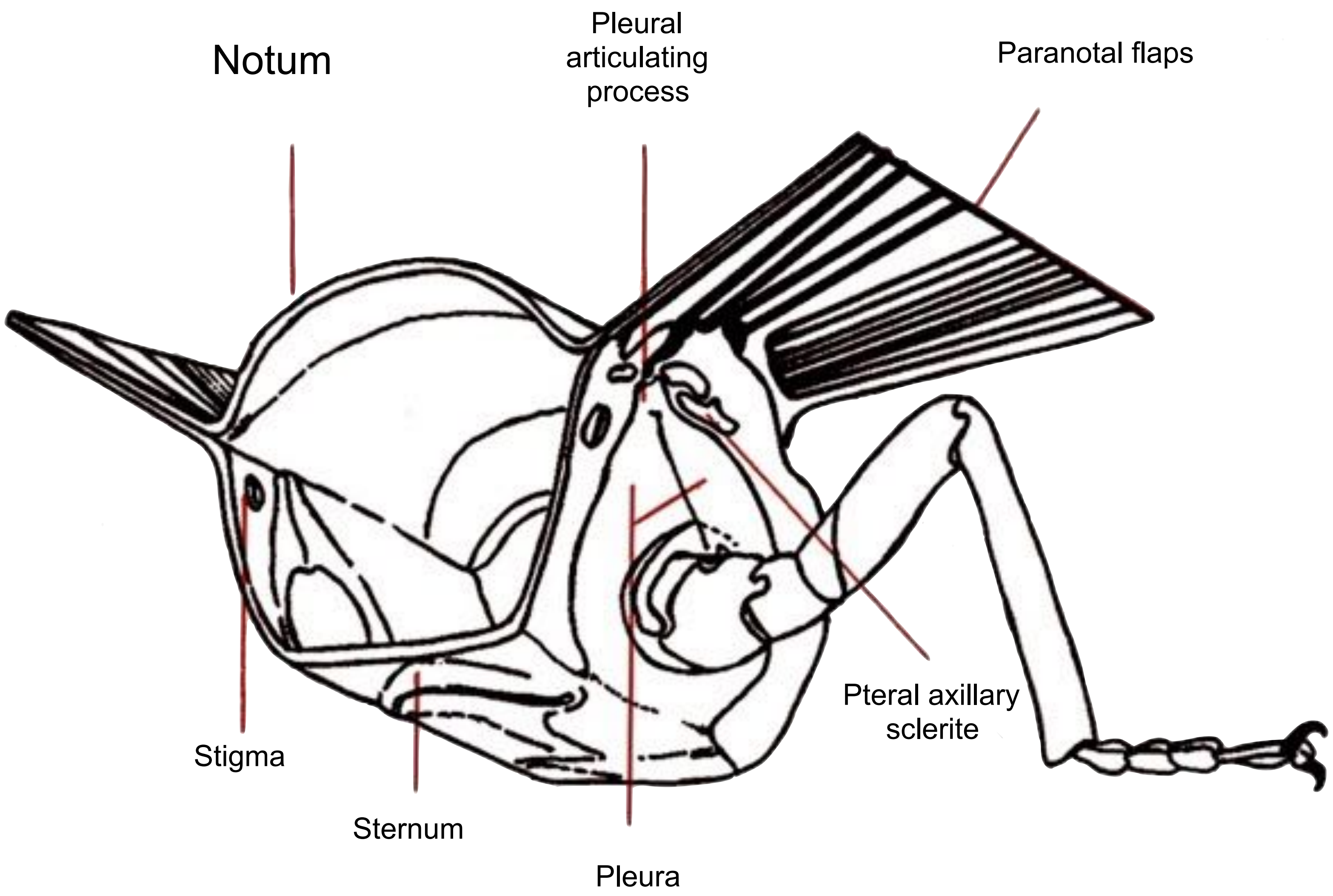
After the inner layer is formed the embryo is divided into segments by transverse furrows. In members of most orders each of the segments develops a pair of appendages, the antennae and three gnathal appendages (prospective mouthparts) in the cephalic region, three pairs of thoracic legs, ten pairs of 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.

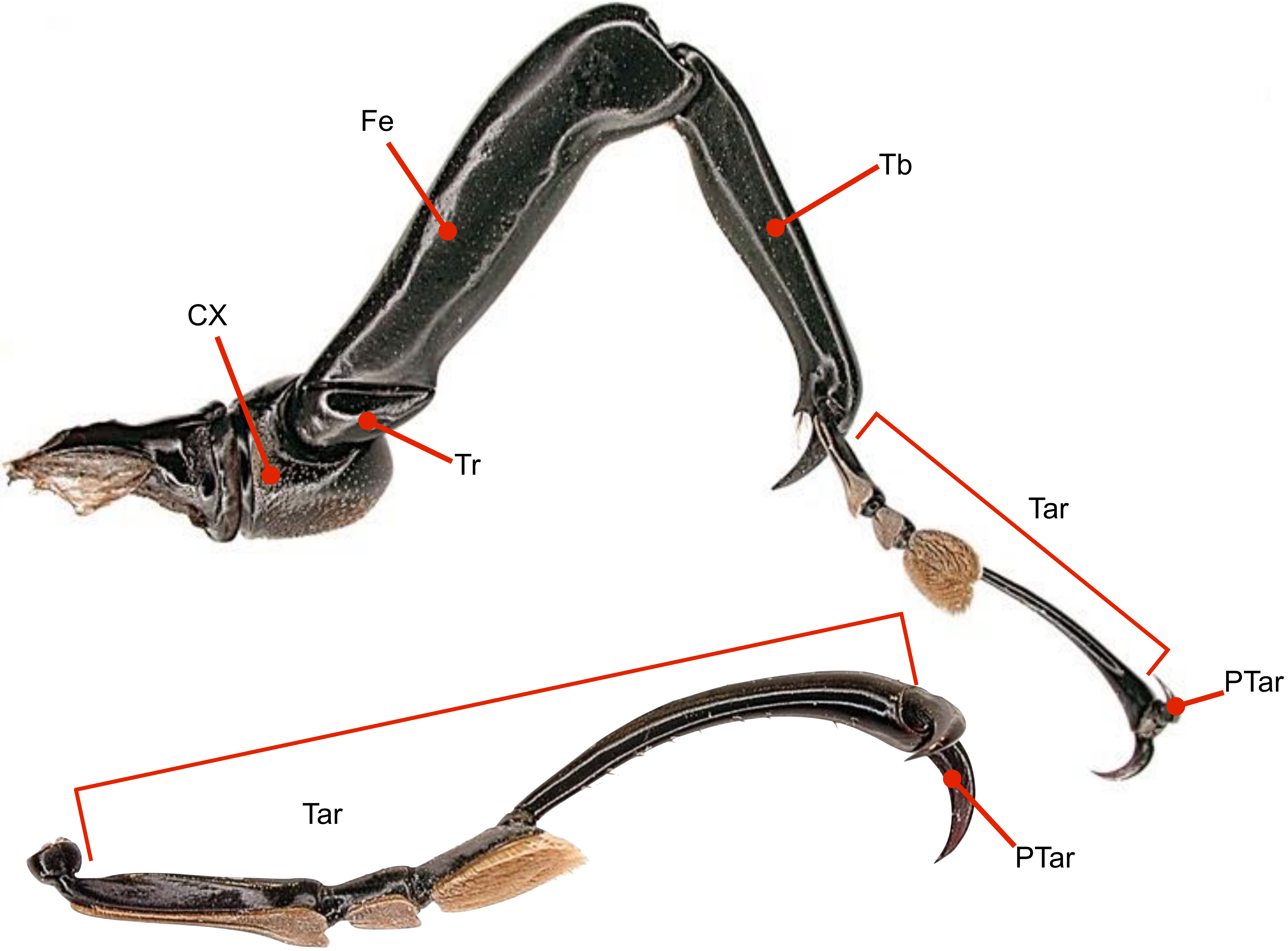
Sternum The primary sclerotizations on the ventral side are segmental and inter segmental plates which often remain separate in the thorax.

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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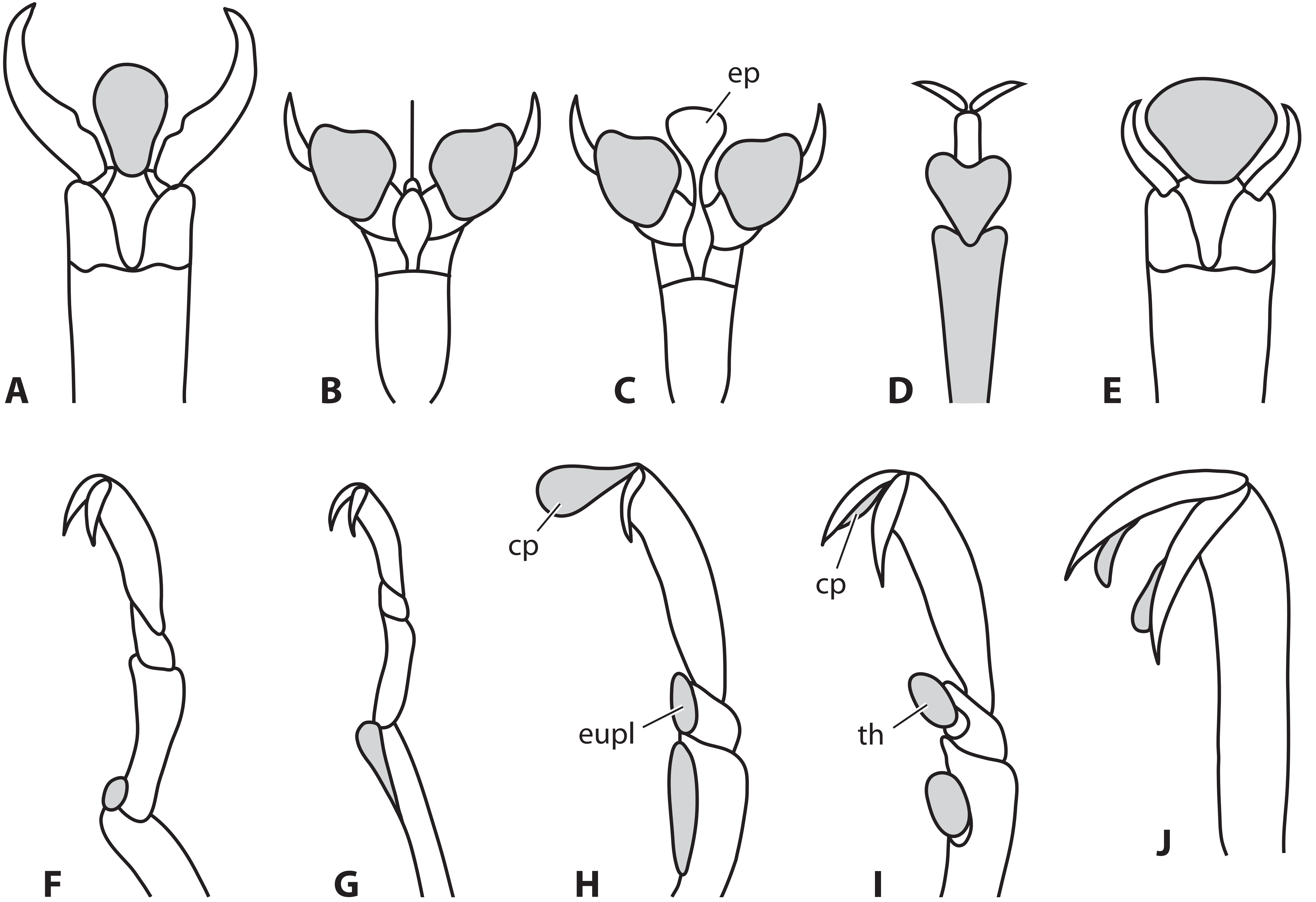
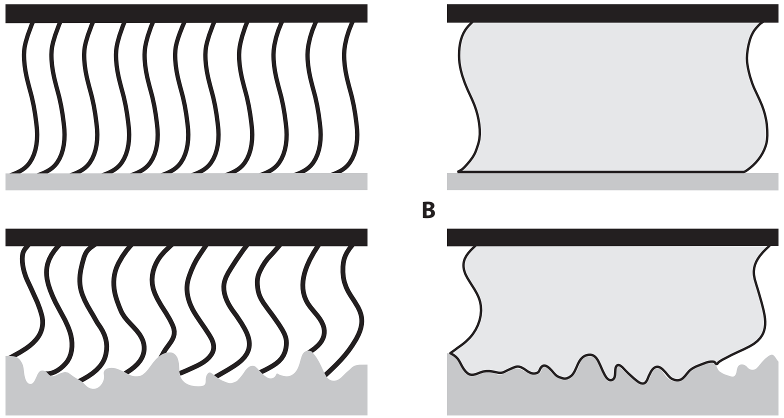
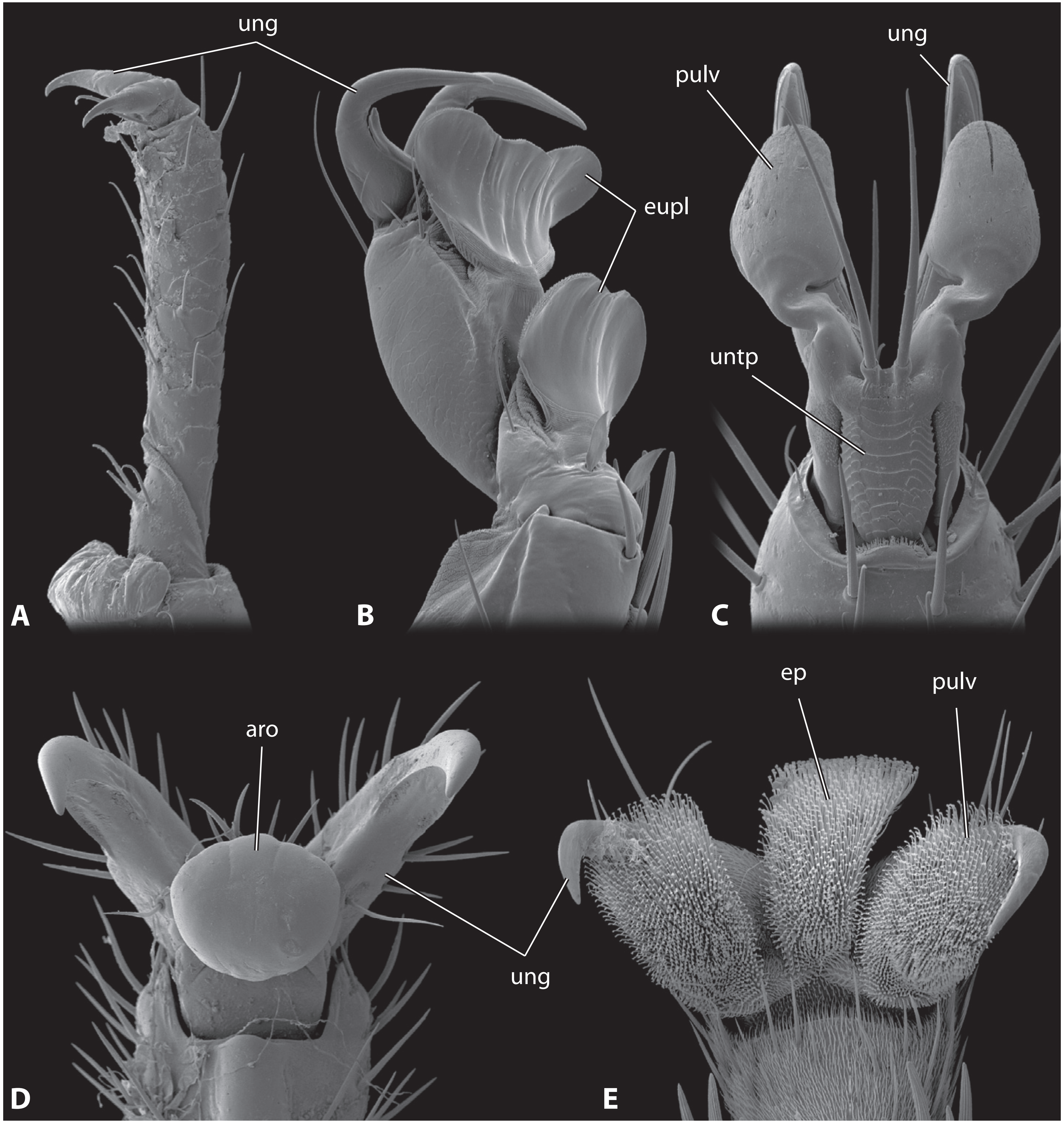


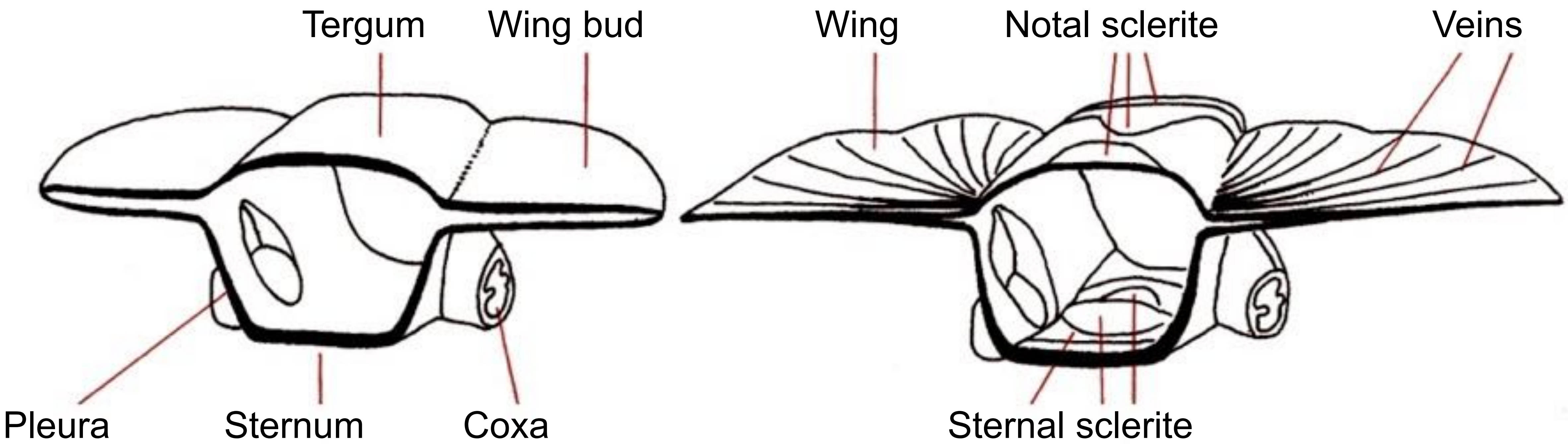
Attachment structures (grey) A: pretarsal arolium (almost always smooth); **B:** pretarsal pulvilli (smooth or hairy); **C:** widened empodium with adhesive microtrichia; **D:** hairy adhesive soles of tarsomeres; **E:** pretarsal protrusible vesicle (arolium); **F:** eversible adhesive structure between 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.



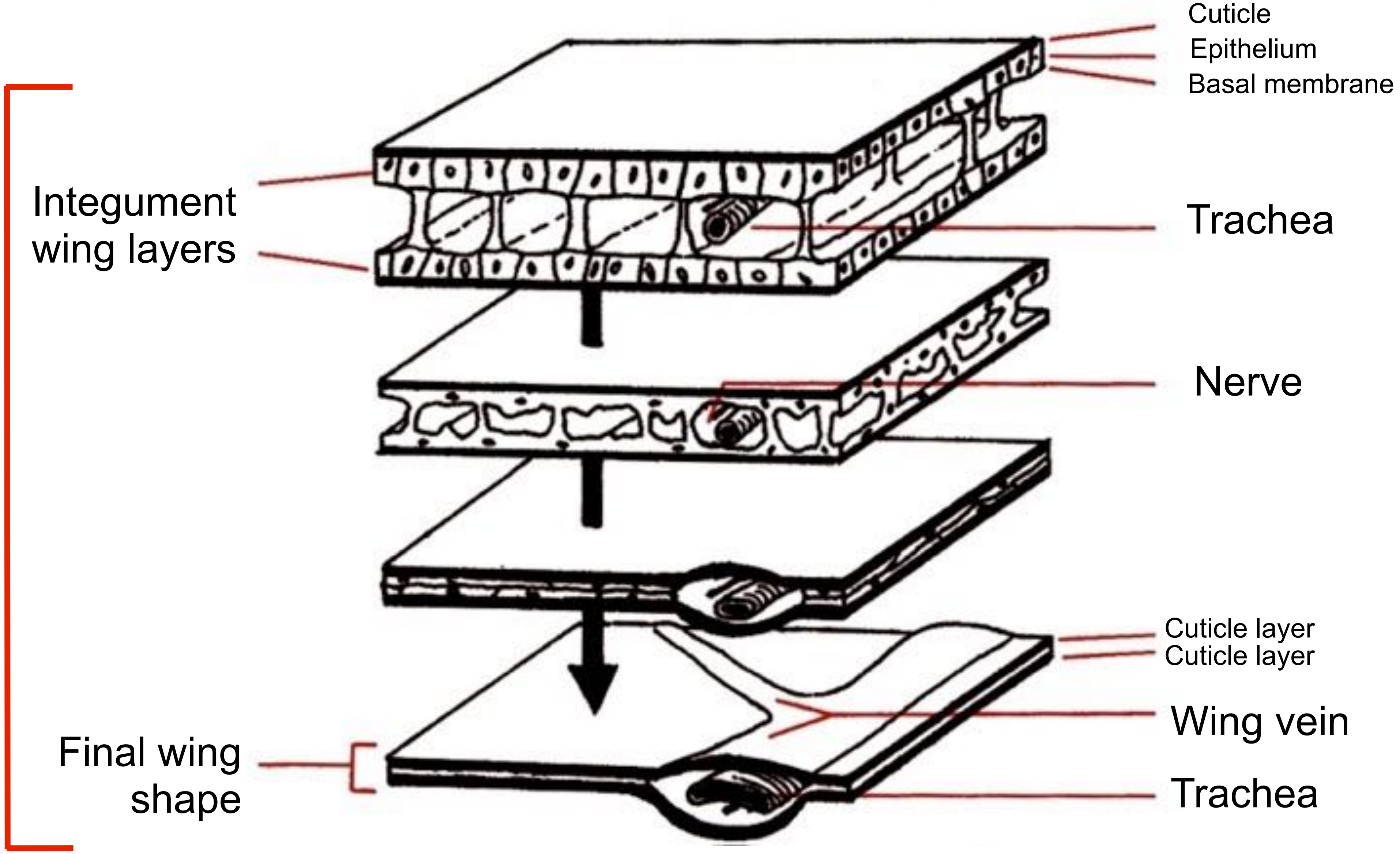
Function of different types of tarsal or pretarsal attachment structures. **A:** hairy type; **B:** smooth type.

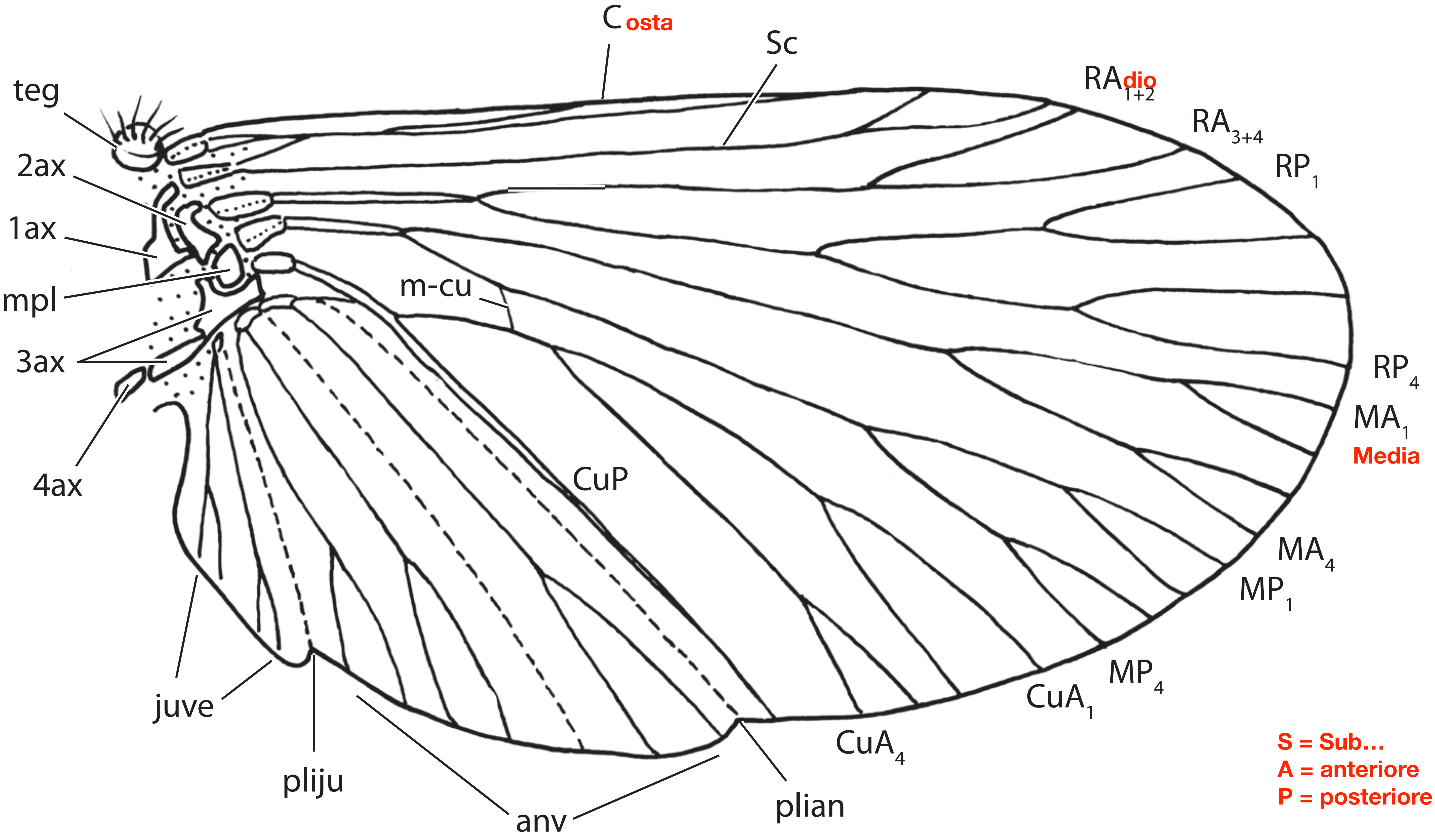


Attachment structures SEM micrographs. **A:** *Aphis sambuci* (Sternorrhyncha, Aphididae); **B:** *Trinoton anserinum* (Amblycera, Menoponidae); **C:** *Graphosoma lineatum* (Heteroptera, Pentatomidae); **D:** *Locusta migratoria* (Orthoptera, Acrididae); **E:** *Tabanus* sp. (Diptera, Tabanidae). Abbr.: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

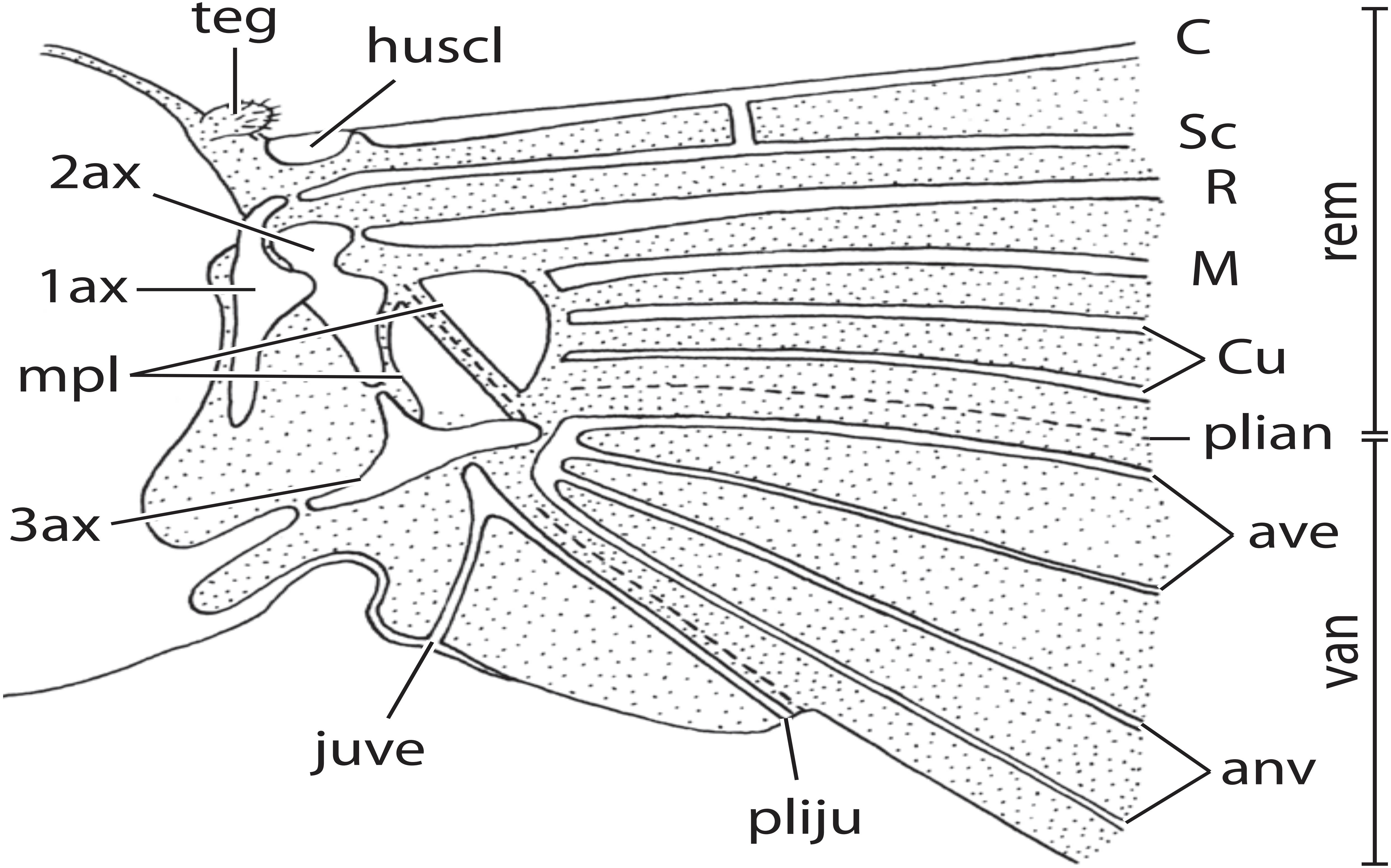


Wing growth during insect development





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 **postcu bitus** (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.

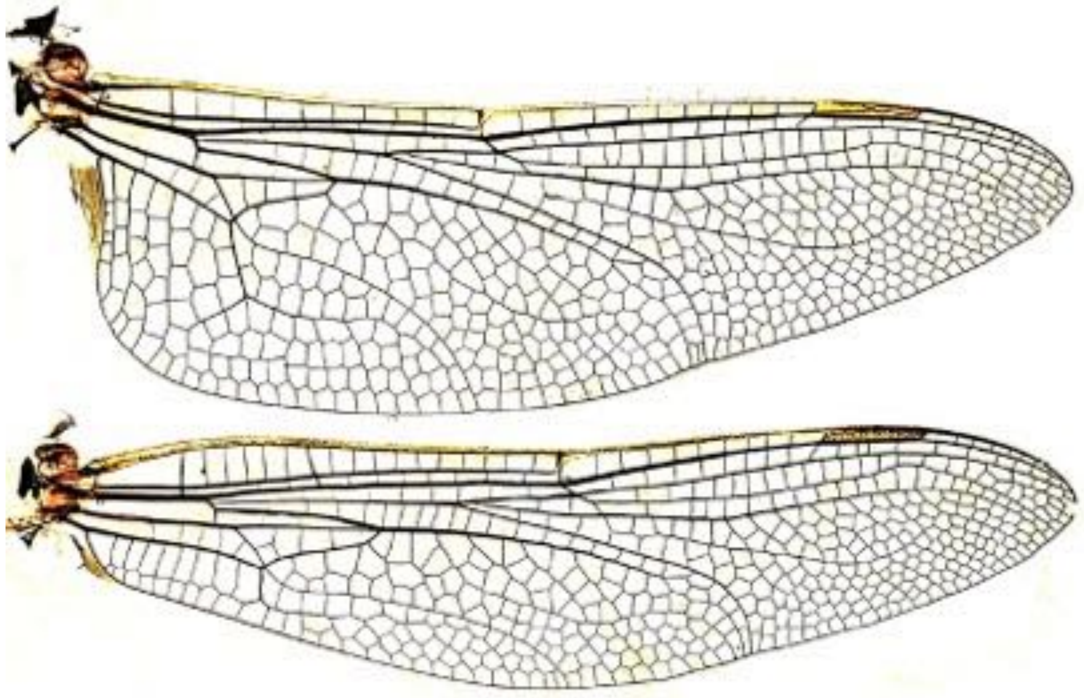
The first and strongest vein of the remigium is the unbranched **costa** (C). The following vein, the **subcosta** (Sc), often branches once. The **radius** (R) usually divides several times. Its anterior primary branch is referred to as **radius anterior** (RA) and the posterior one as **radial sector** 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).

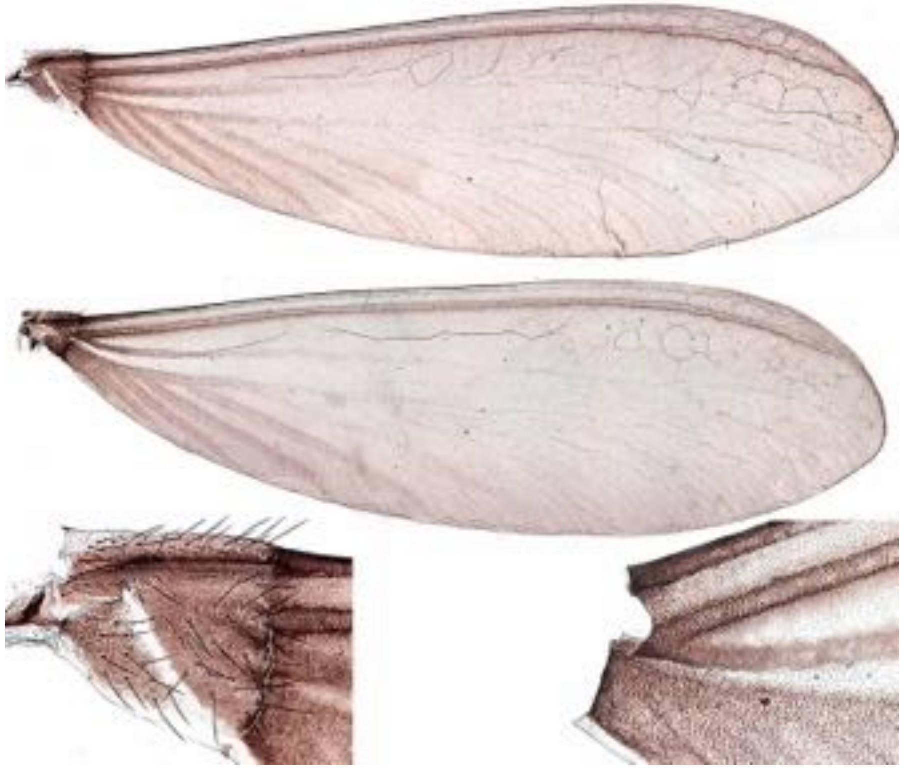
The surface of the wing is usually more or less densely covered with very short microtrichia. The wing membrane can be partly or entirely transparent (e.g., Hymenoptera) but color patterns occur frequently, most conspicuously in Lepidoptera. A specialized structure of the anterior margin is the **pterostigma**,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

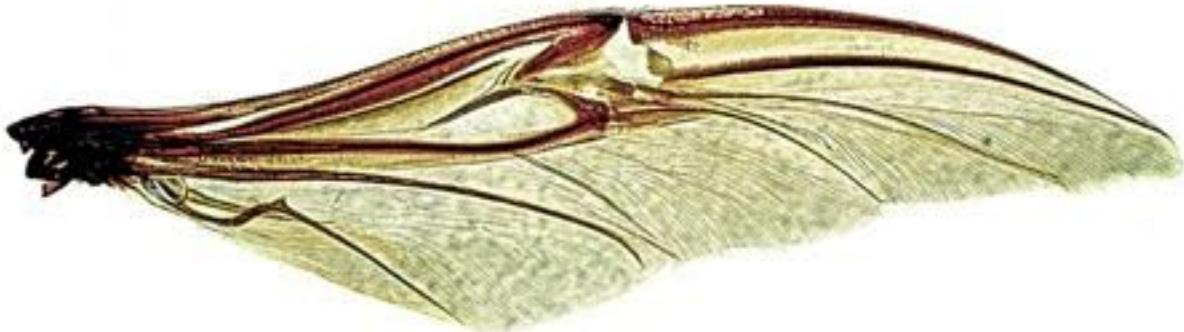
Different modifications and reductions of wings occur in pterygote insects. They are completely absent in all known species of Grylloblattodea, Mantophasmatodea and Siphonaptera and also in subordinate lineages of other groups (e.g., Phasmatodea). Alate and wingless morphs occur in Zoraptera and some 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).

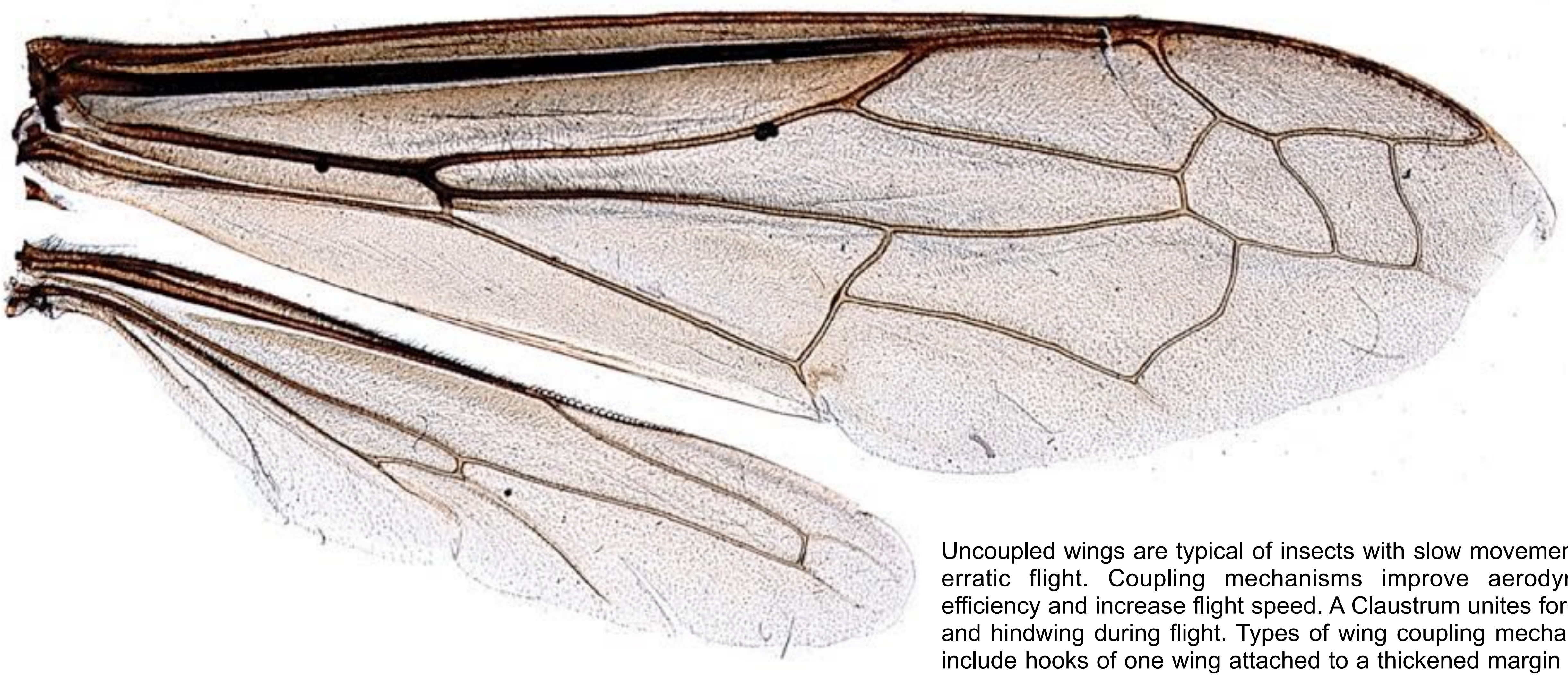
Aside from the ability to fold back the wings (autapomorphy of Neoptera) different transverse or longitudinal folding patterns occur. This is always linked with modifications of veins such as articulations (Scarabaeoidea) or bending zones (e.g., other groups of Coleoptera). A complicated mechanism of 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).

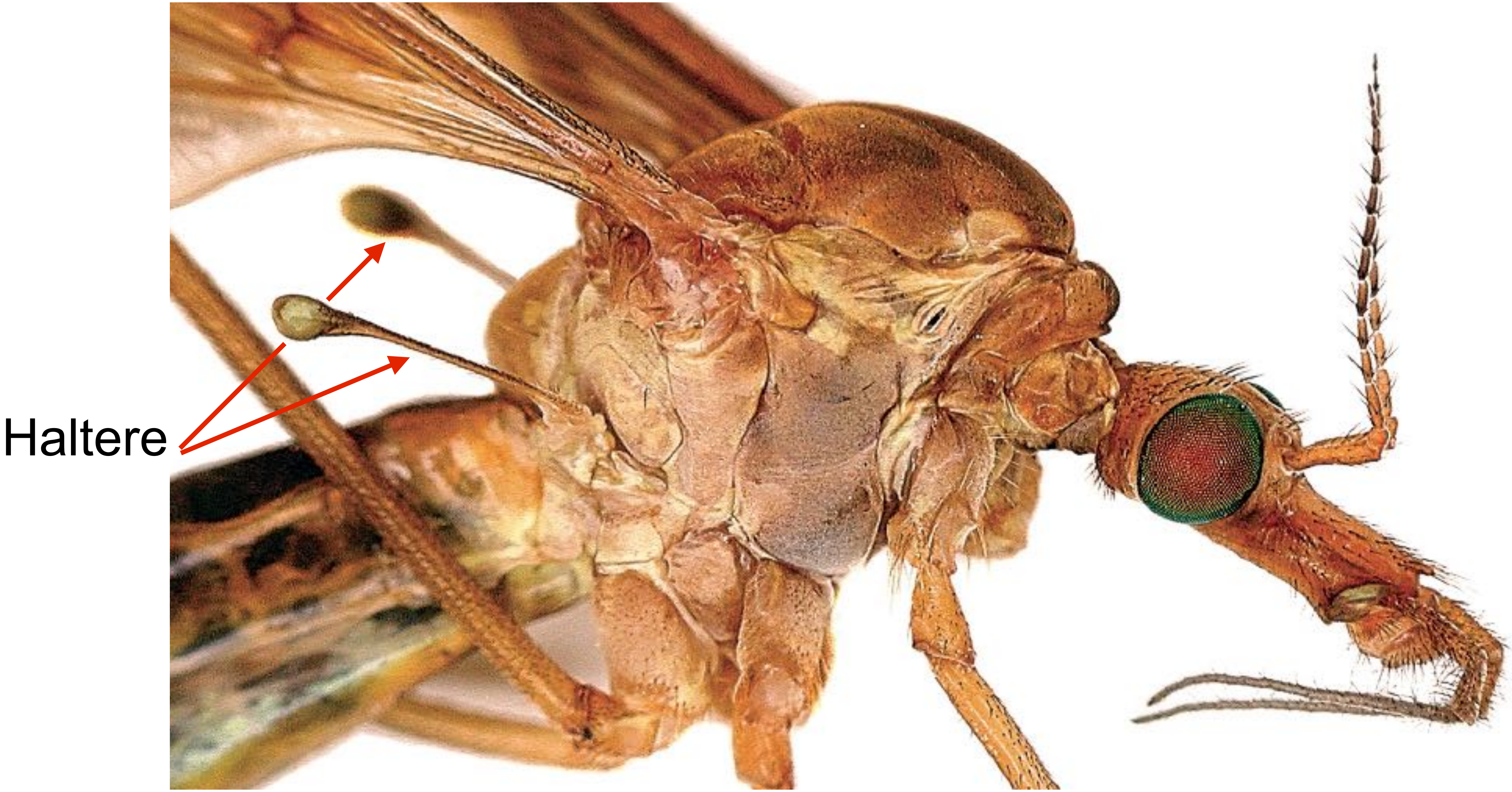




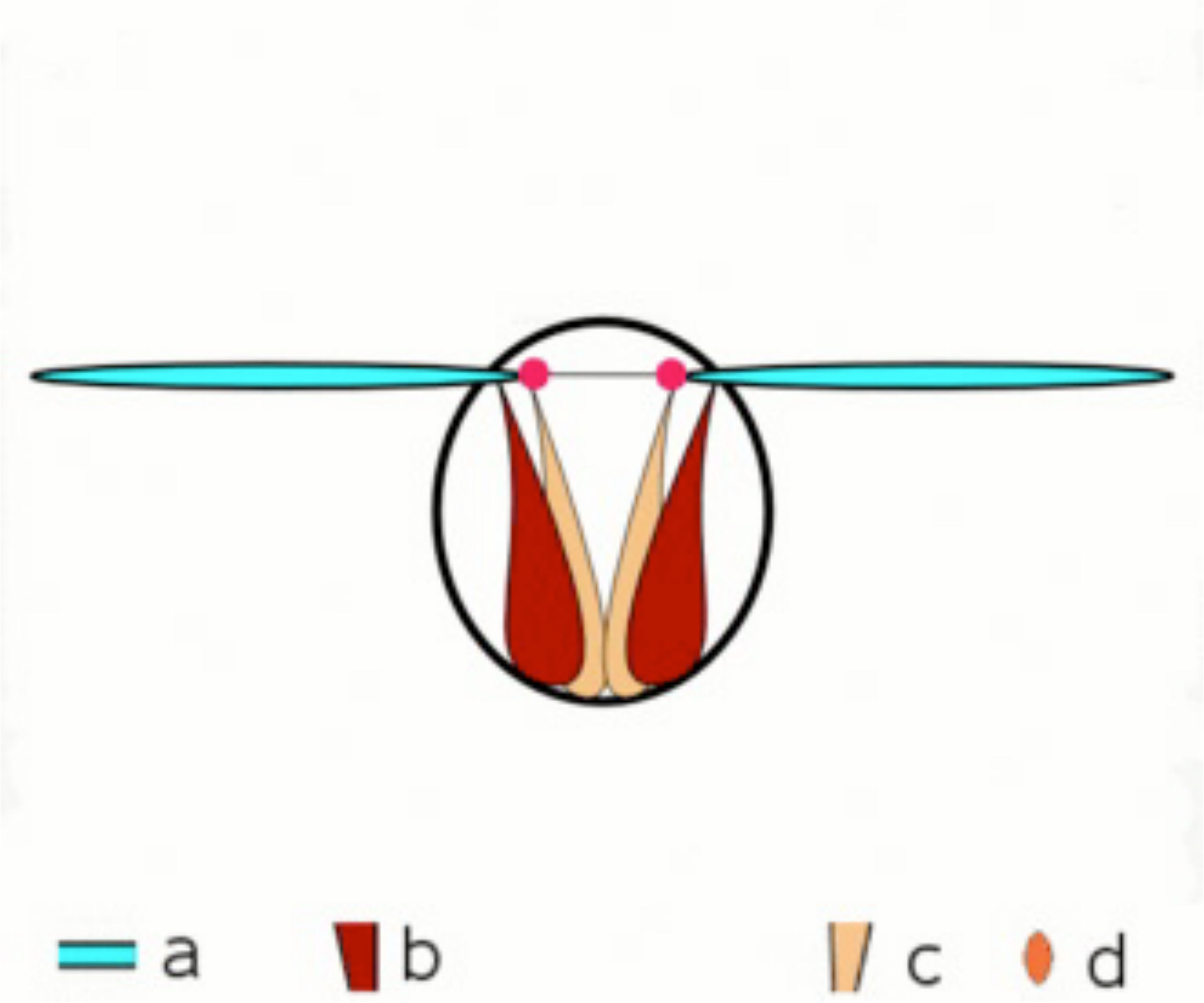


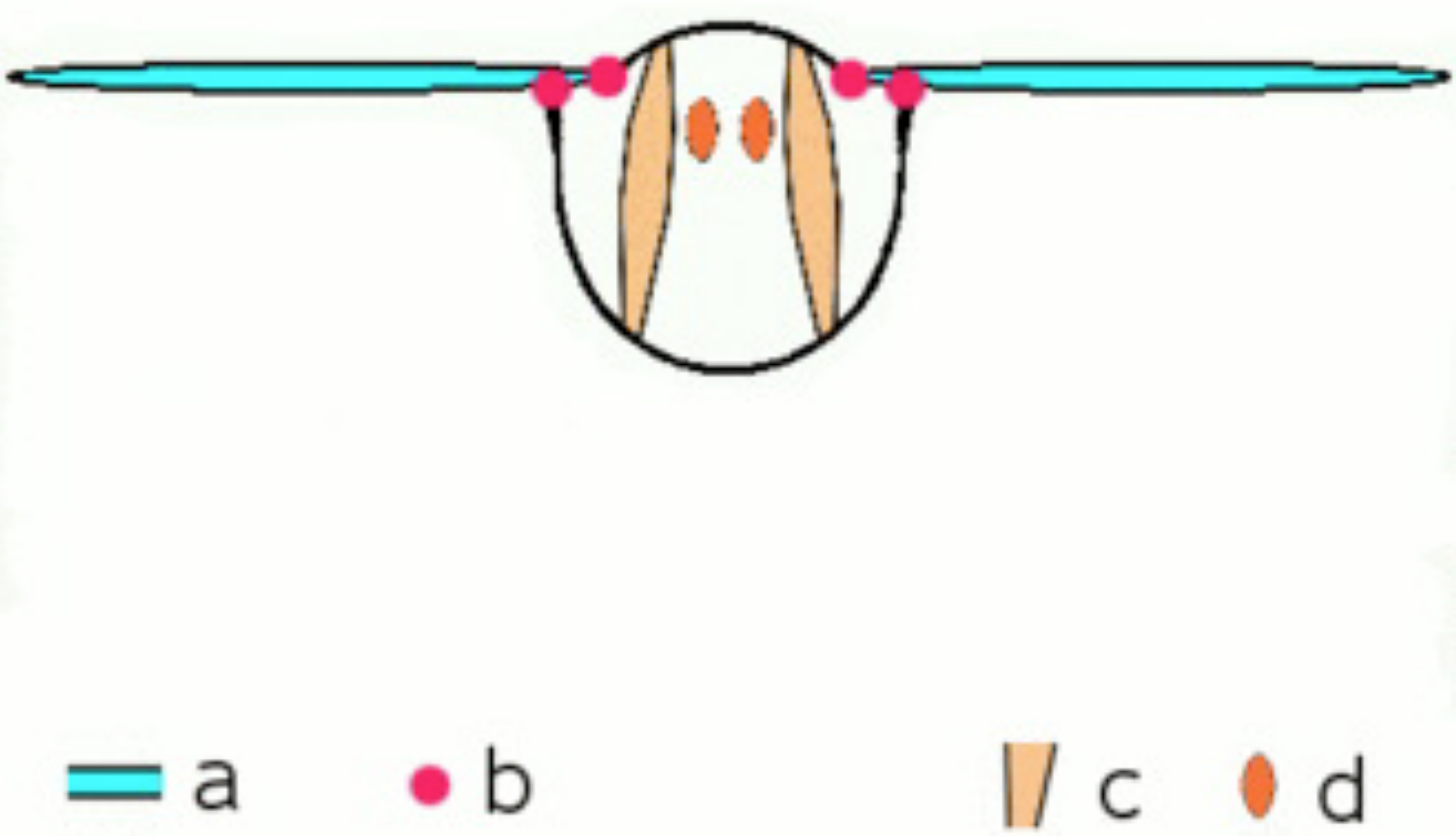


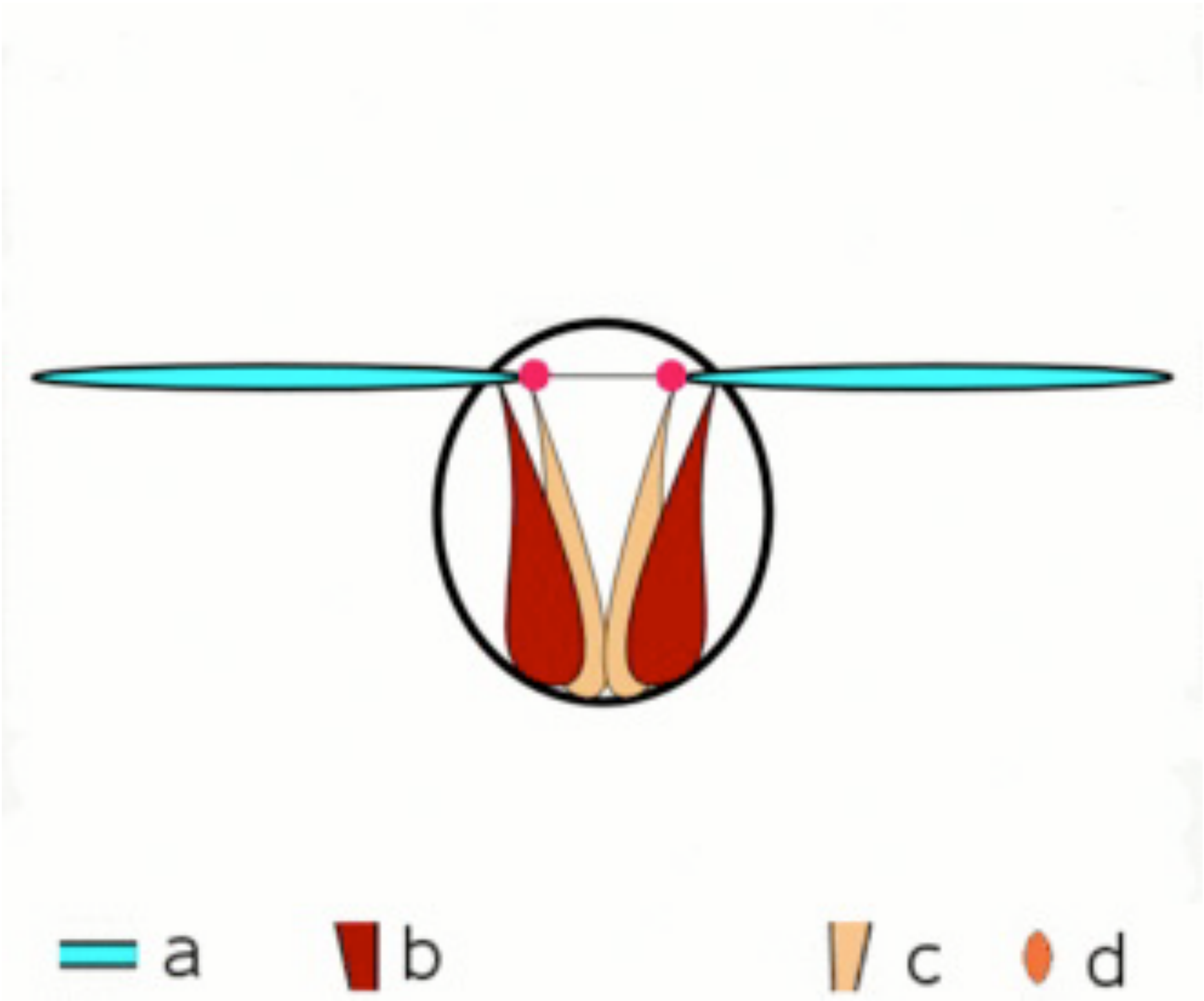
Uncoupled wings are typical of insects with slow movement and erratic flight. Coupling mechanisms improve aerodynamic efficiency and increase flight speed. A Claustrum unites forewing and hindwing during flight. Types of wing coupling mechanisms include hooks of one wing attached to a thickened margin 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.

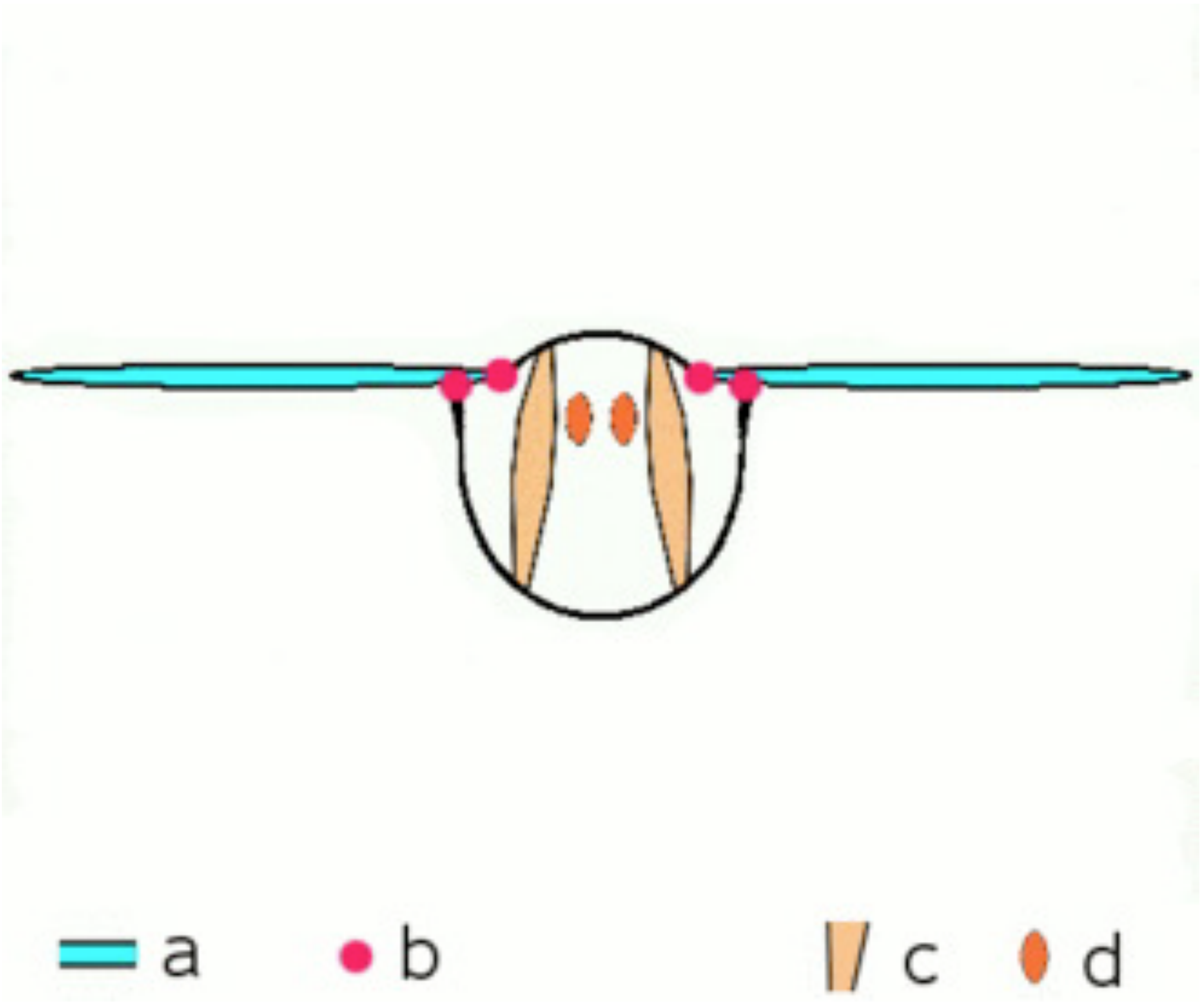


The Haltere forms a complex orientation device. Anatomically, the Haltere consist of a base (Scabellum), an elongate pedicel and an apically enlarged knob (Capitulum). The base of the Haltere is invested with campaniform Sensilla, Hicks' Papillae and chordotonal organs. The Haltere is a balancing organ 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.


a
b
c
d


a
b
c
d


a
b
c
d


a
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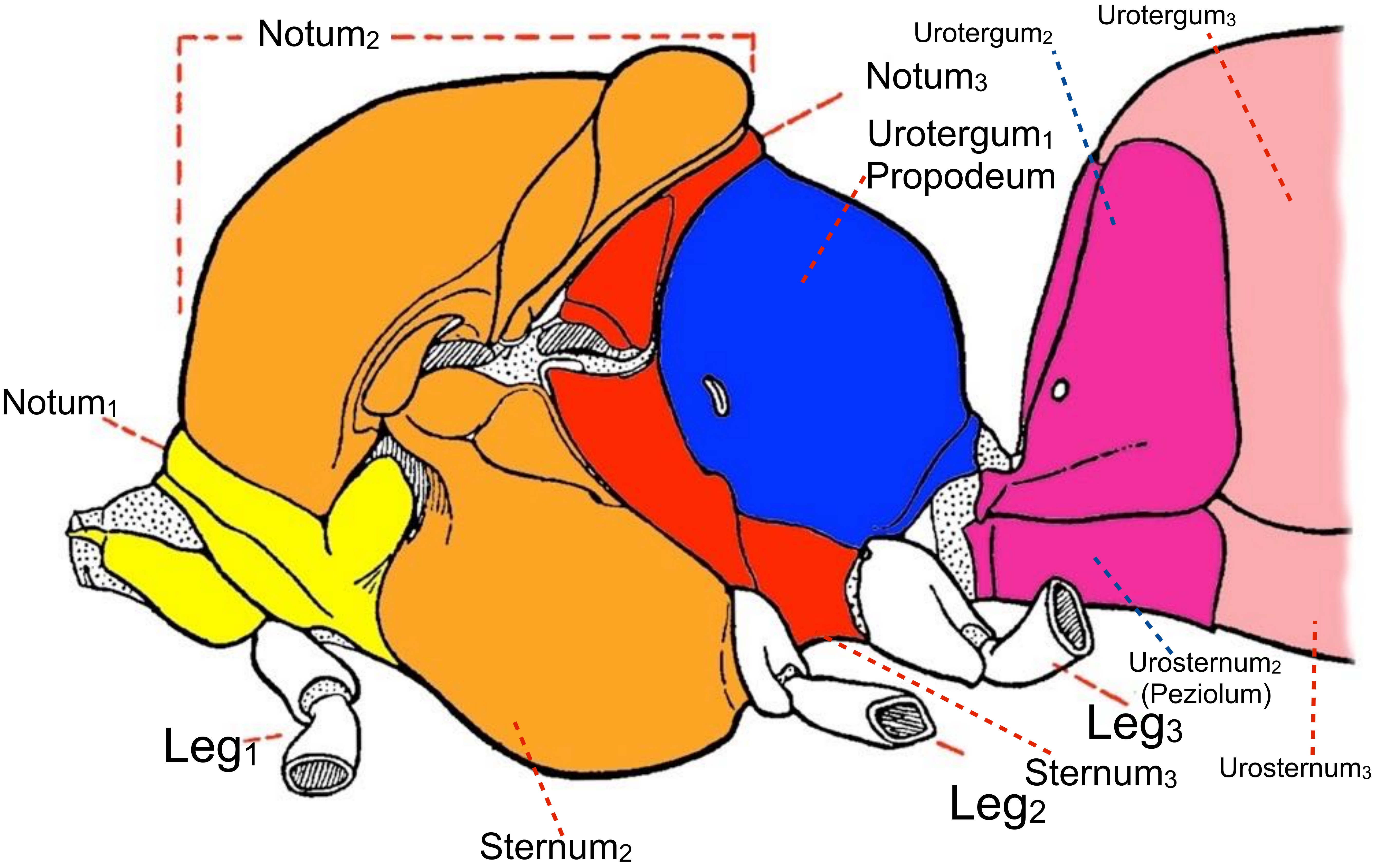
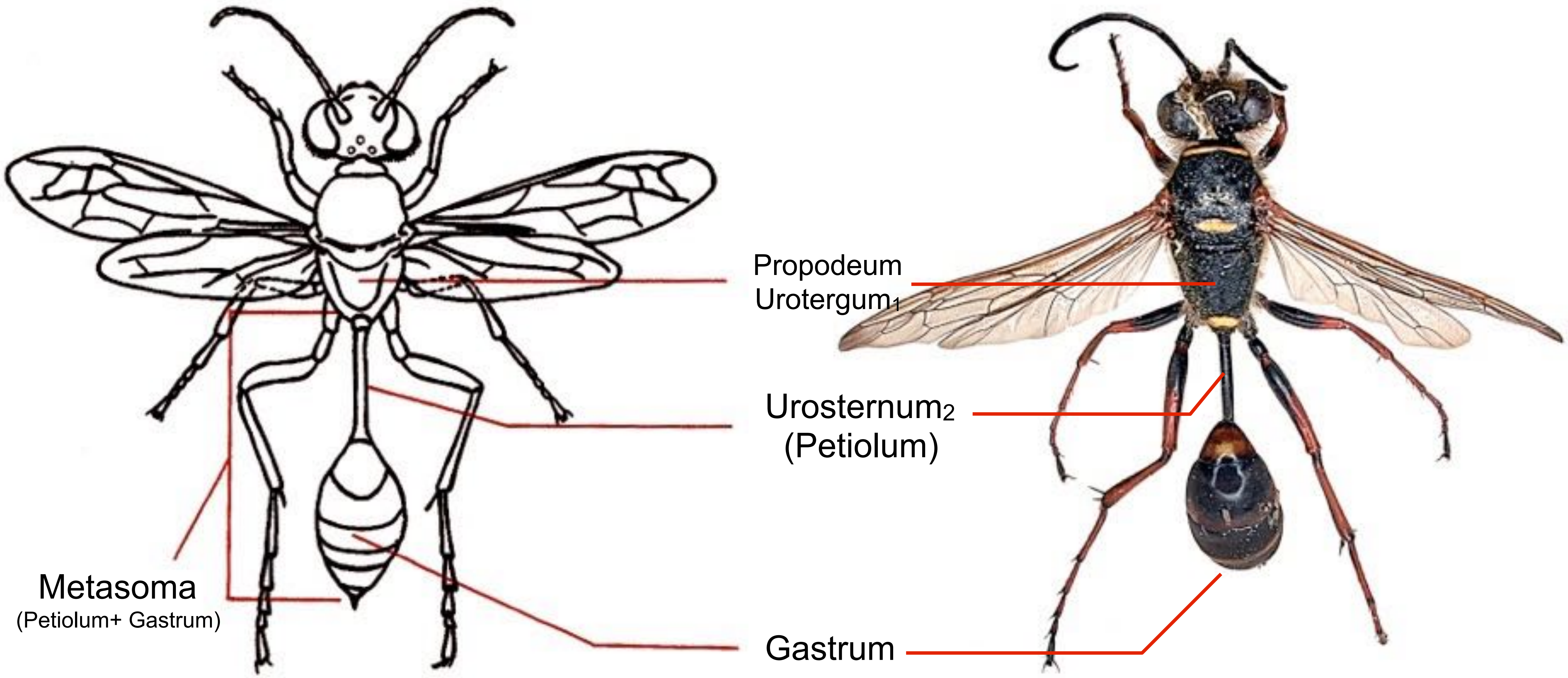
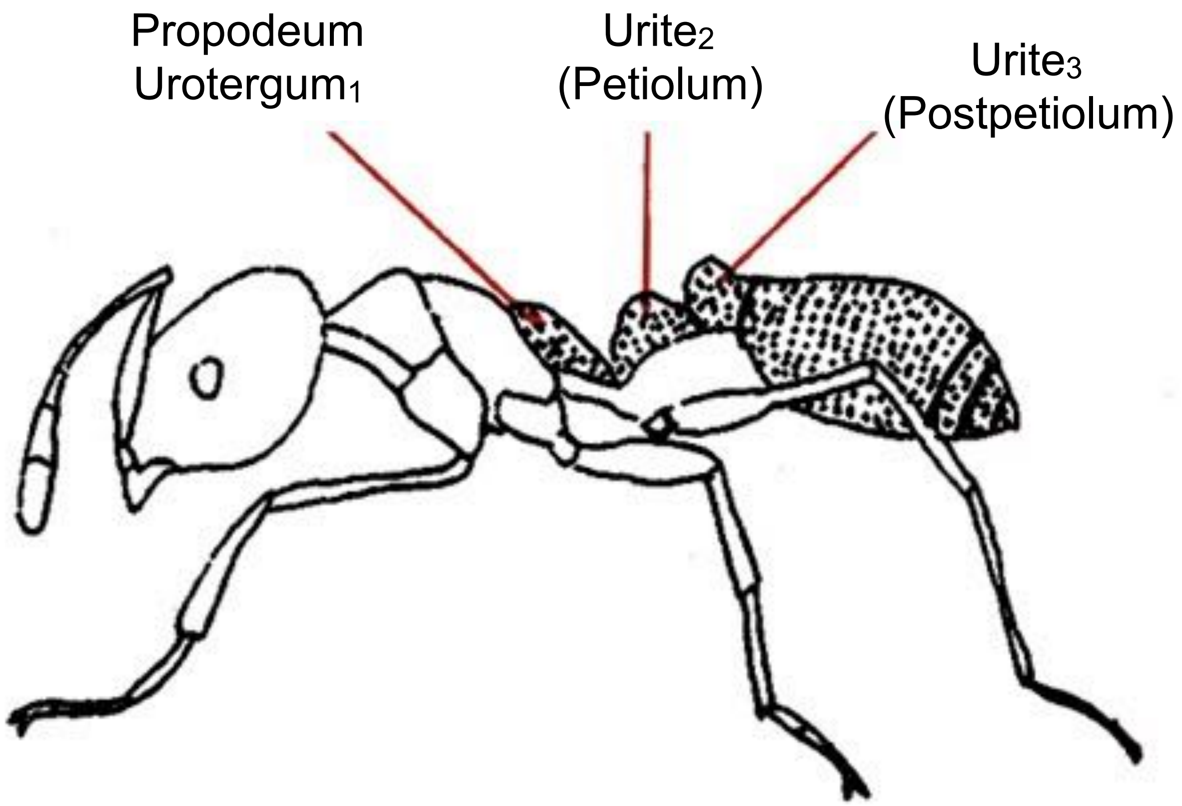
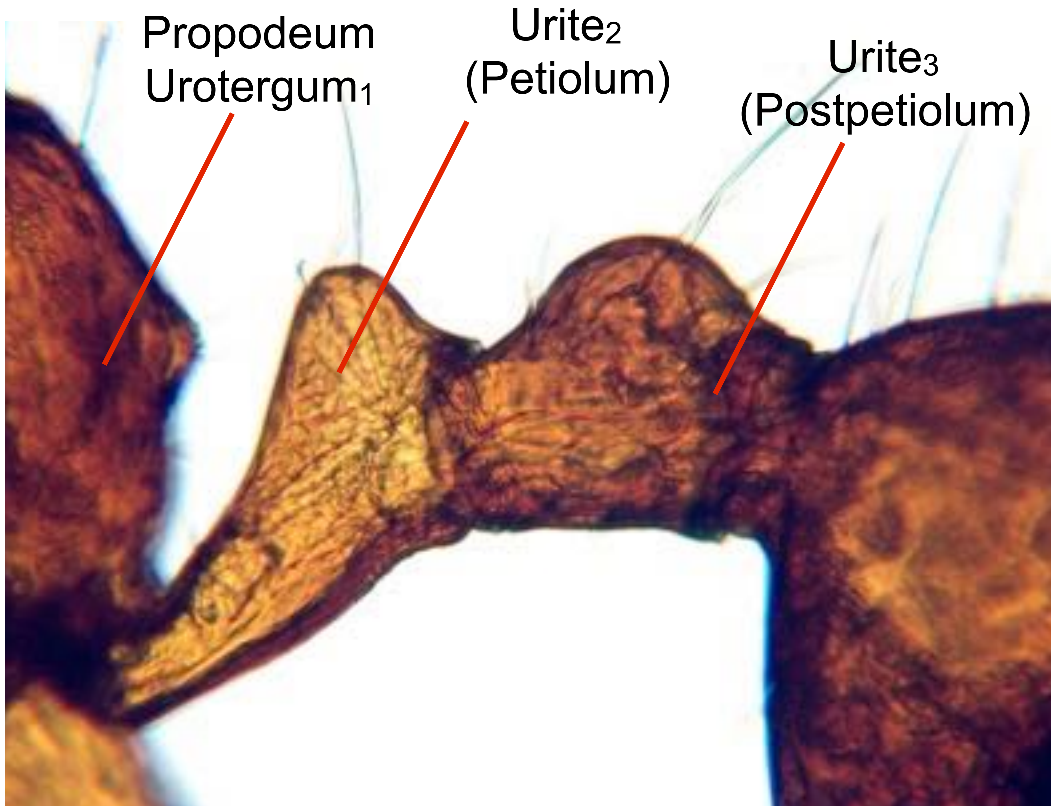
d

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.

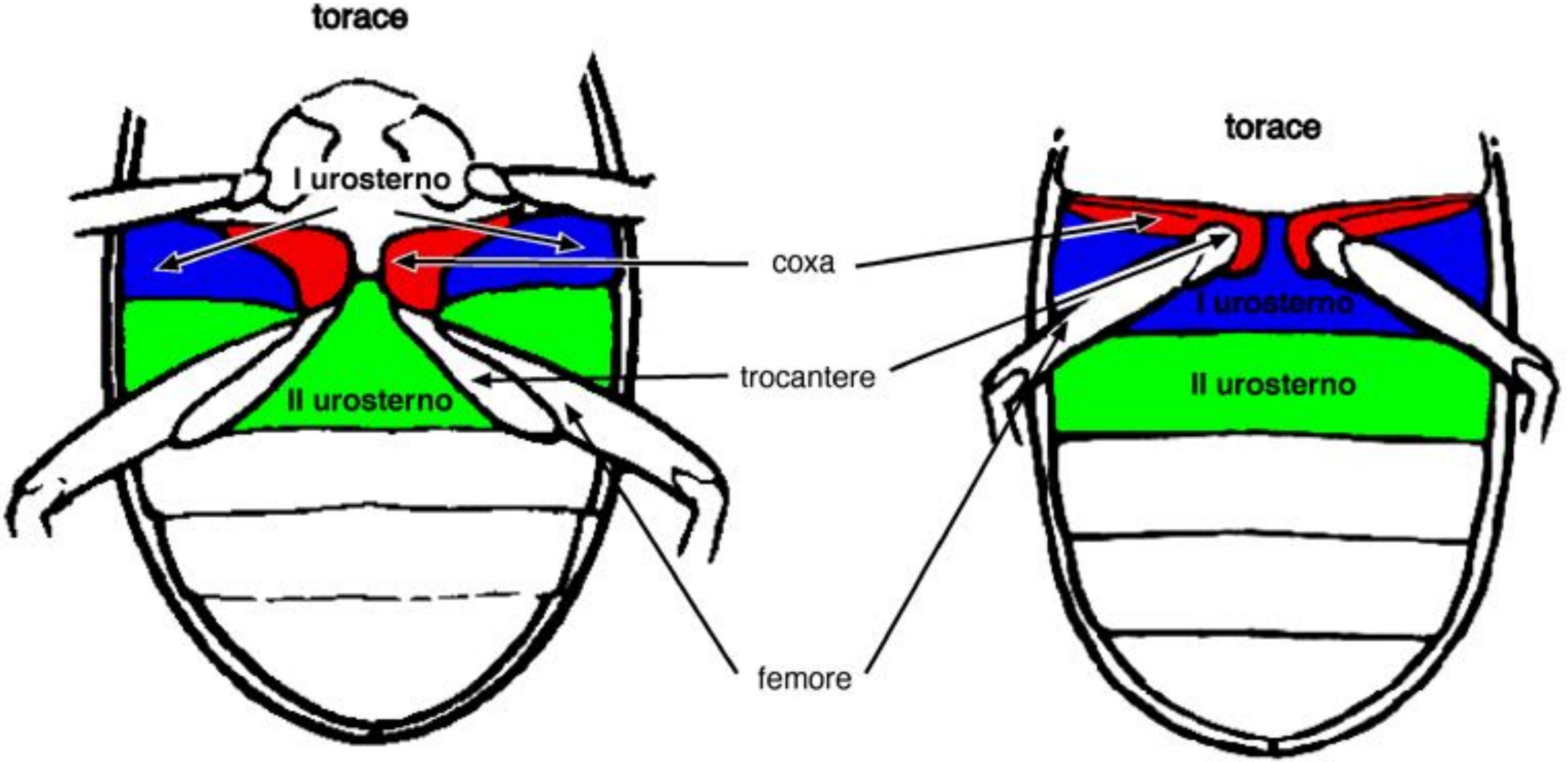



Propodeum
Urotergum$_1$
Urosternum$_2$
(Petiolum)
Metasoma
(Petiolum+ Gastrum)
Gastrum


Propodeum
Urotergum$_1$
Urite$_2$
(Petiolum)
Urite$_3$
(Postpetiolum)


Propodeum
Urotergum$_1$
Urite$_2$
(Petiolum)
Urite$_3$
(Postpetiolum)

Coleoptera

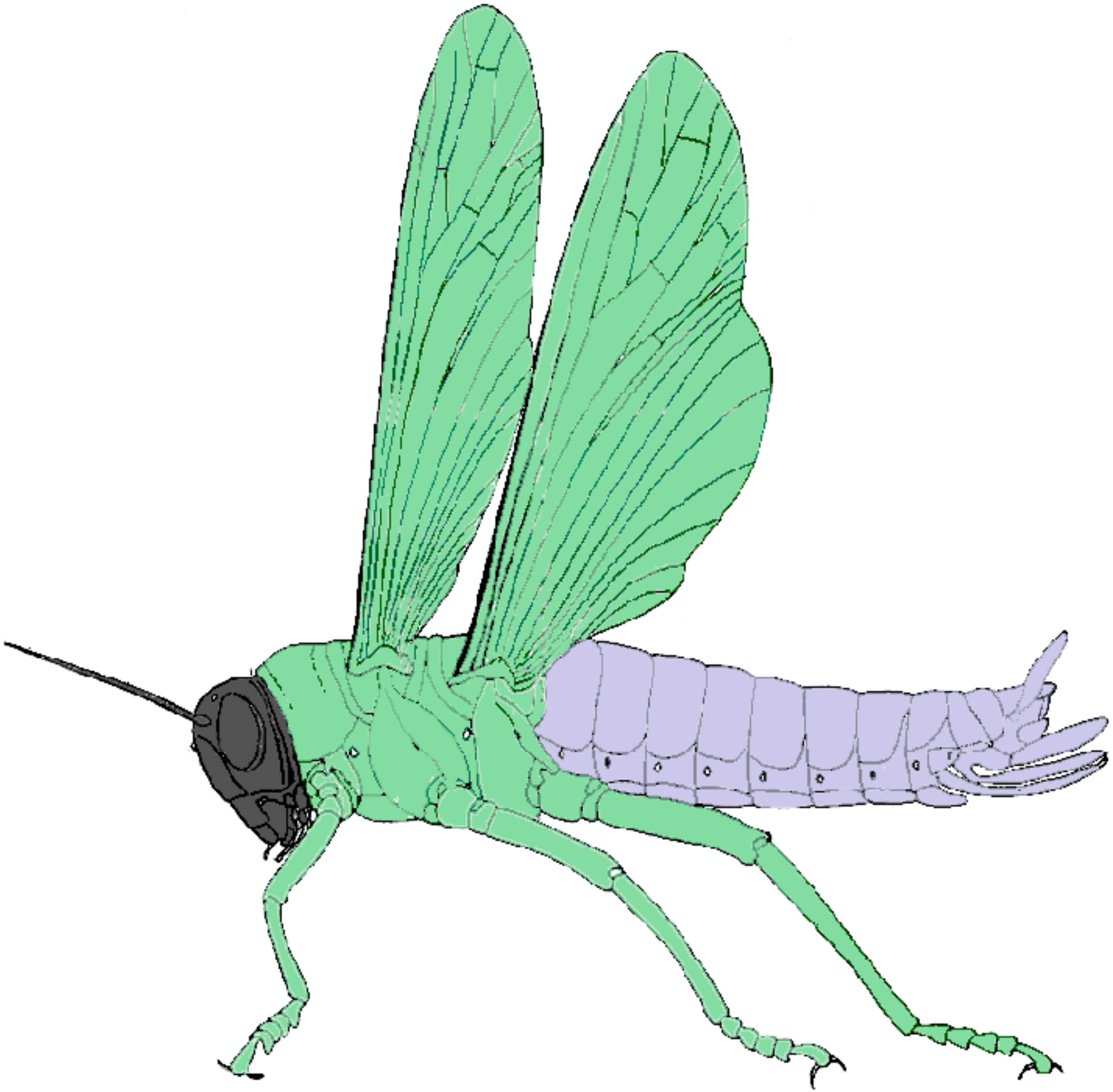


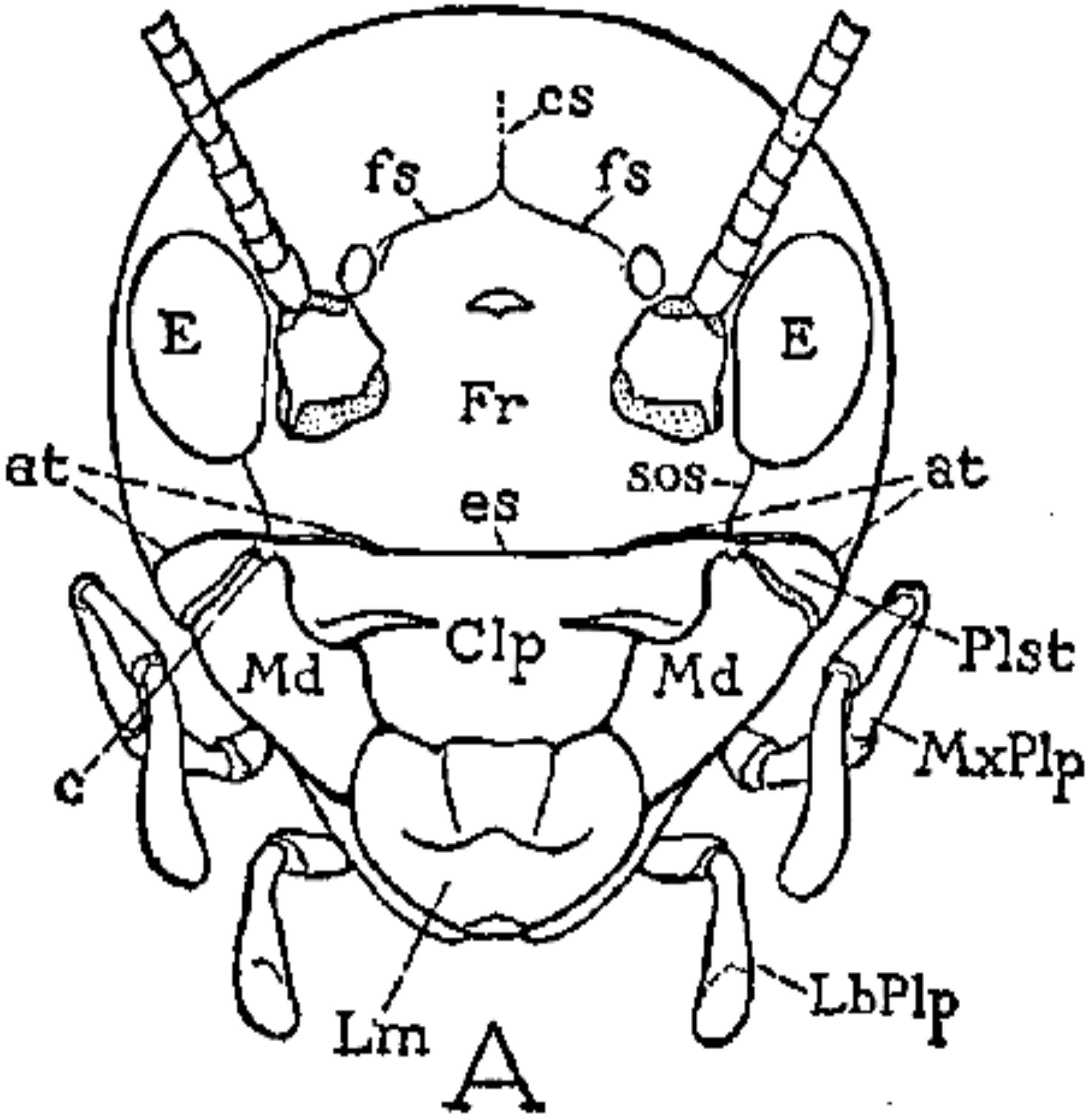
Adephaga

Polyphaga

06 Head

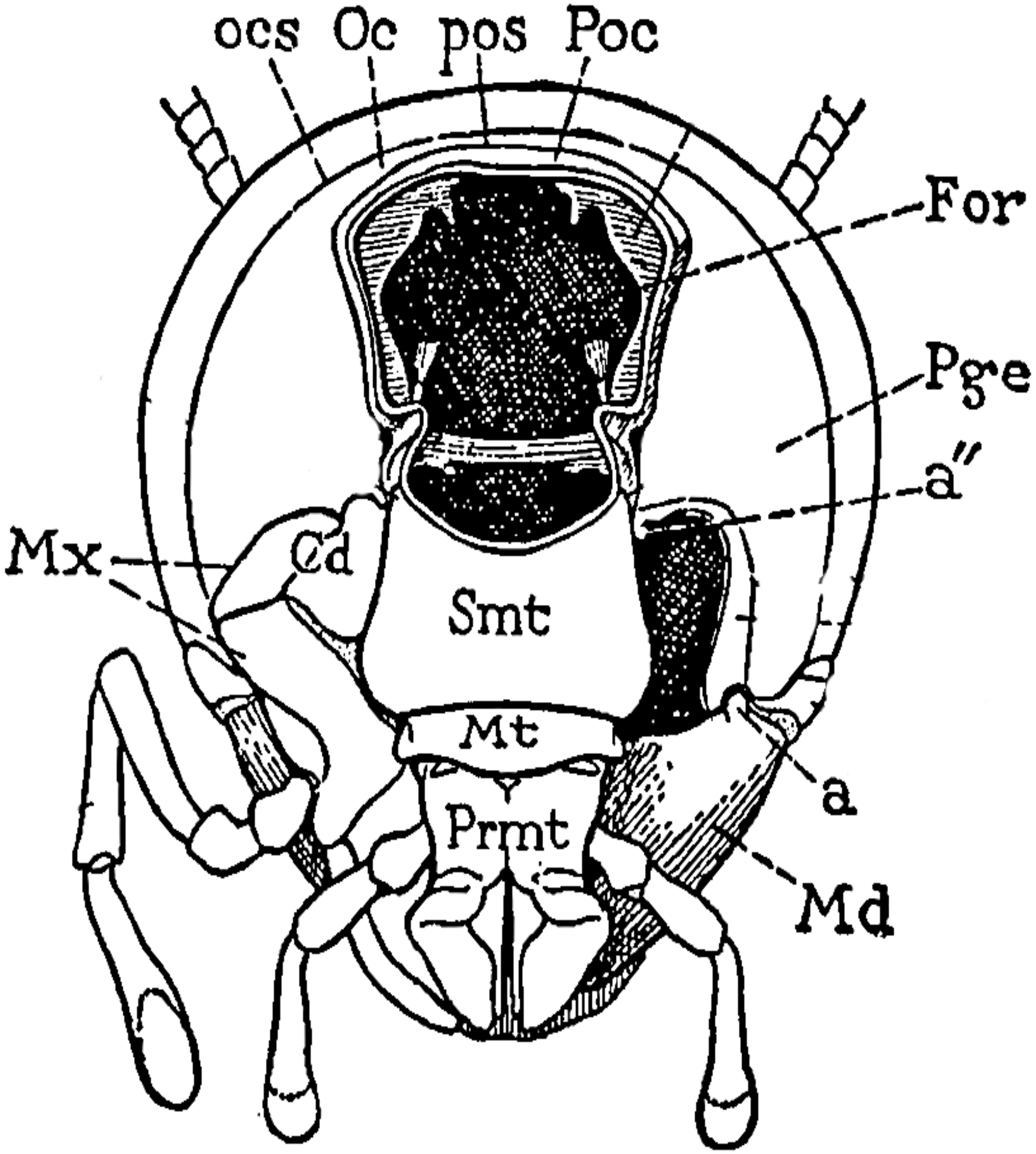
III



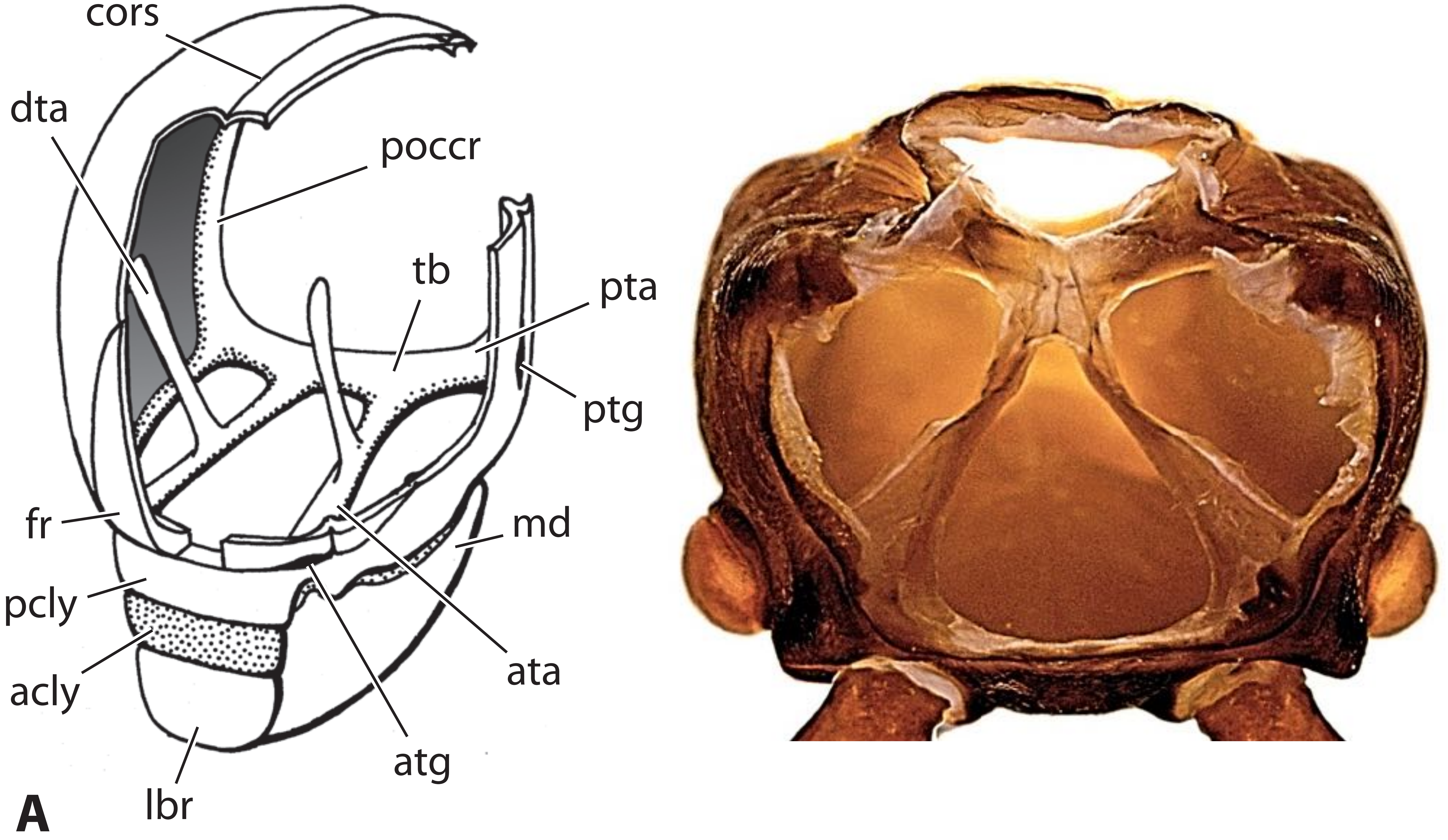


Mouthparts are cranial appendages specifically adapted for the acquisition and processing of food. Principal mouth parts include Mandible, Maxilla and Labium; Each appendage is subdivided into component parts of varing complexity and functional interaction among different groups of insects. The Labrum 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.

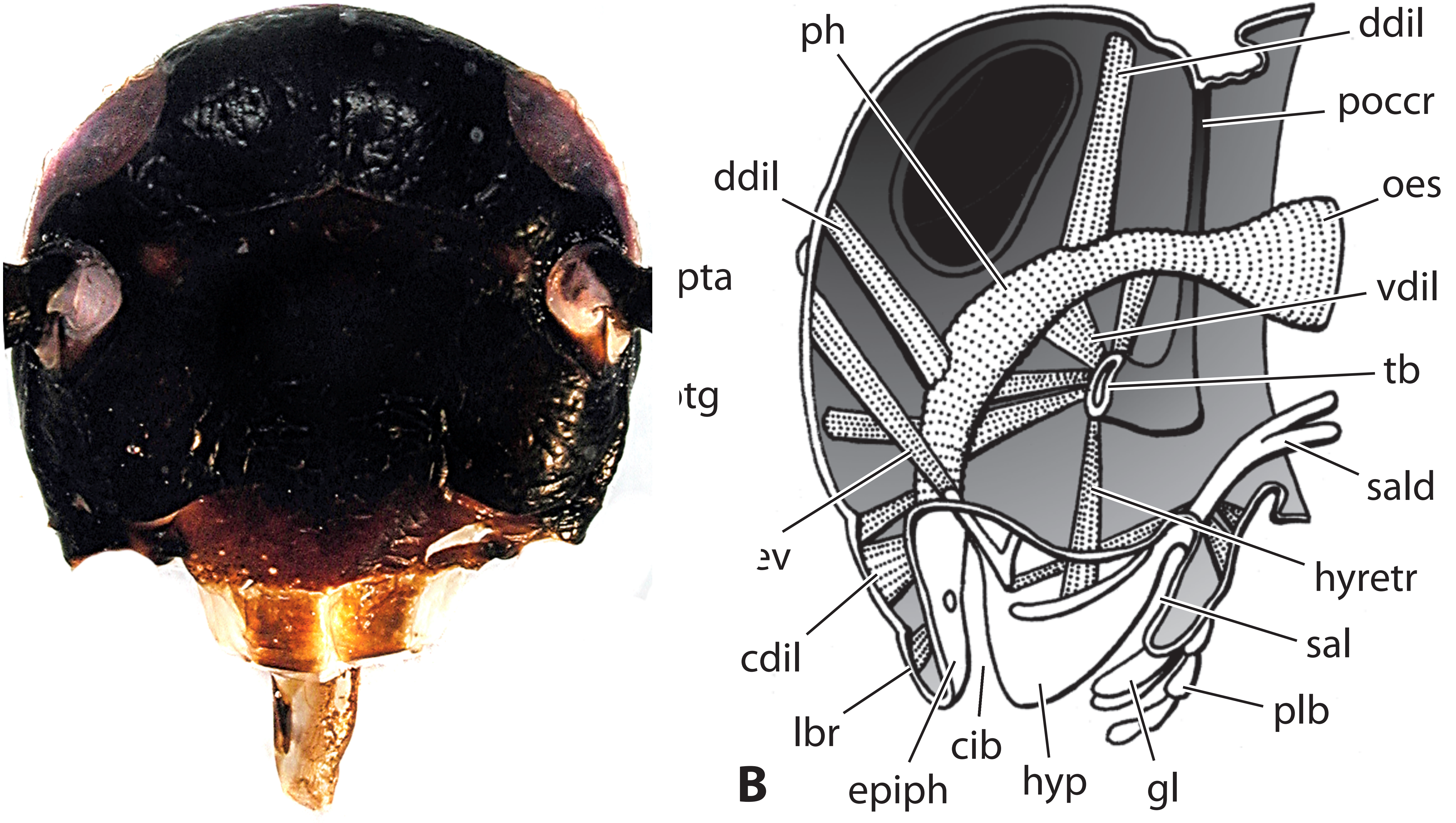
Labrum is the 'upper lip' of the insect head which covers the base of the Mandible and forms the roof of the mouth. Labrum traditionally has been viewed as a preoral feature that is not homologous with segmental appendages. Labrum articulates with the cranial capsule via membrane (Ciypeolabral 'Suture') 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.



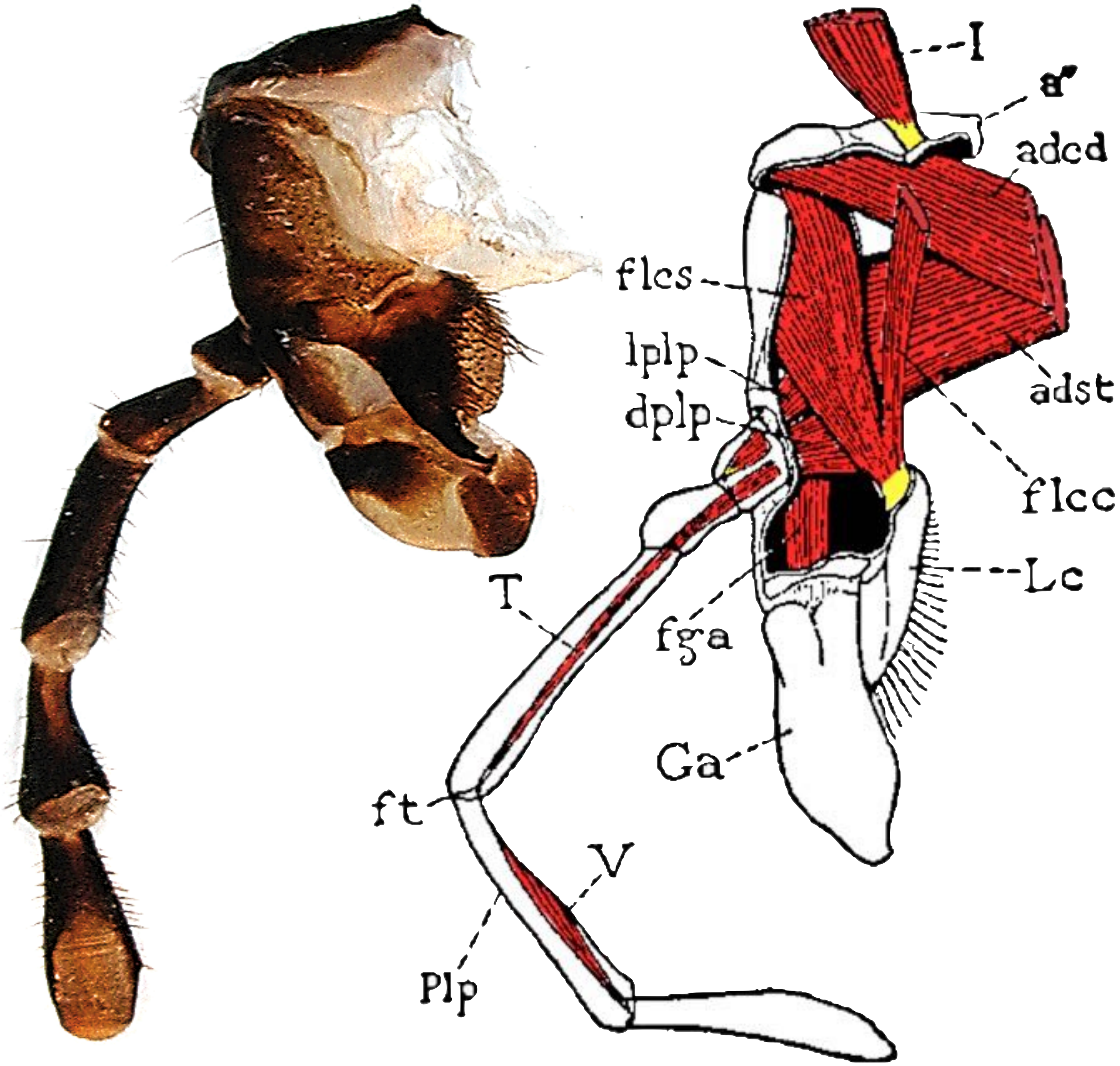
The Mandibles are the anterior-most pair of oral appendages on the insect head. Mandibles are lateral appendages, immediately behind Labrum and may represent segmental appendages of fourth segment of head groundplan. Early in their evolutionary history, insects perfected Mandible as an appendage for 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.



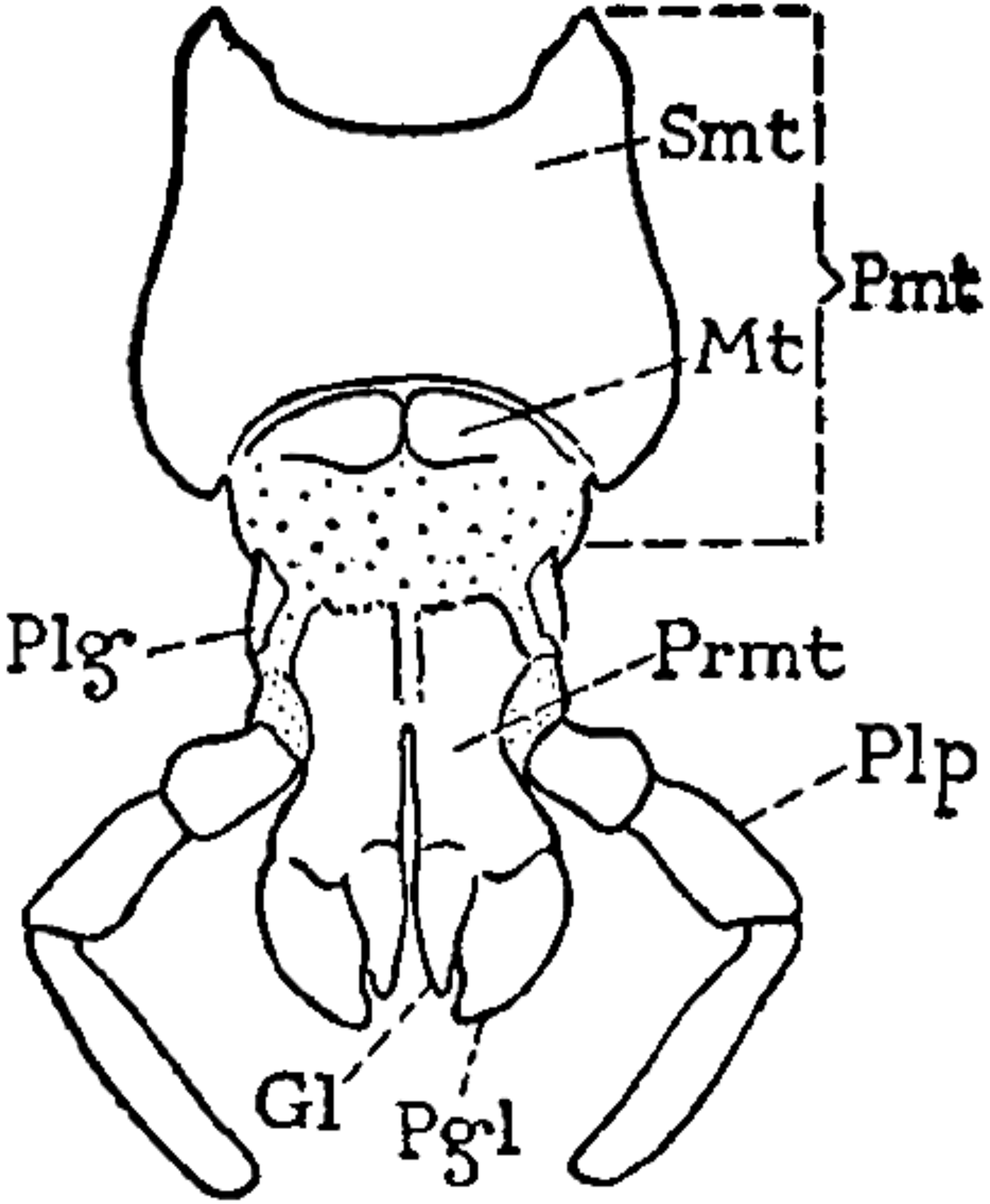
Generalized hexapod head, internal structures. **A: anterolateral view, frontal side of head capsule opened; B, sagittal section, brain and suboesophageal complex removed**. **ata:** anterior tentorial arm, **acly:** anteclypeus, **atg:** anterior tentorial groove, **cib:** cibarium, **cdil:** cibarial 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).



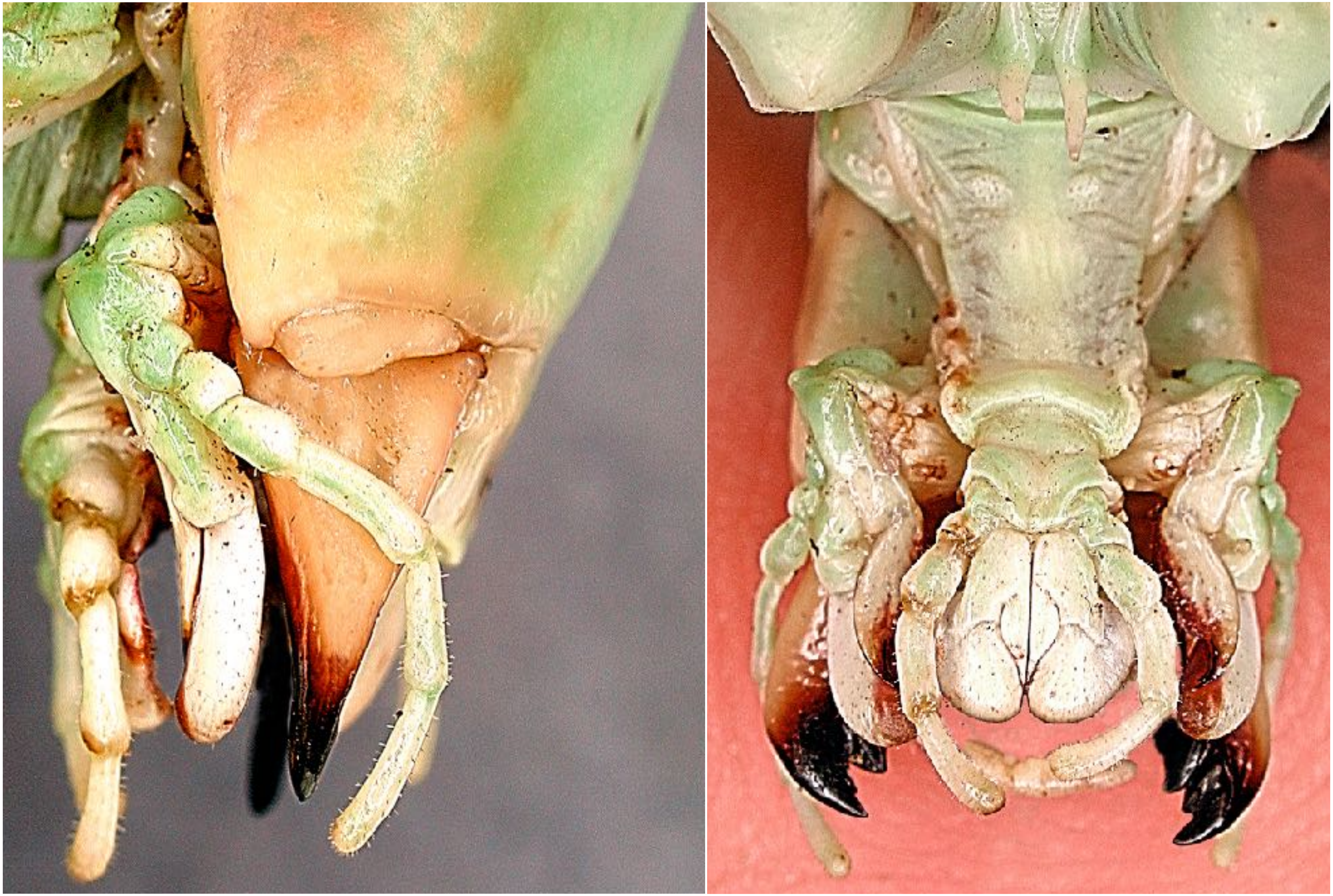
Generalized hexapod head, internal structures. **A: anterolateral view, frontal side of head capsule opened; B, sagittal section, brain and suboesophageal complex removed**. **ata:** anterior tentorial arm, **acly:** anteclypeus, **atg:** anterior tentorial groove, **cib:** cibarium, **cdil:** cibarial 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).



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.



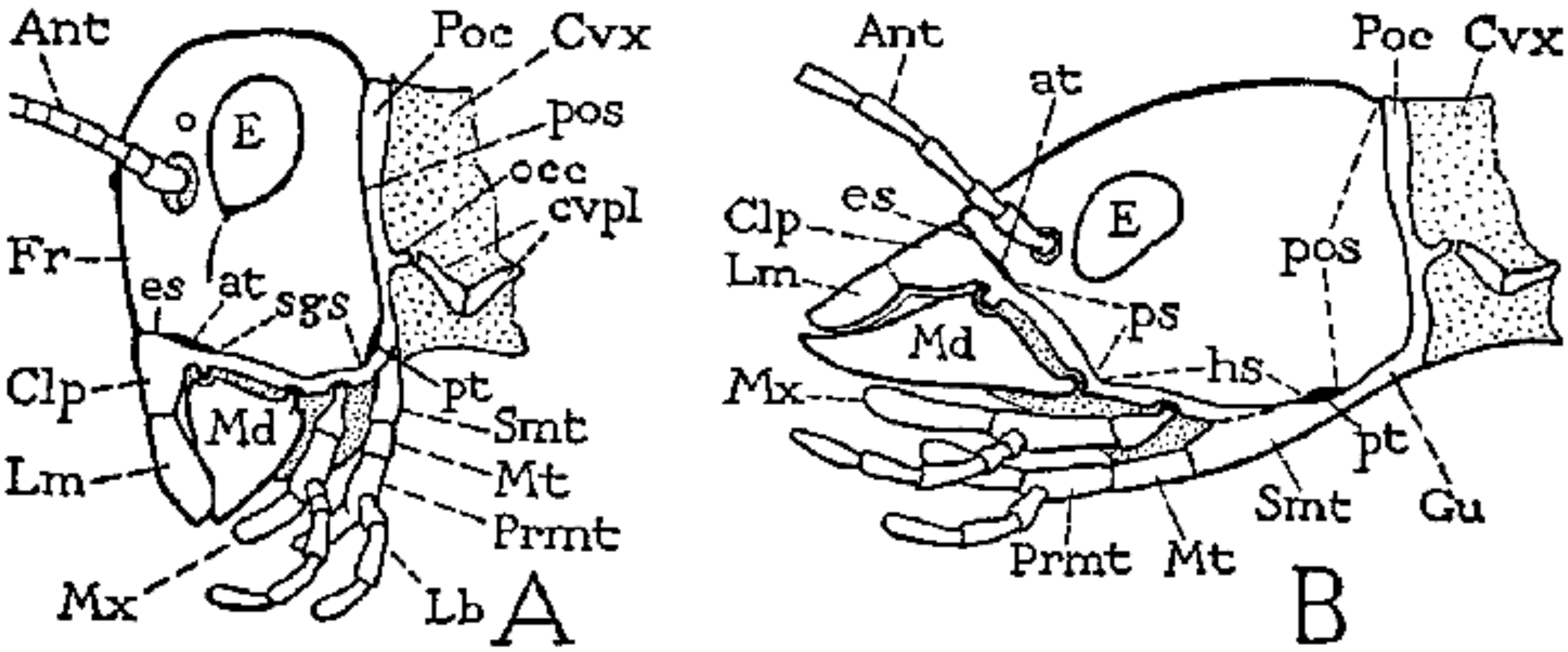
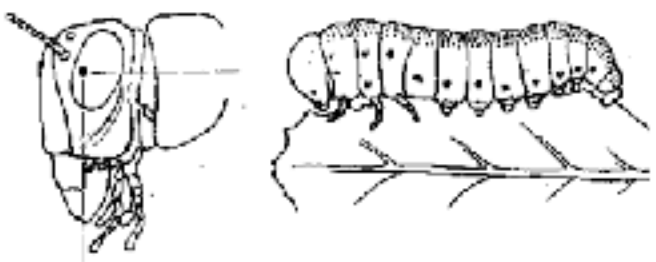
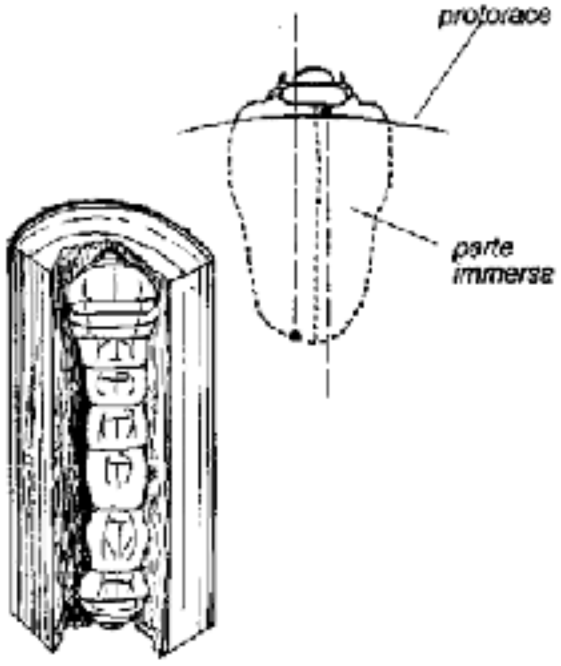


FIG. 66.—Diagrams illustrating the hypognathous (A) and prognathous (B) types of head structure.

Figure 12.6 (Snodgrass, 1935)

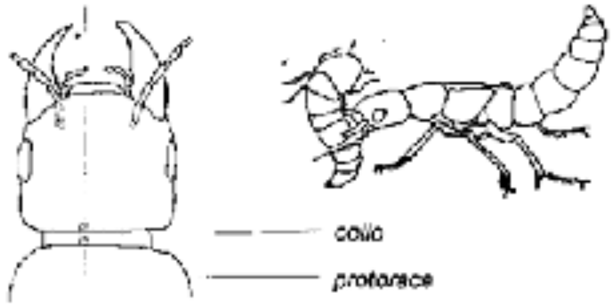

▽ CAPO PROGNATO


▽ CAPO IPOGNATO


▽ CAPO IMMERSO NEL TORACE


▽ CAPO EPIGNATO


▽ CAPO METAGNATO

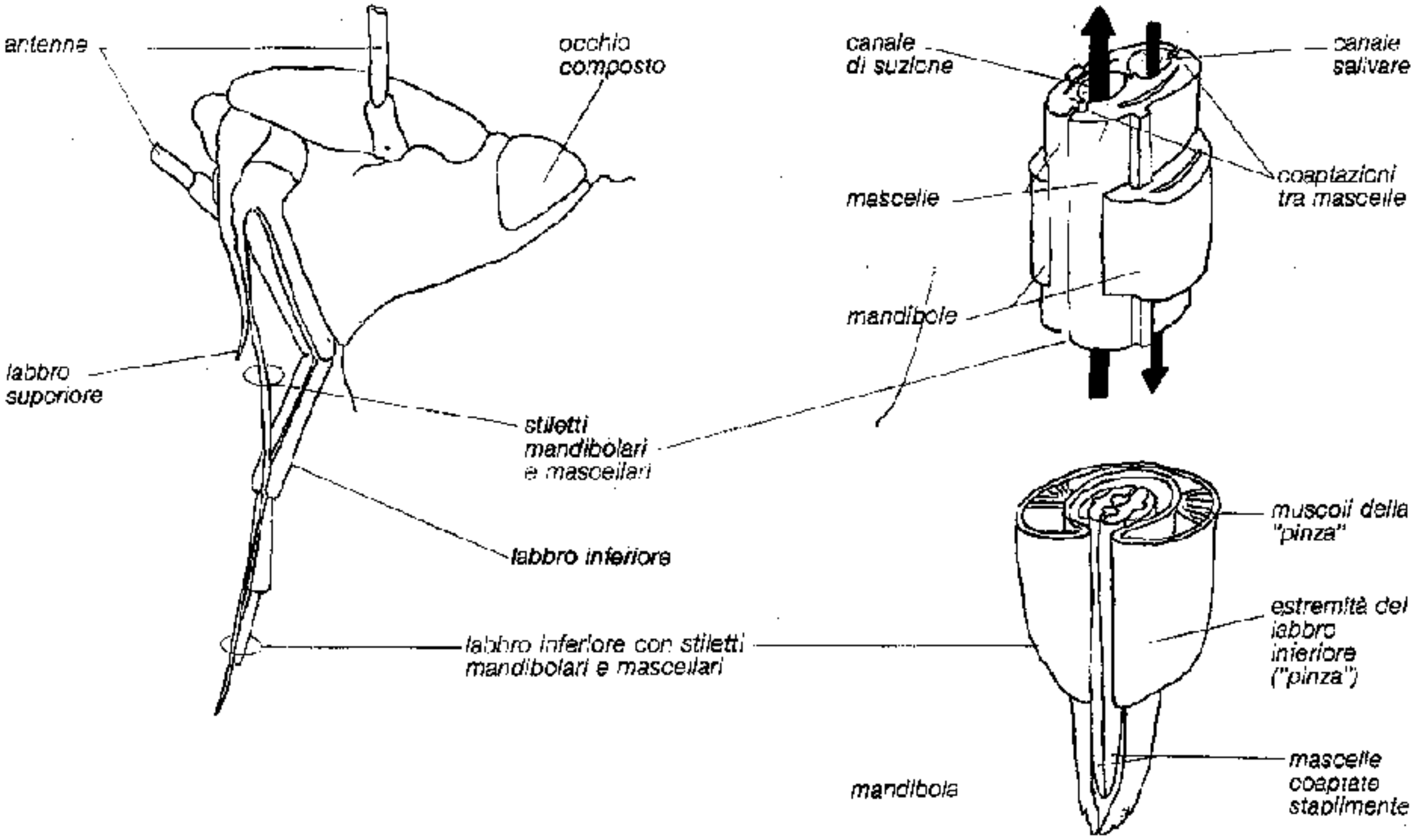

▽ CAPO LIBERO DAL TORACE

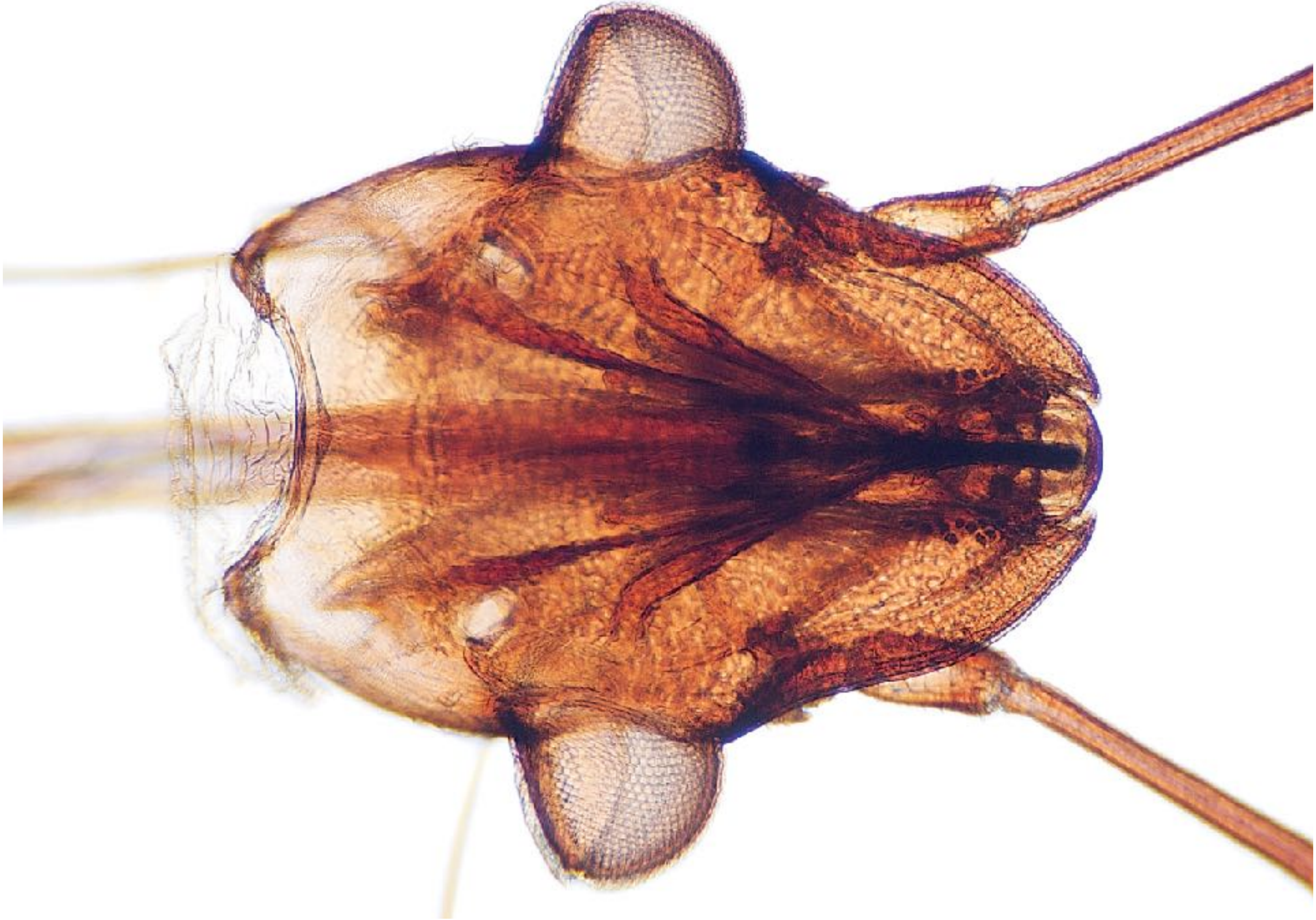
Bugs posses piercing, sucking mouthparts in the form of a long beak or rostrum. In heteropteran bugs, the rostrum arises from the front part of the head and can be hinged forward to point down or forwards, in front of the head. This allows much greater flexibility and a larger choice of food. In the Auchenorrhyncha and Sternorrhyncha, the rostrum, which arises from the posterior part of the head, or seemingly from between the front legs, is permanently directed backwards. With the exception of non-feeding male scale insects and the sexual forms of a few aphids, whose mouthparts are vestigial or lacking, the bug rostrum is similar throughout the order. The outer covering of the rostrum, the protective labium (with 1-4 segments), is grooved for most of its length and surrounds the slender, toughened feeding stylets.

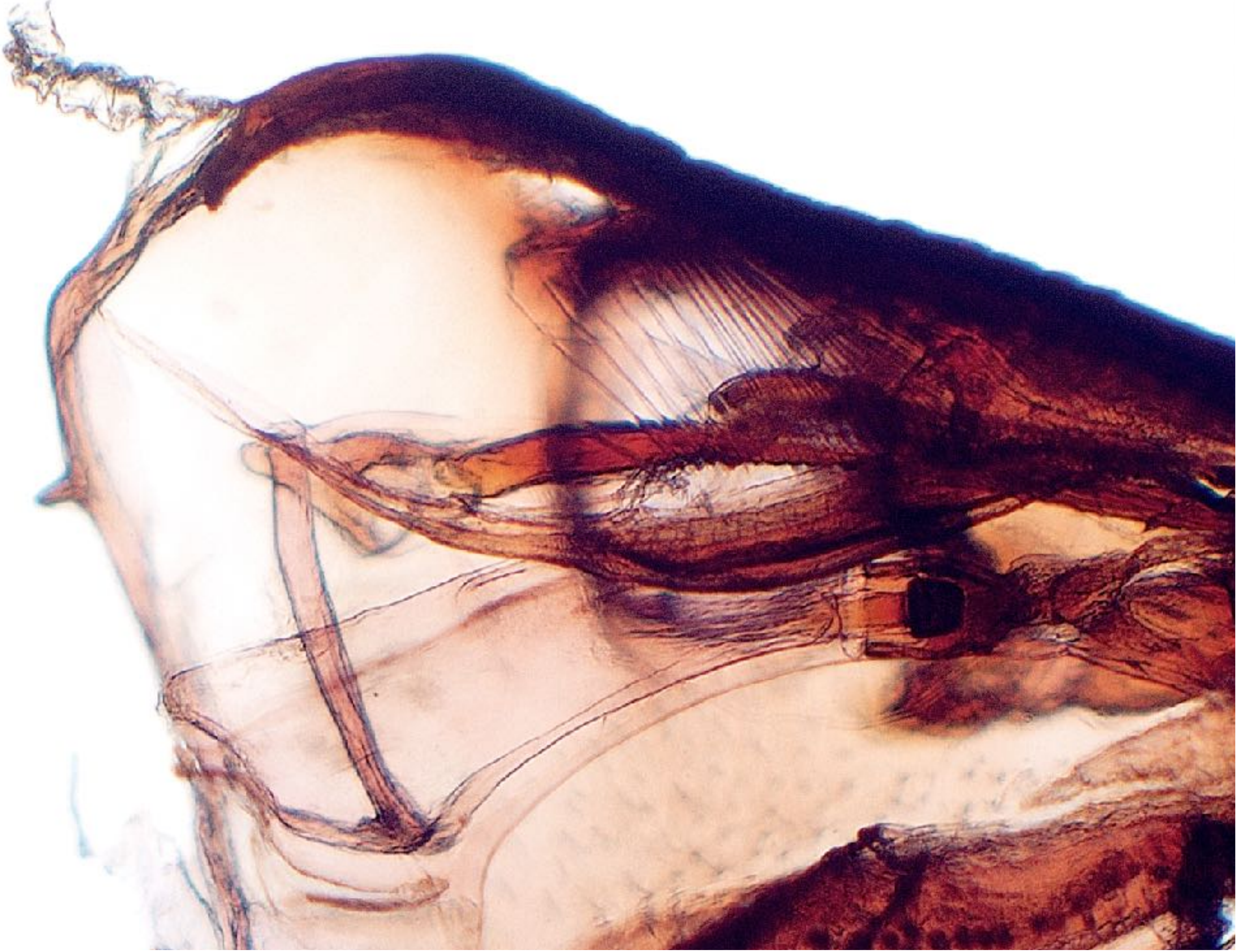
The stylet bundle is made up of a pair of mandibular and a pair of maxillary stylets. The mandibular stylets enclose the maxillary stylets and can be closely connected by means of longitudinal ridges and grooves on their surfaces fitting together like the seal of a zip-lock plastic bag. The two pairs of stylets can slide freely on each other but are difficult to pull apart. The mandibular stylets have saw-like serrations, teeth, and, sometimes, barbs to penetrate plant and animal tissues. Predacious bugs penetrate the cuticle of their prey through a weak spot and use their long stylets and saliva to macerate the internal tissues before they are sucked out. The inner surfaces of the maxillary stylets are folded into longitudinal ridges and grooves, which firmly unite the two and provide two very fine, parallel canals running along their entire length. The ventral canal is the salivary canal, which carries digestive enzymes from the salivary glands in the anterior part of the thorax, the other is the food canal.

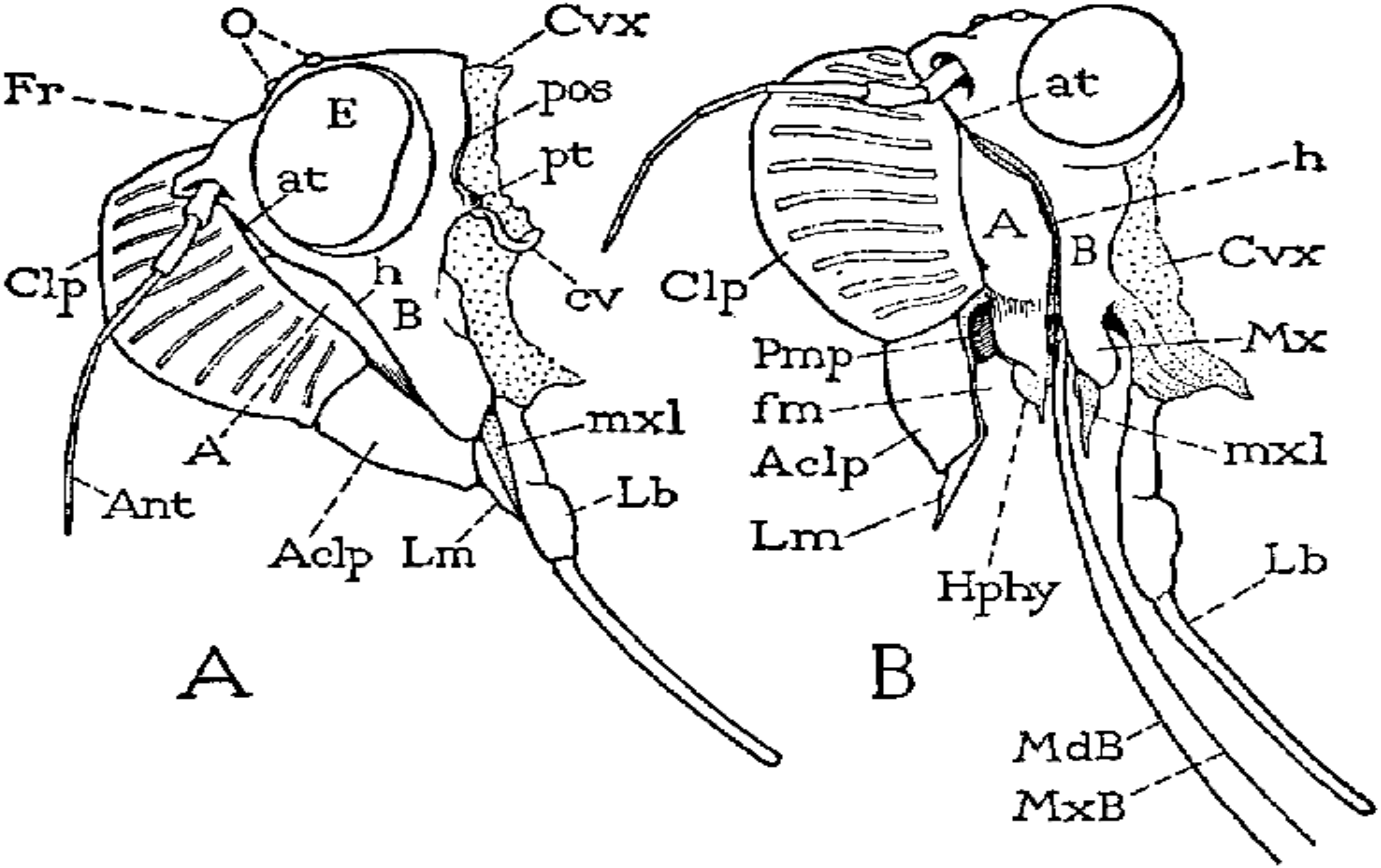
▽ CAPO CON PARTI BOCCALI

▽ SPACCATO DELLE PARTI BOCCALI A DIVERSO INGRANDIMENTO E LIVELLO








O
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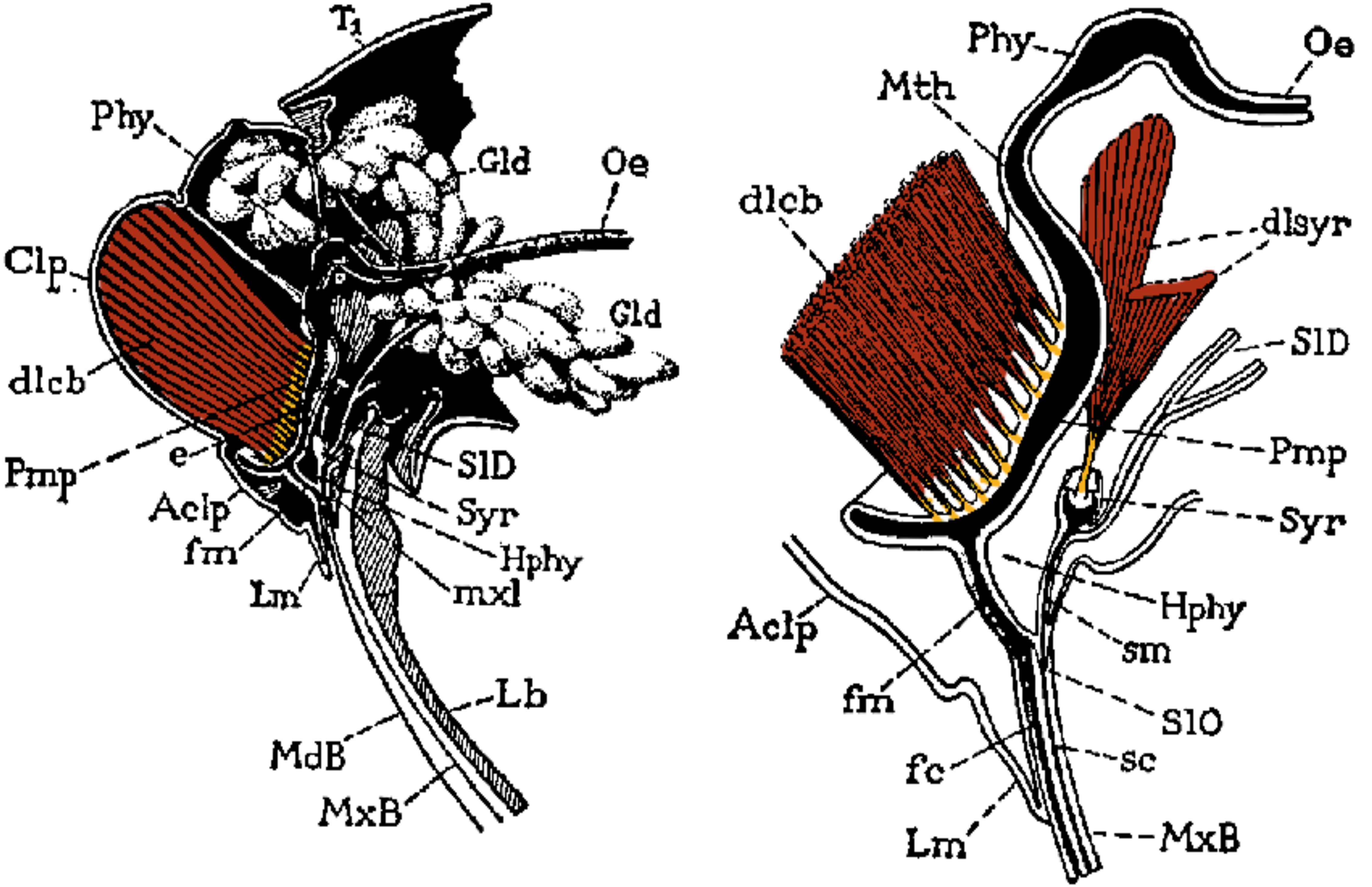
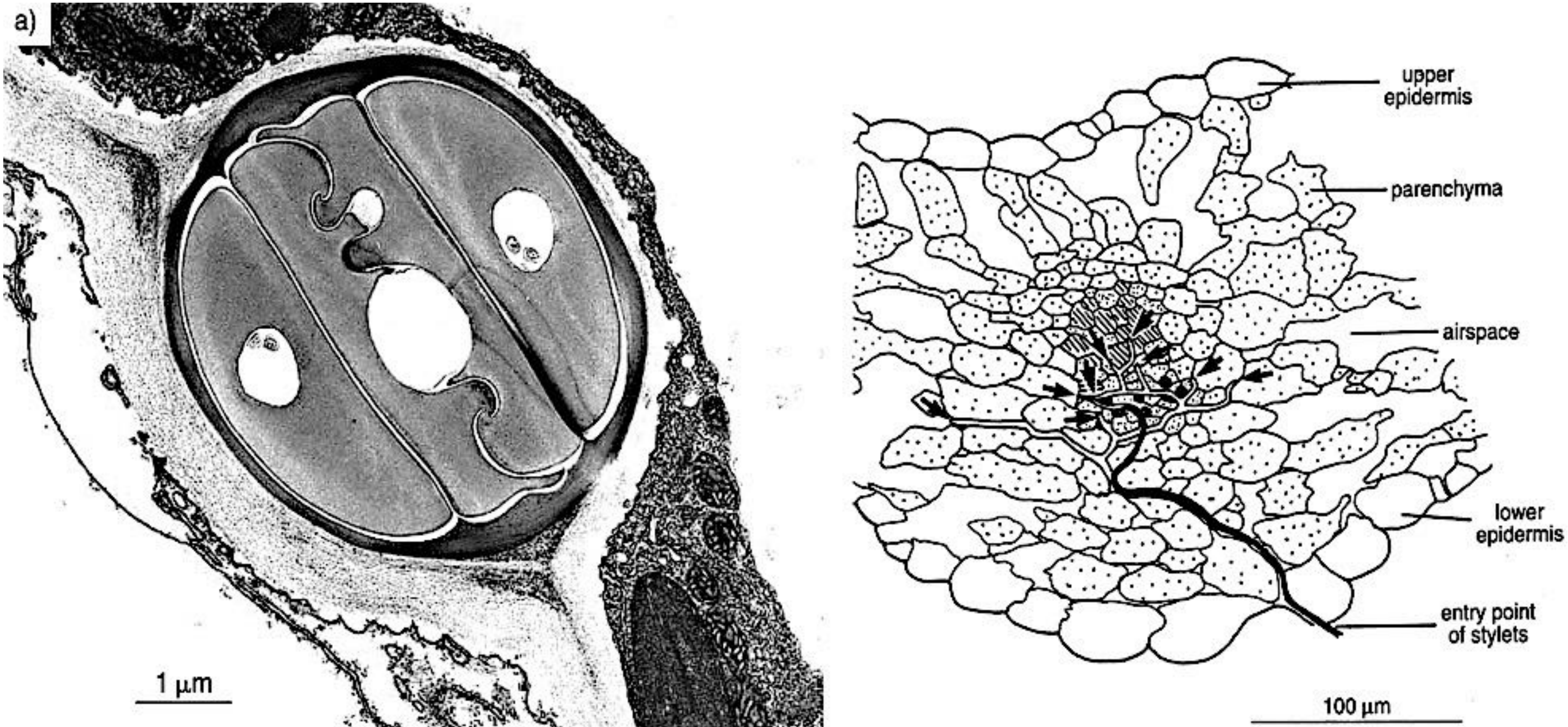
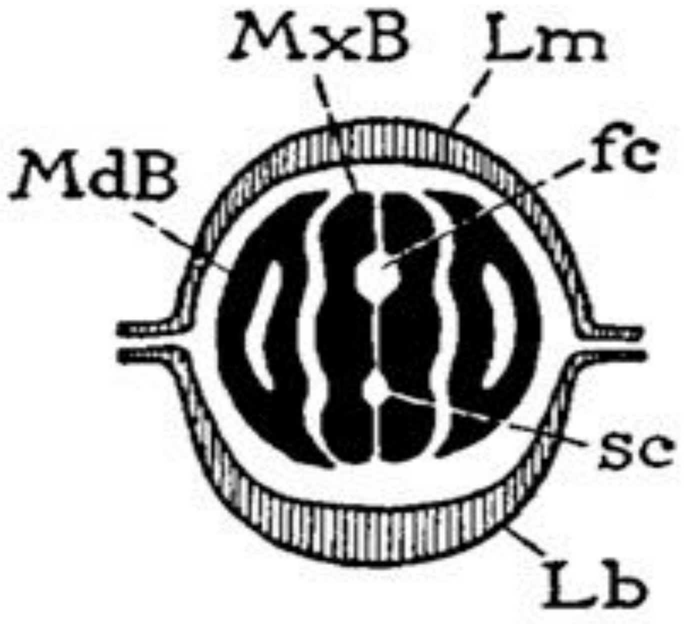
MdB
MxB



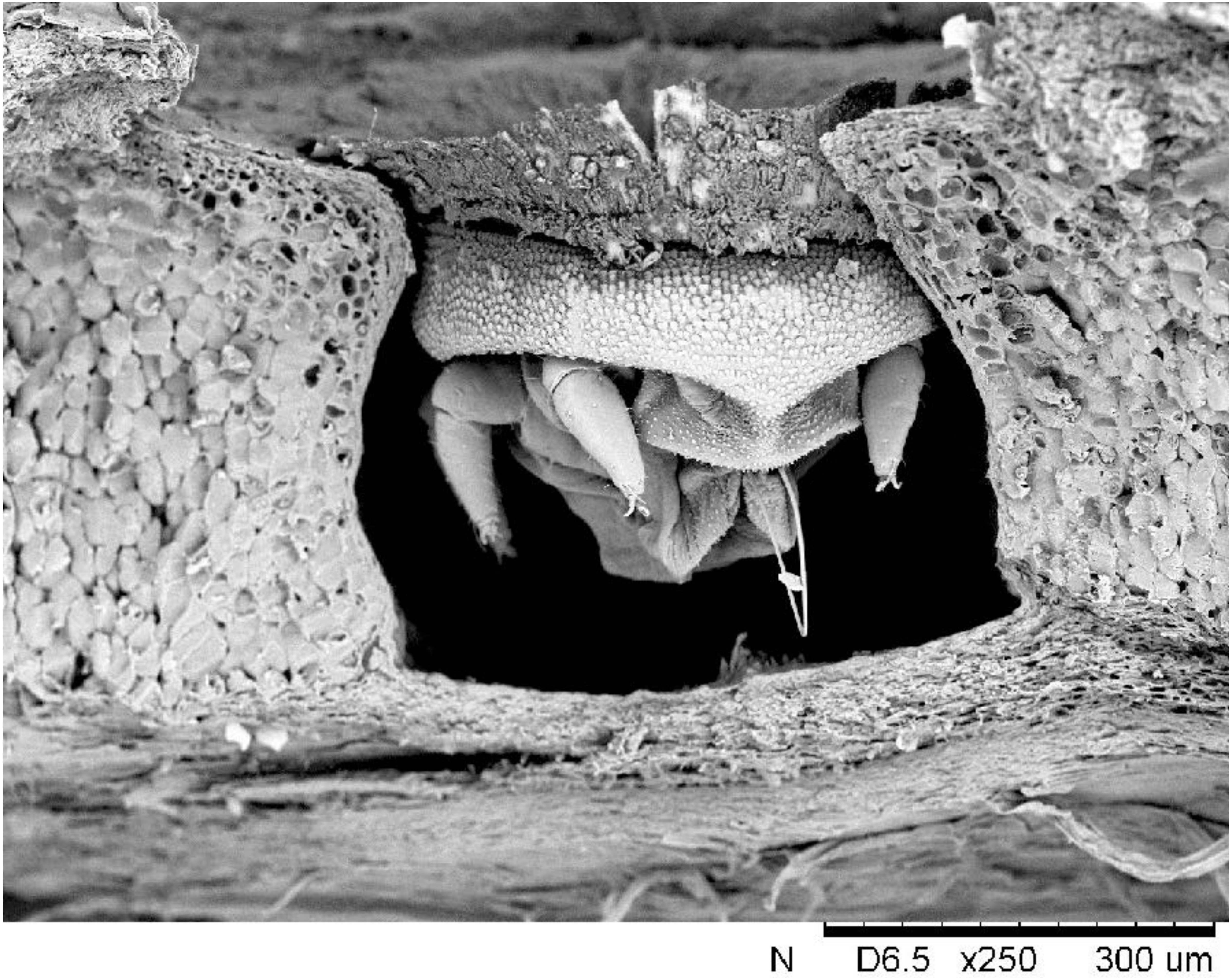
Bug saliva is a complex mixture of a number of different enzymes, toxins, lubricants, and other substances. Herbivorous bugs need enzymes, such as pectinases, to break down plant cell walls, while the saliva of carnivorous heteropteran bugs may contain powerful enzymes causing the instantaneous paralysis and death of prey. In plant sap feeding bugs, such as aphids, the site of the phloem vessels in the plant may be some distance from the surface, and the stylet bundle has to wander between the tough-walled cells of the plant's epidermis before reaching a feeding site. The stylets are protected by the formation of a proteinaceous sheath formed by the hardening of special salivary gland secretions, which are produced throughout the course of penetration. In the head, powerful muscles operating the sucking or cibarial pump draws the liquid or pre-dissolved food up the stylet bundle and passes it into the pharynx. Bugs feeding on the sap in phloem vessels do not require very strong cibarial pumps as their diet is under slight positive pressure.

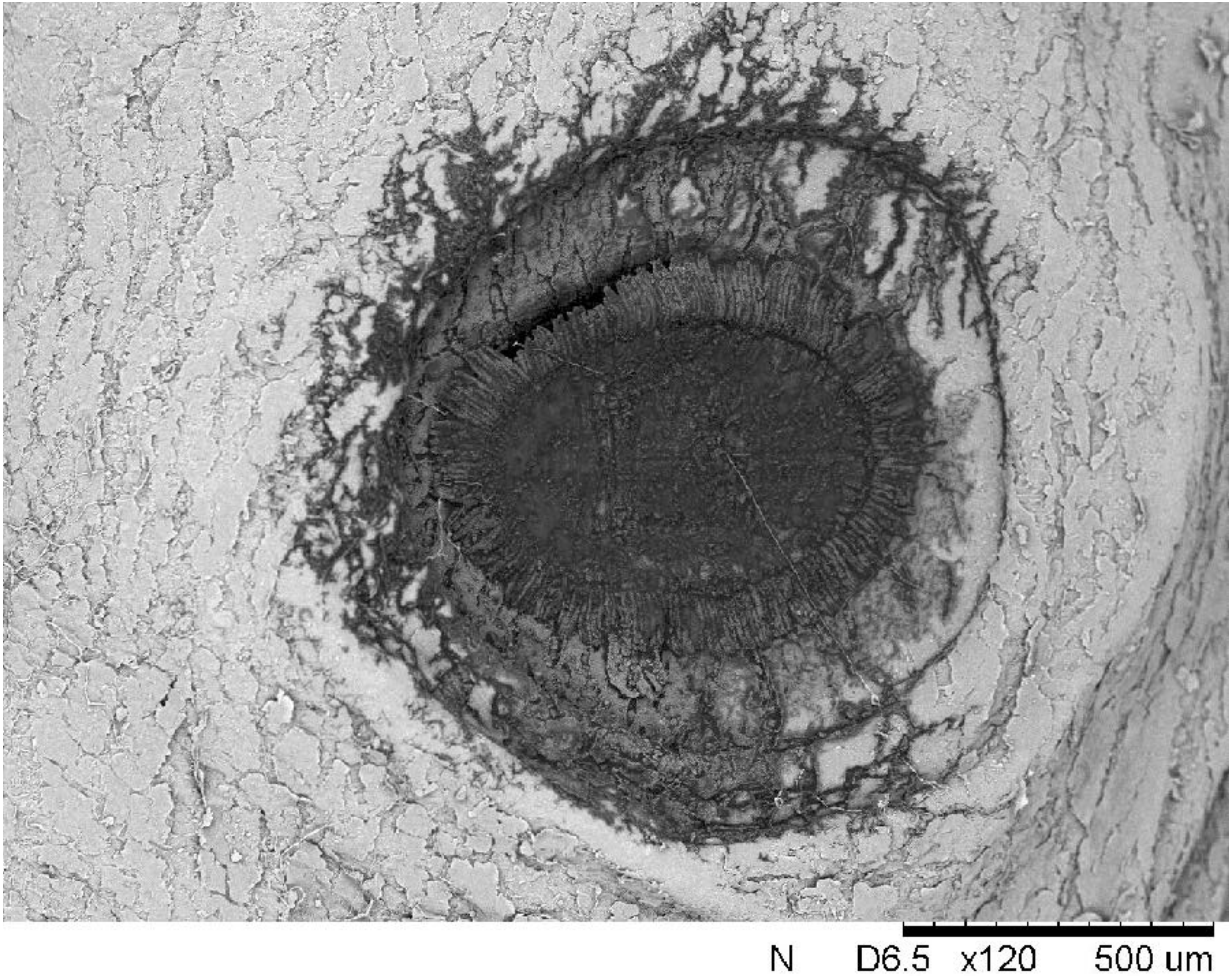


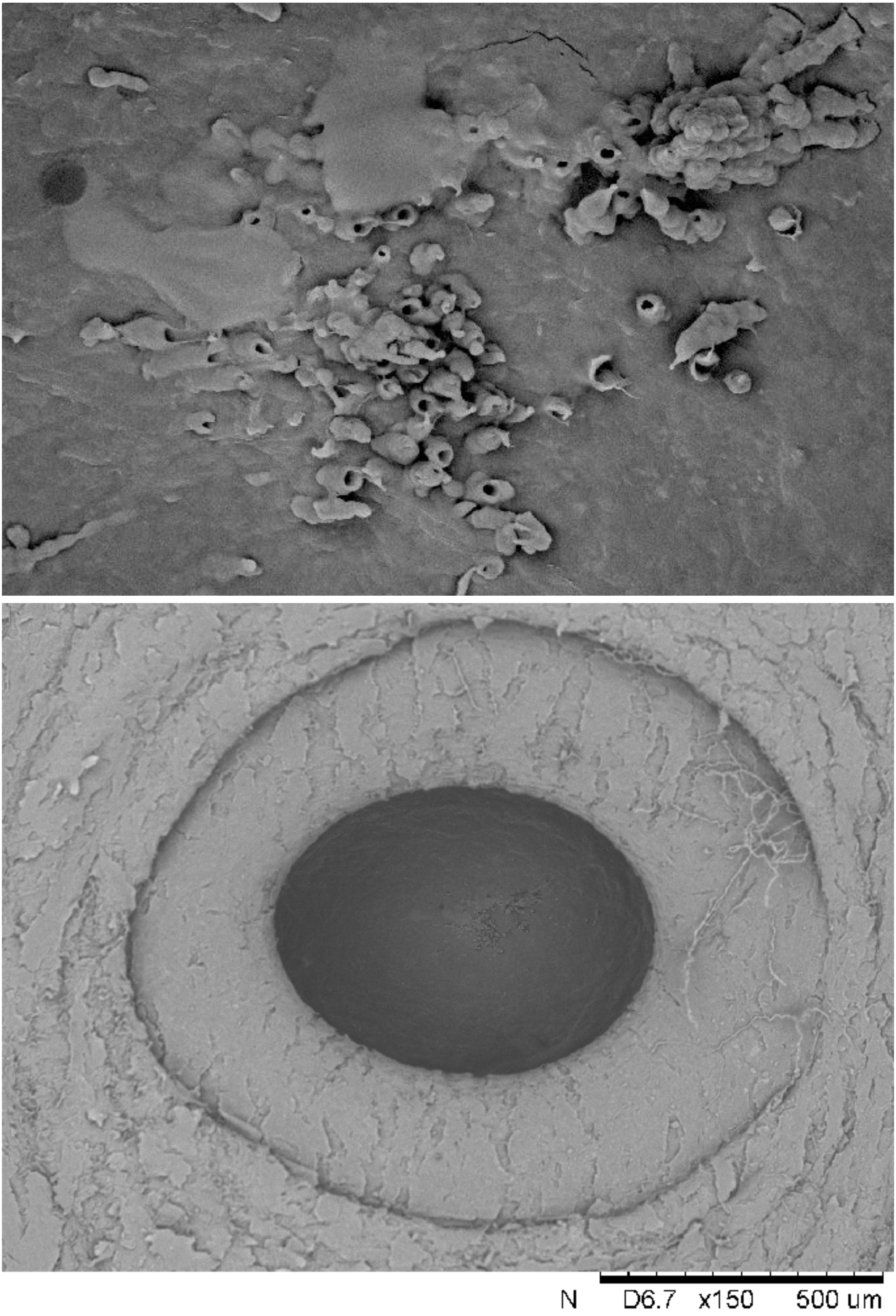
Feeding by an aphid (after Tjallingii & Esch, 1993). (a) Transverse section through the stylets and salivary sheath in a leaf. The maxillary stylets interlock to form the food canal (center) and the salivary canal (above). Each mandibular stylet has a narrow lumen, an extension of the hemocoel, containing mechanoreceptor neurons. The dark ring surrounding the stylets is the salivary sheath. Outside it, the pale fibrous material is plant cell wall. Notice that the stylets are contained within the cell wall; they do not enter the surrounding cytoplasm. (b) Pathways taken by the stylets of an aphid at the start of feeding. Abortive pathways are shown white with the ends of the paths indicated by arrows. The final pathway, reaching the phloem, is shown black. Phloem sieve tubes, black; xylem, cross-hatched; parenchyma, stippled.

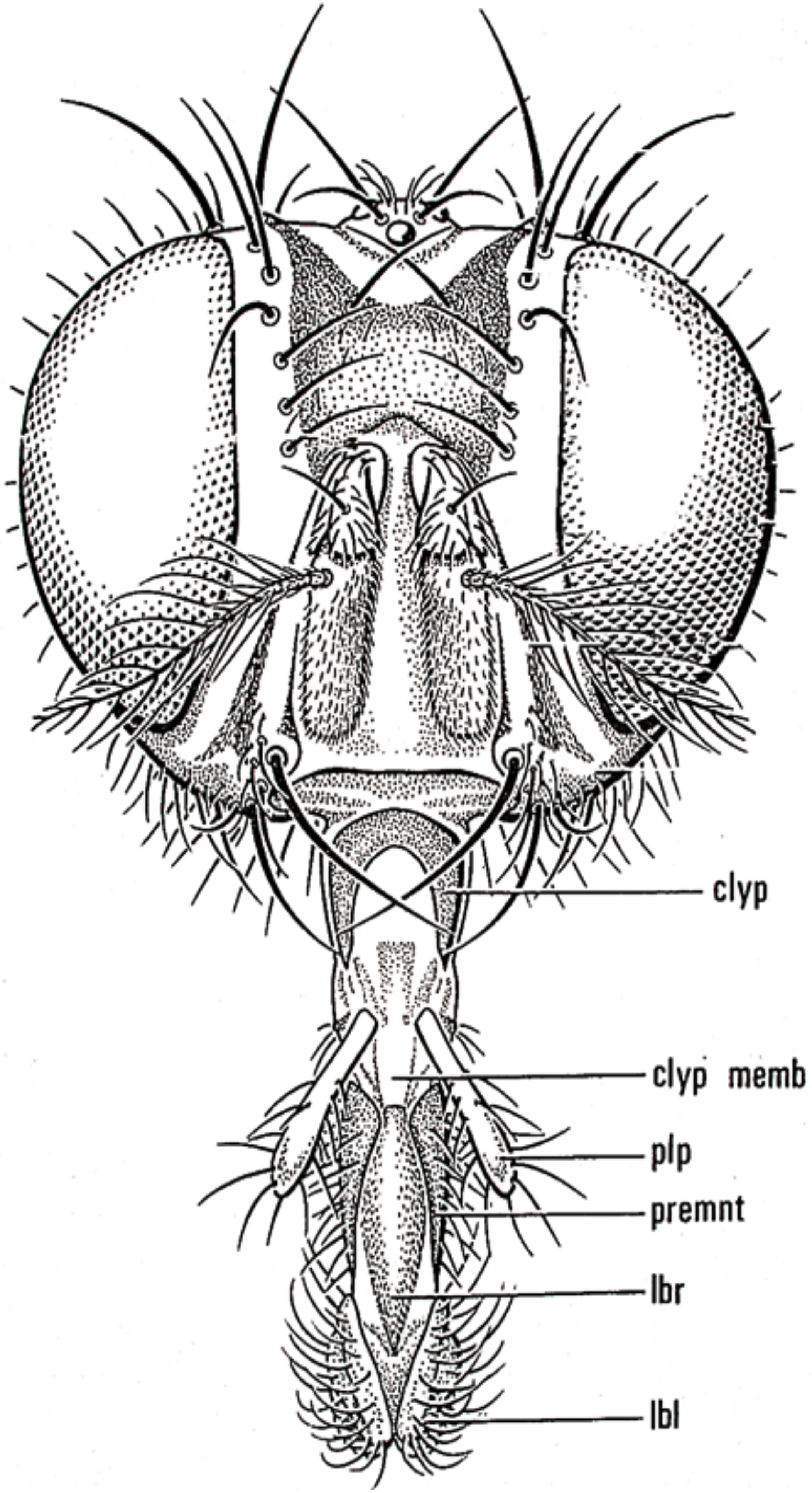


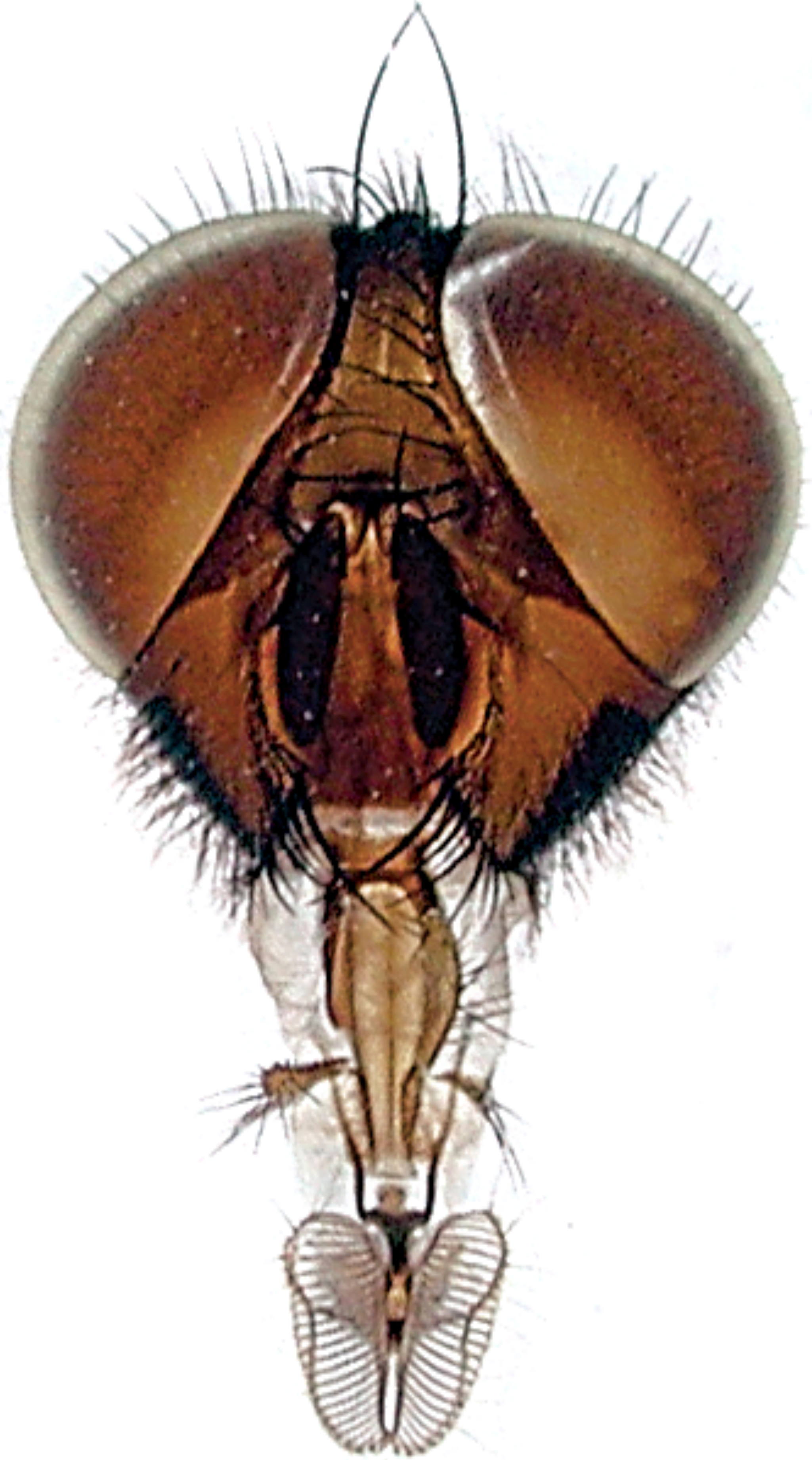
1 mm
N D6.3 x60

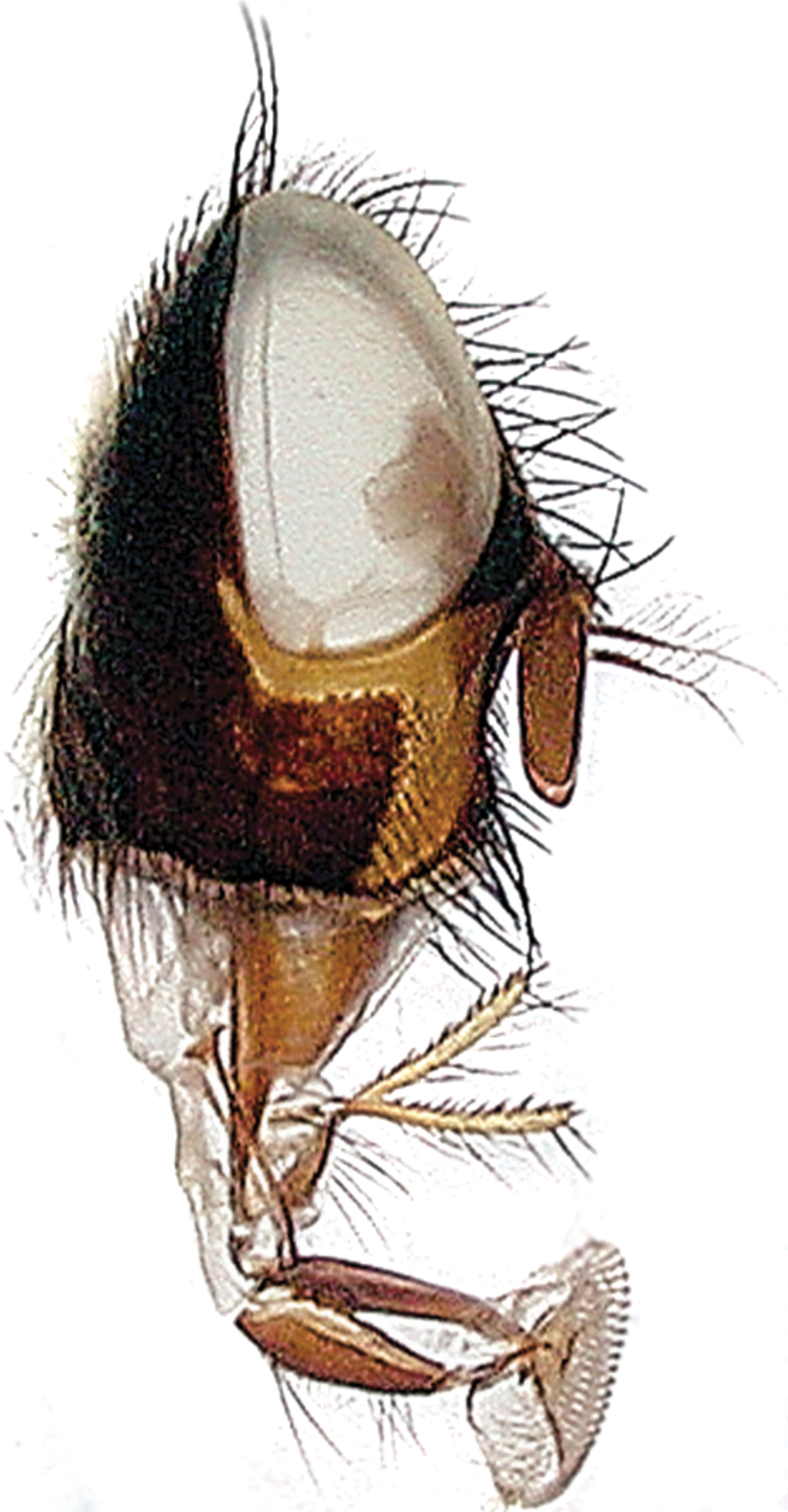

N
D6.5
x250
300 um

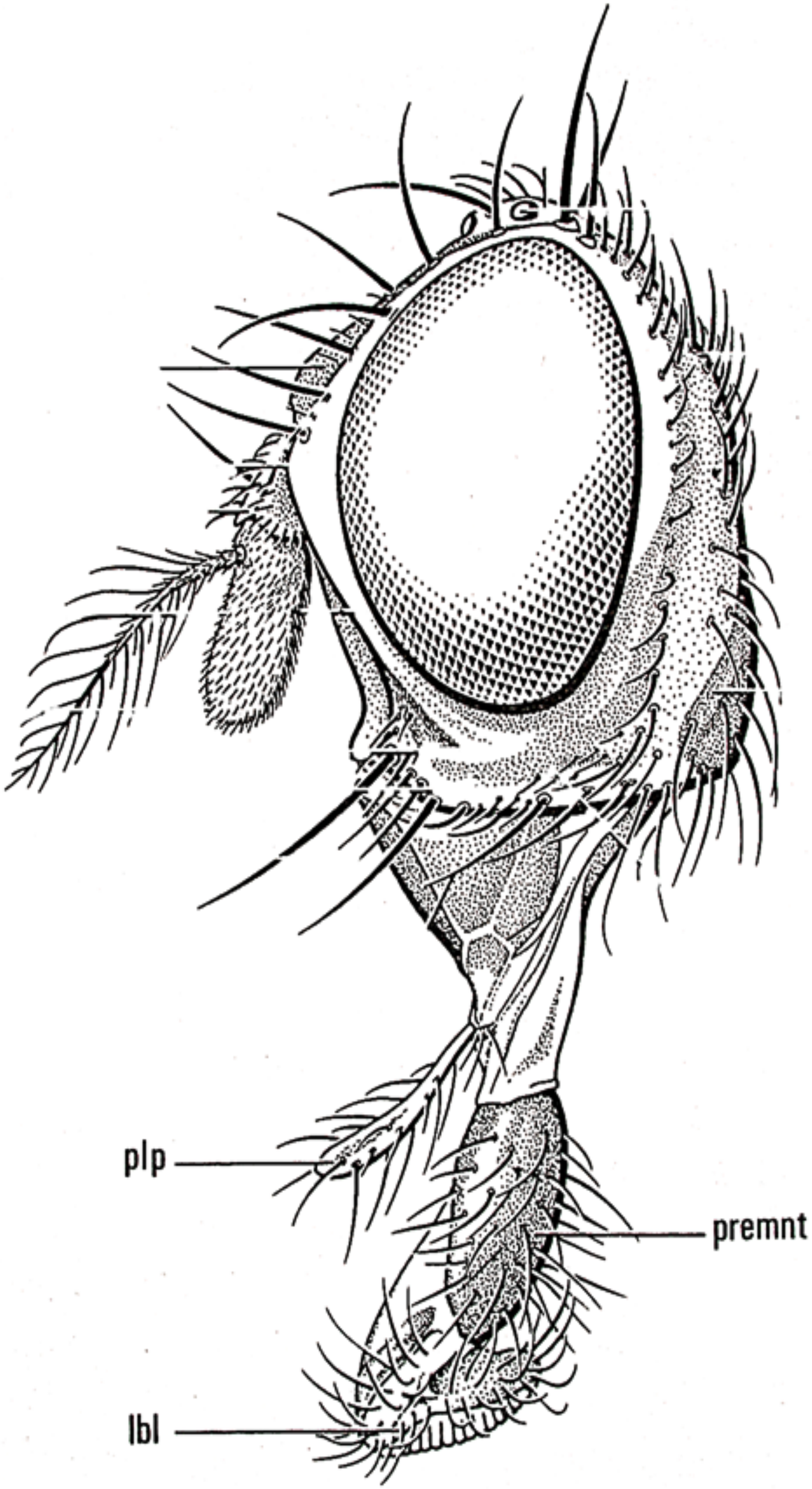

N
D6.5
x120
500 um


N D6.7 x150 500 um

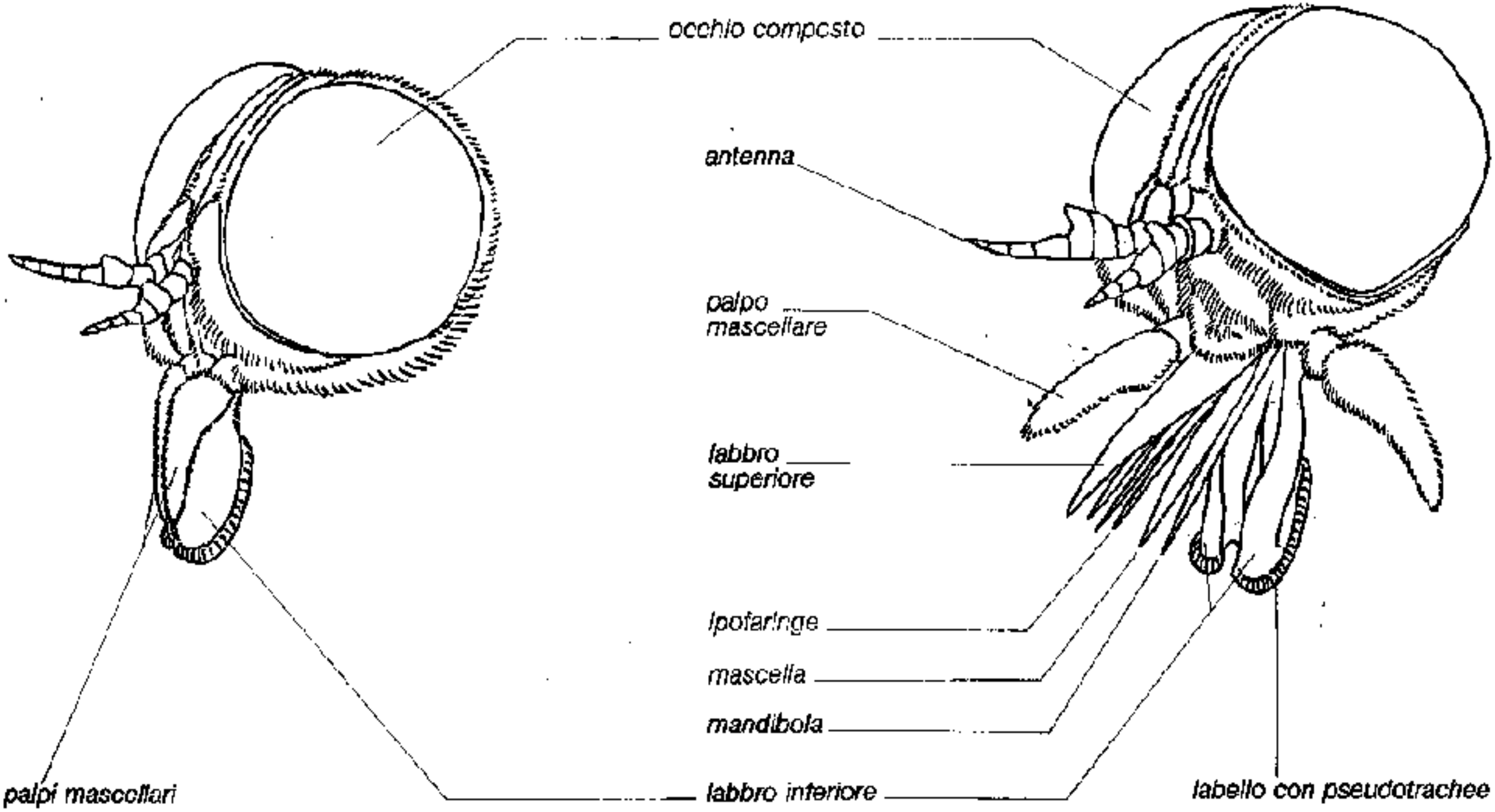

clyp
clyp memb
plp
premnt
lbr
lbl



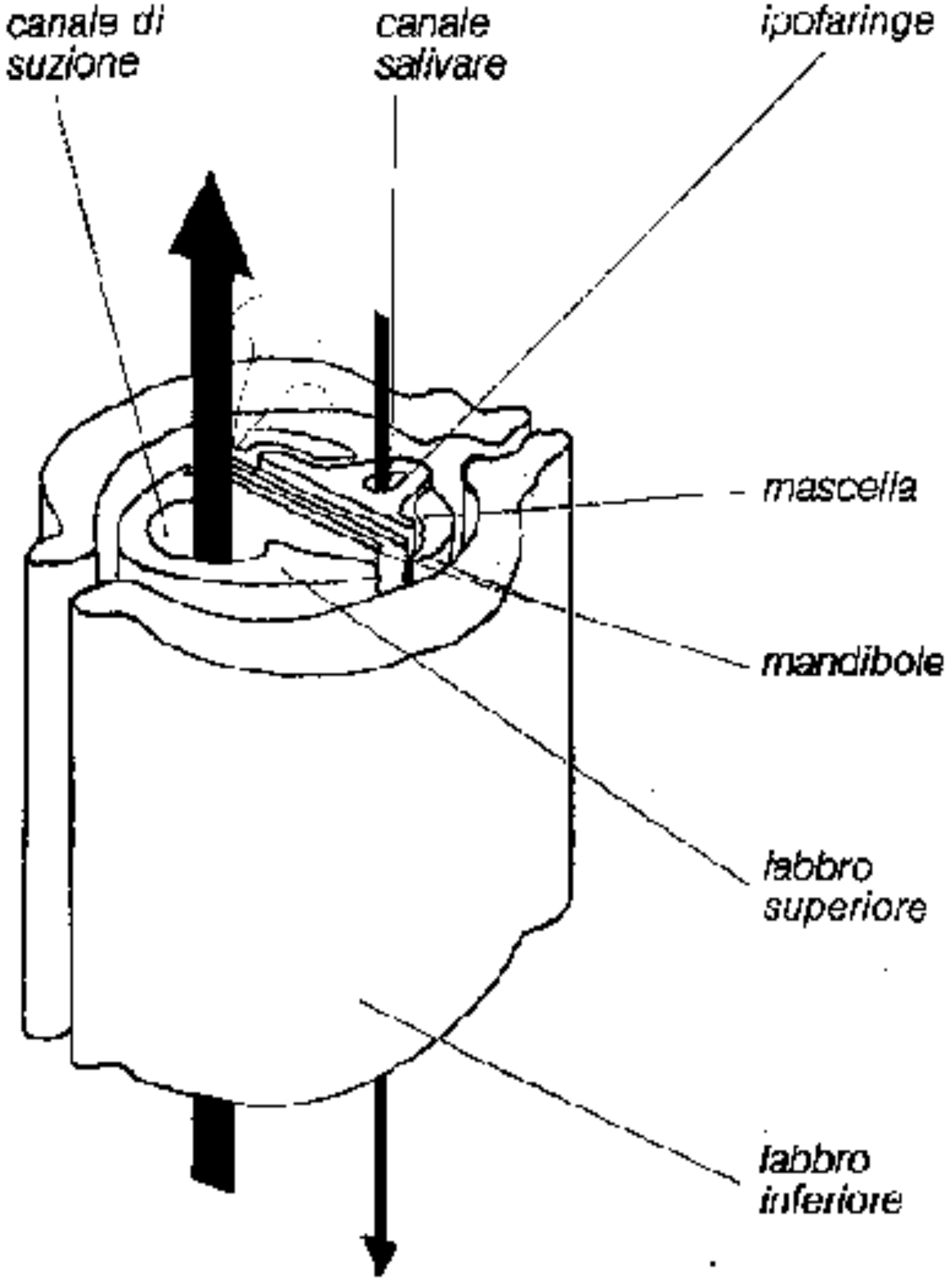



plp
premnt
lbl

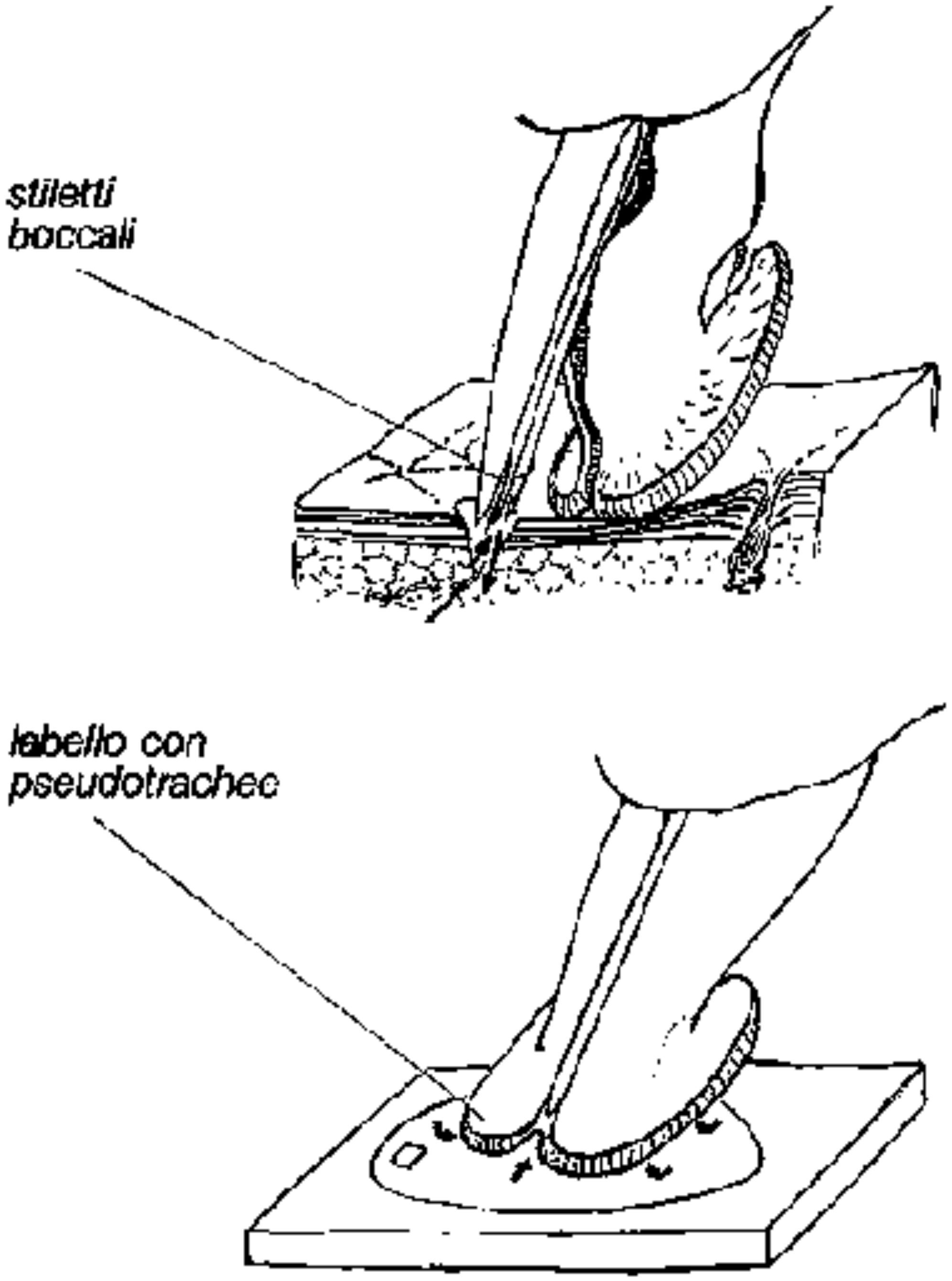
▽ CAPO VISTO SUBFRONTALMENTE CON PARTI BOCCALI RACCOLTE (A SINISTRA) E SEPARATE ARTIFICIALMENTE (A DESTRA)



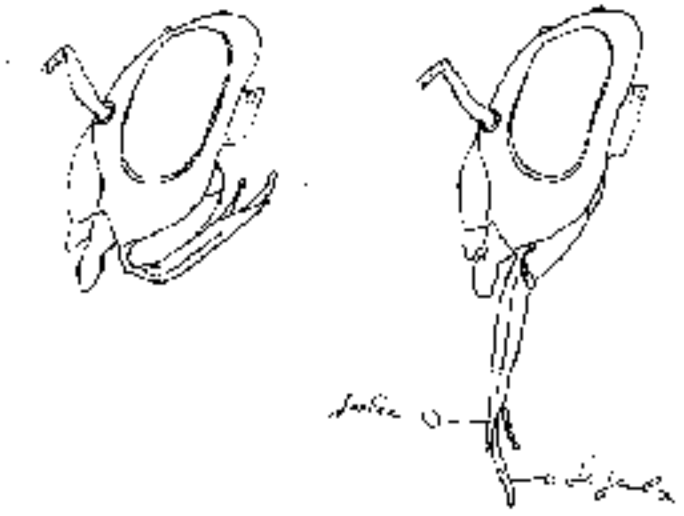
▽ SPACCATO DISTALE DELLE PARTI BOCCALI



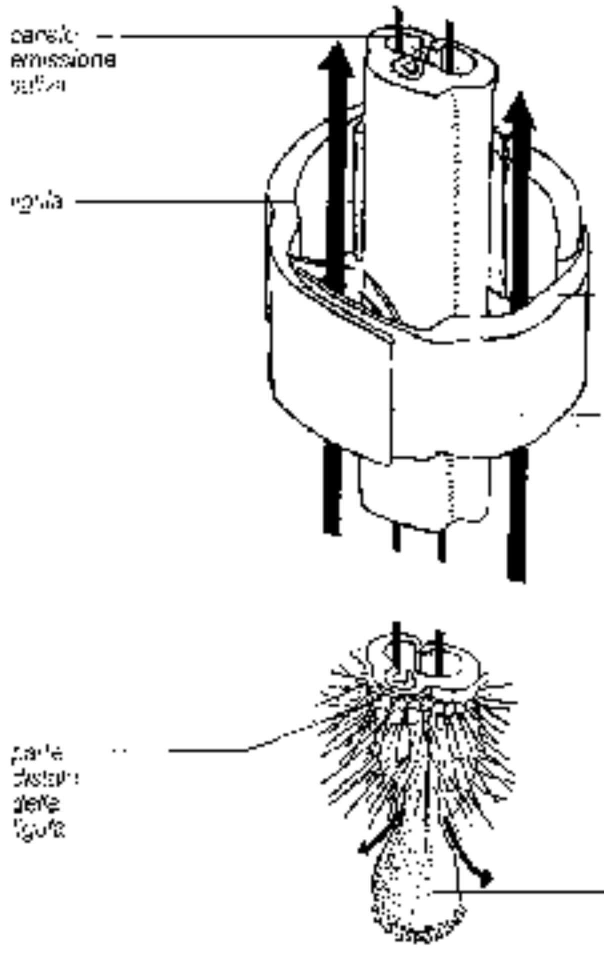
▽ DIFFERENTI MODALITÀ DI NUTRIZIONE: PUNGENTE - SUCCHIANTE (IN ALTO) E LAMBENTE - SUCCHIANTE (IN BASSO)



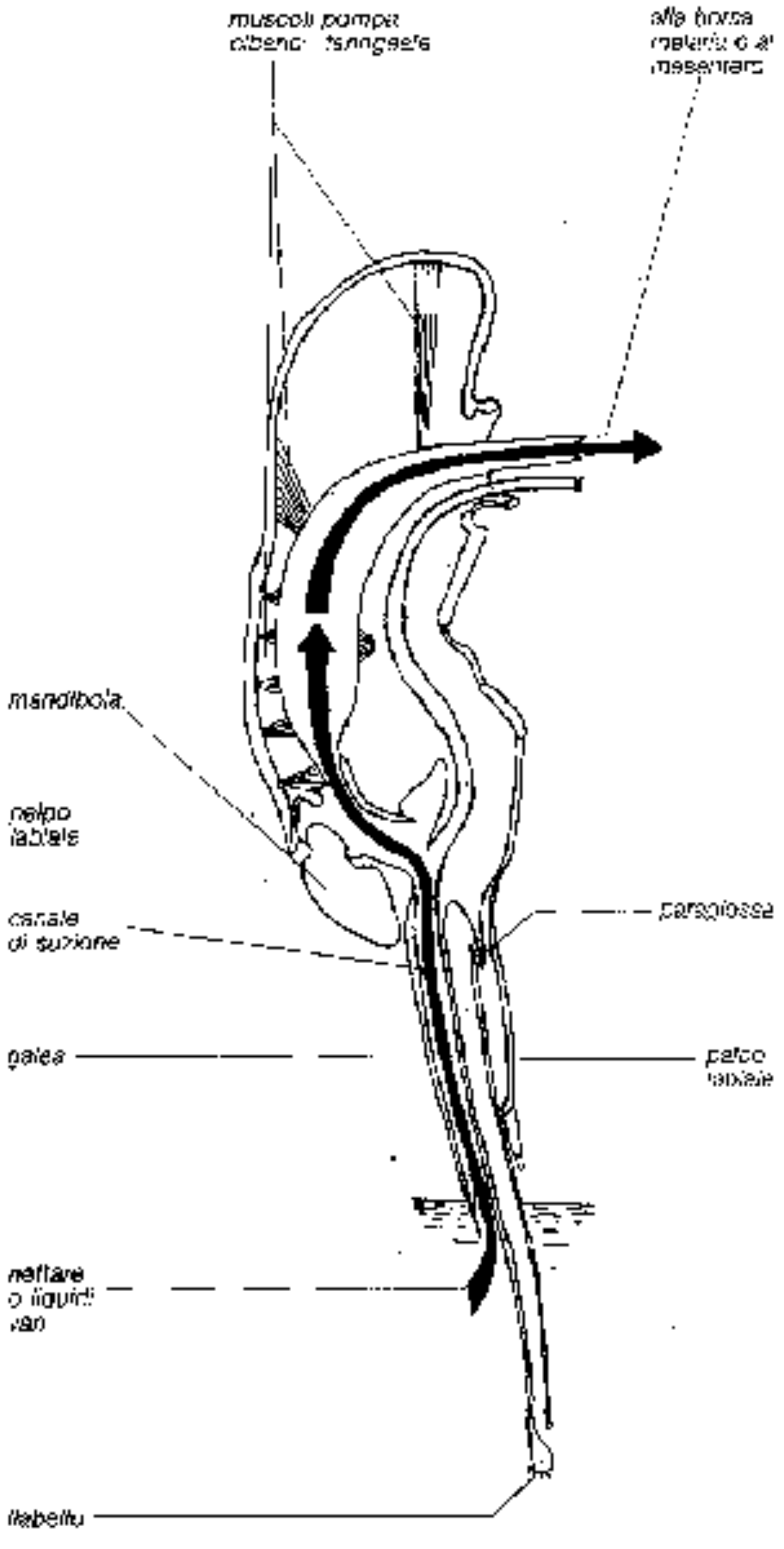
▽ PROBOSCIDE IN POSIZIONE RACCOLTA E DISTESA PER L'ATTIVITÀ TROFICA

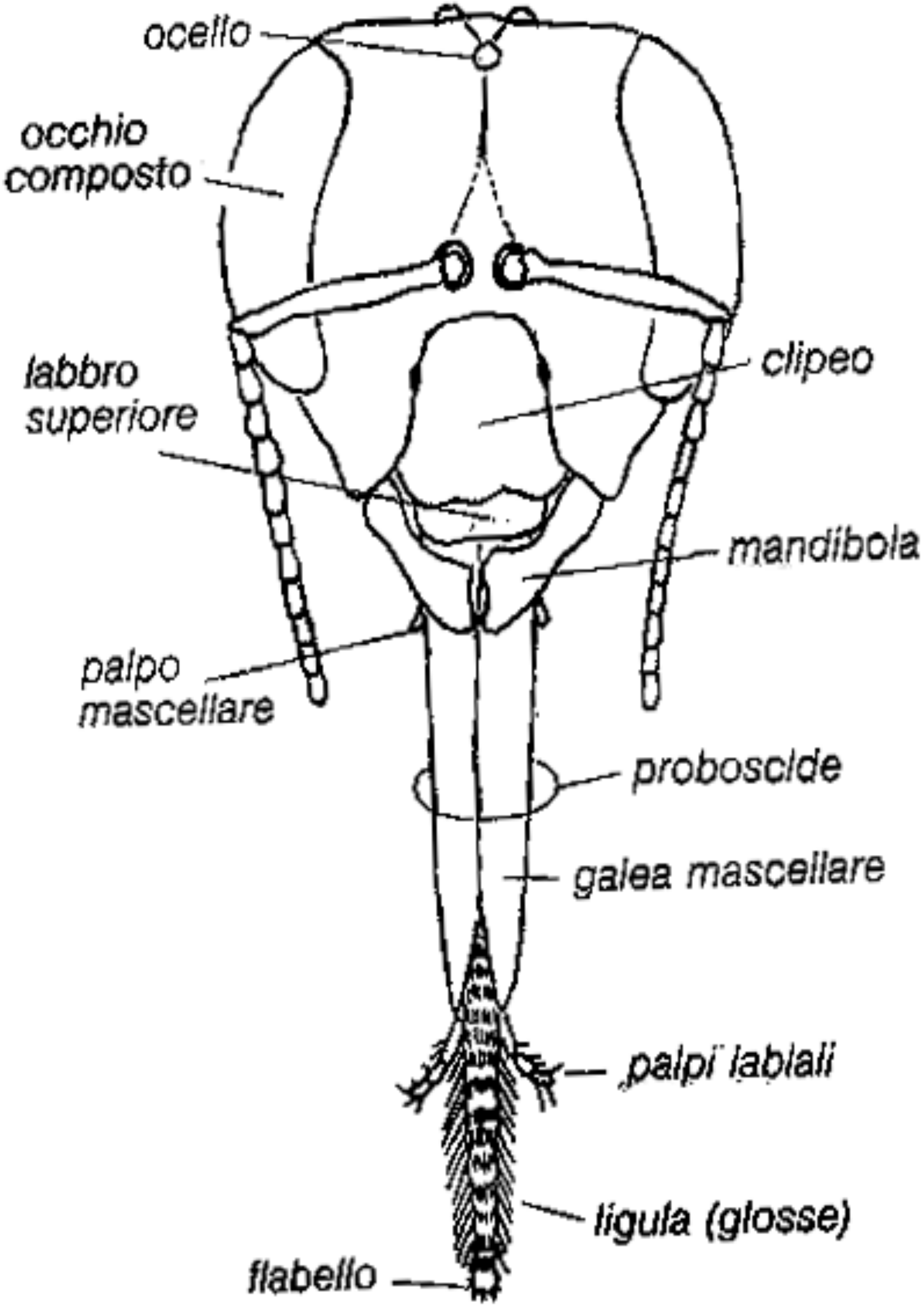


▽ SPACCATO DELLA PROBOSCIDE (IN ALTO) E DELLA LIGULA (IN BASSO) VISTI SUBANTERIORMENTE, CON CANALE DI SUZIONE DEL CIBO E DI EMISSIONE DELLA SALIVA



▽ SEZIONE LONGITUDINALE - MEDIALE E MODALITÀ DI SUZIONE AD OPERA DEL CANALE TEMPORANEO FORMATO DA GALEE E PALPI LABIALI ATTORNO ALLA LIGULA

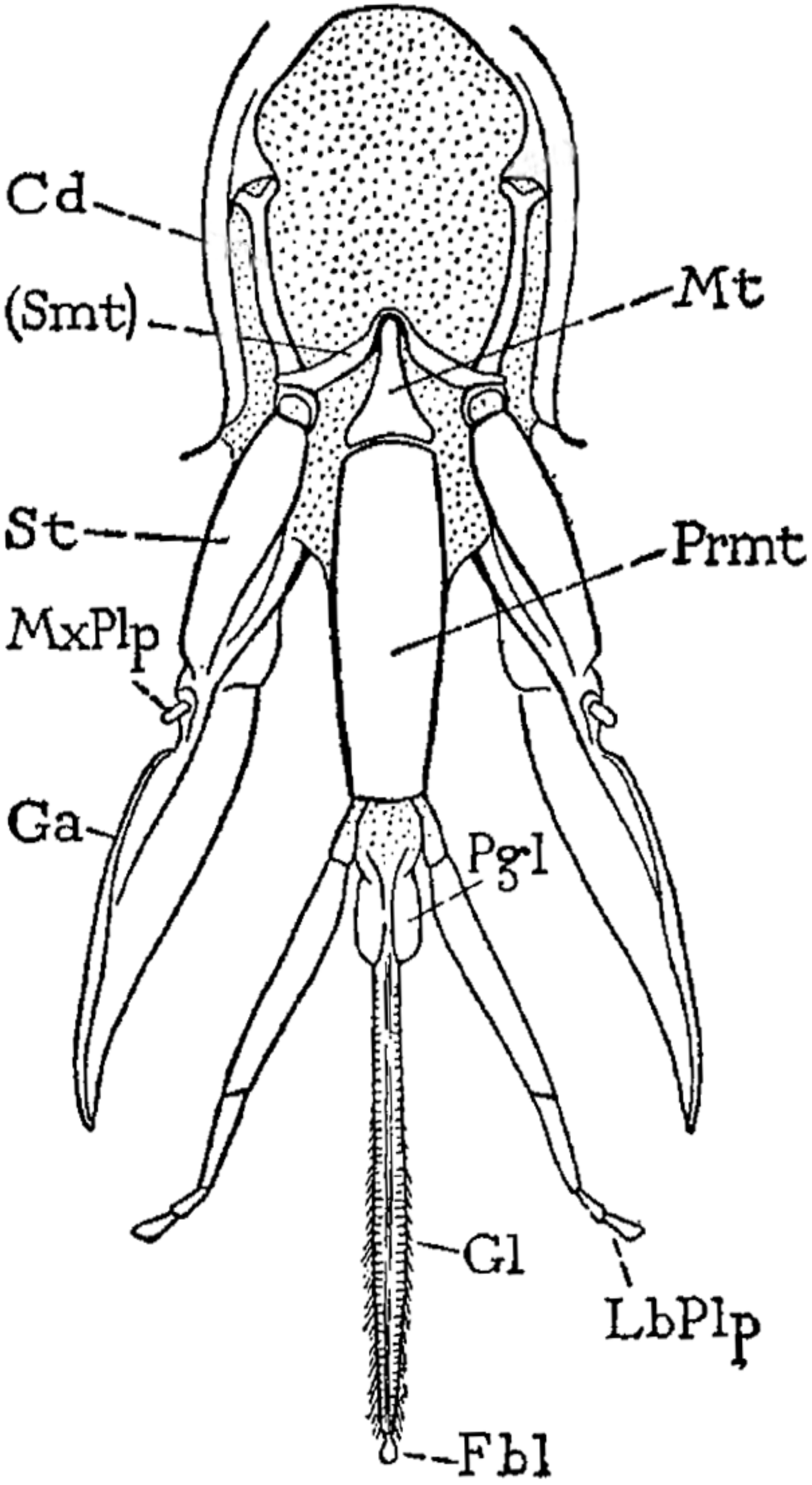


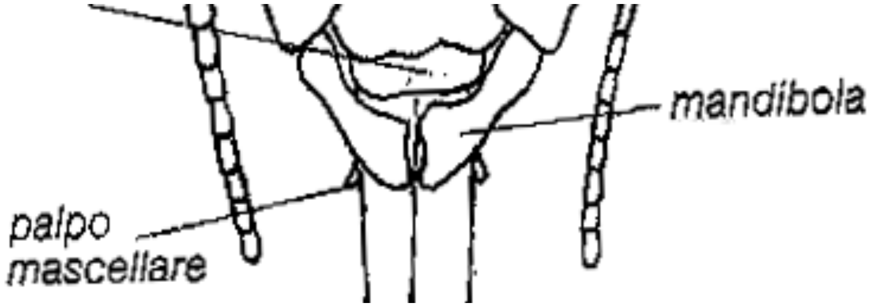

ocello
occhio composto
labbro superiore
palpo mascellare
clipeo
mandibola
proboscide
galea mascellare
palpi labiali
ligula (glosse)
flabello

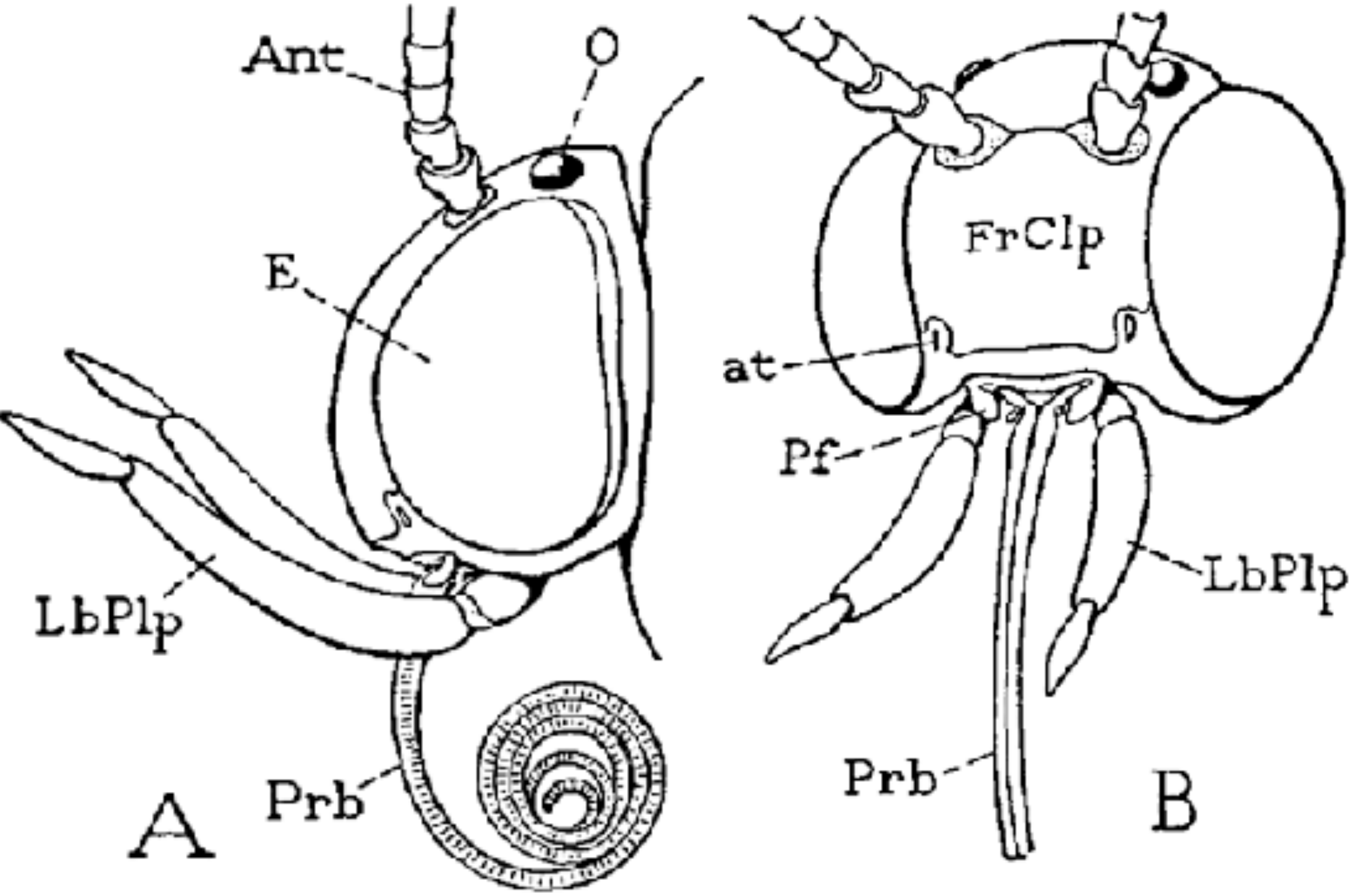
a) le appendici possono accostarsi mosse da muscoli, incastrarsi in modo provvisorio o permanente grazie a **strutture specializzate**;

b) in tutti i casi sono le **caratteristiche superficiali di bagnabilità** che danno il tocco essenziale al funzionamento dell'apparato boccale;

c) il complesso maxillo-labiale si **specializza spesso in modo fondamentale** rispetto alla dieta.




mandibola
palpo mascellare



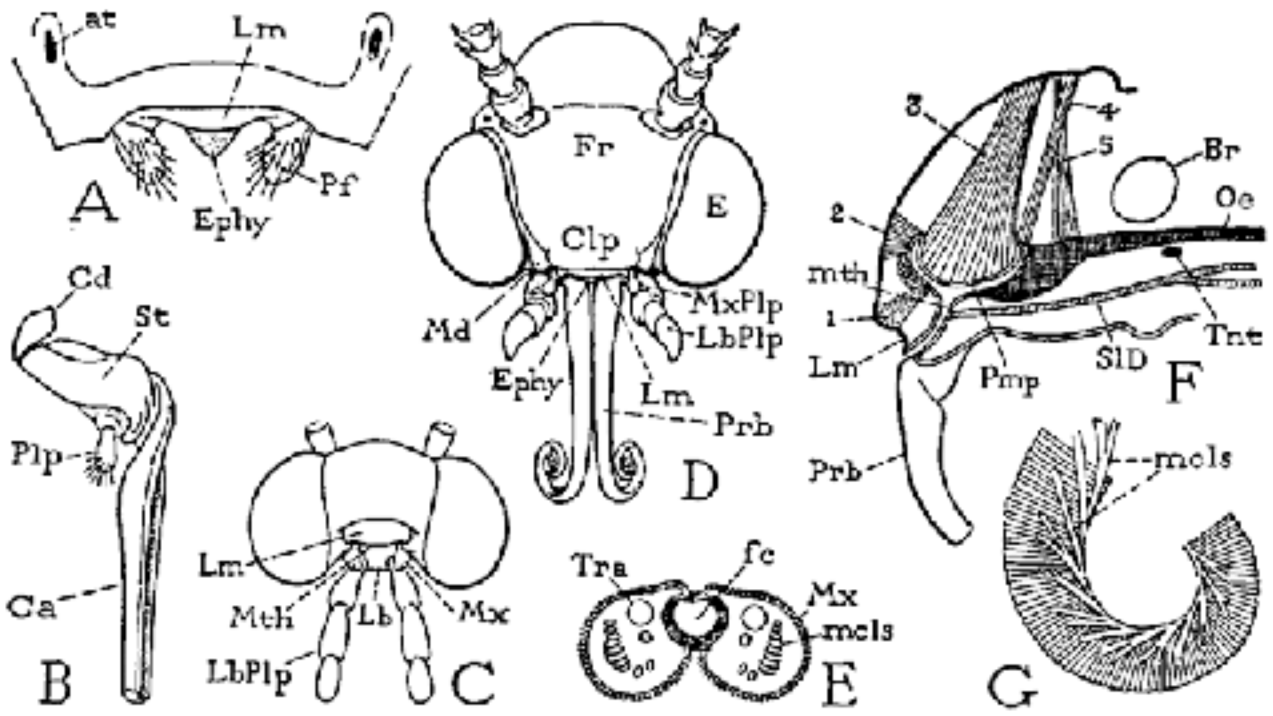
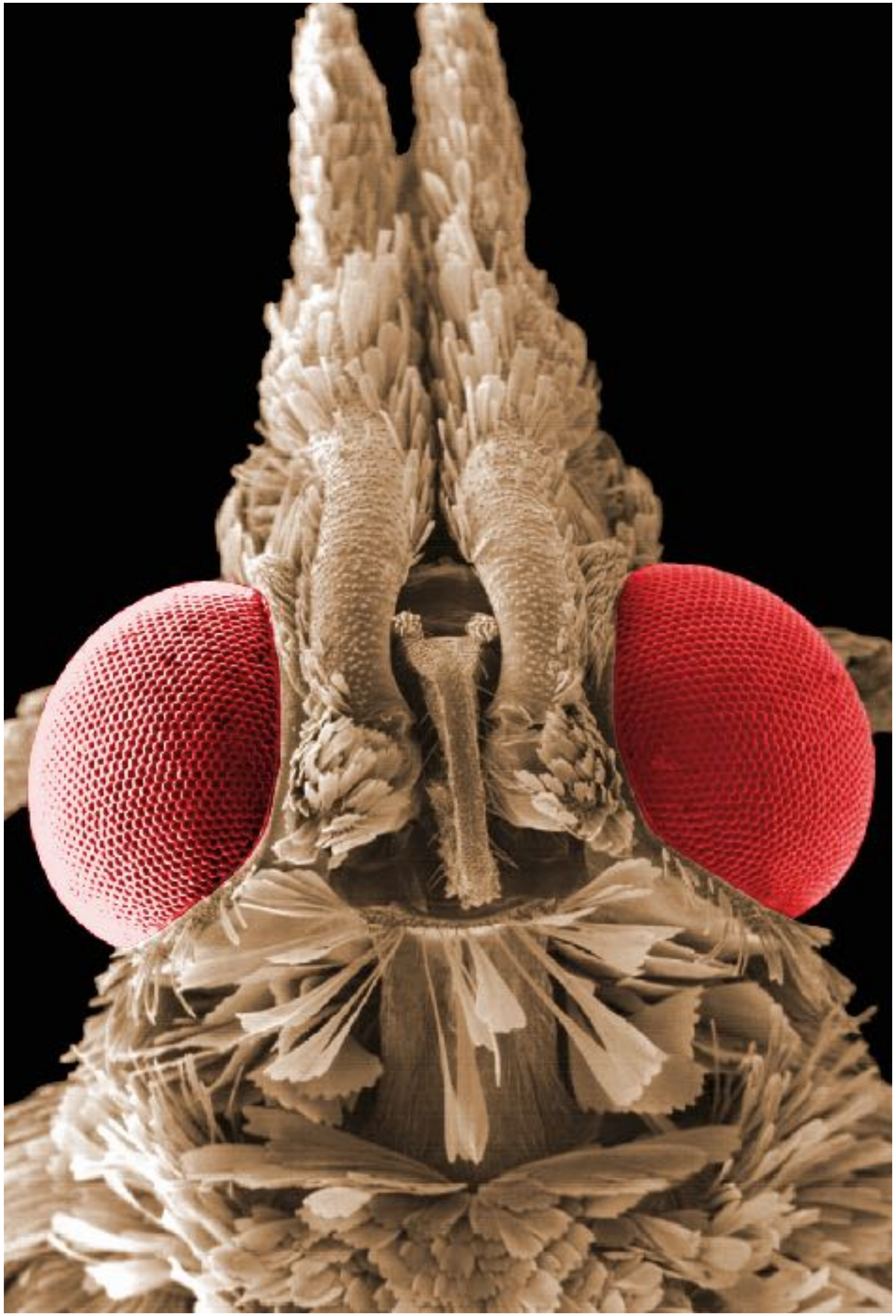
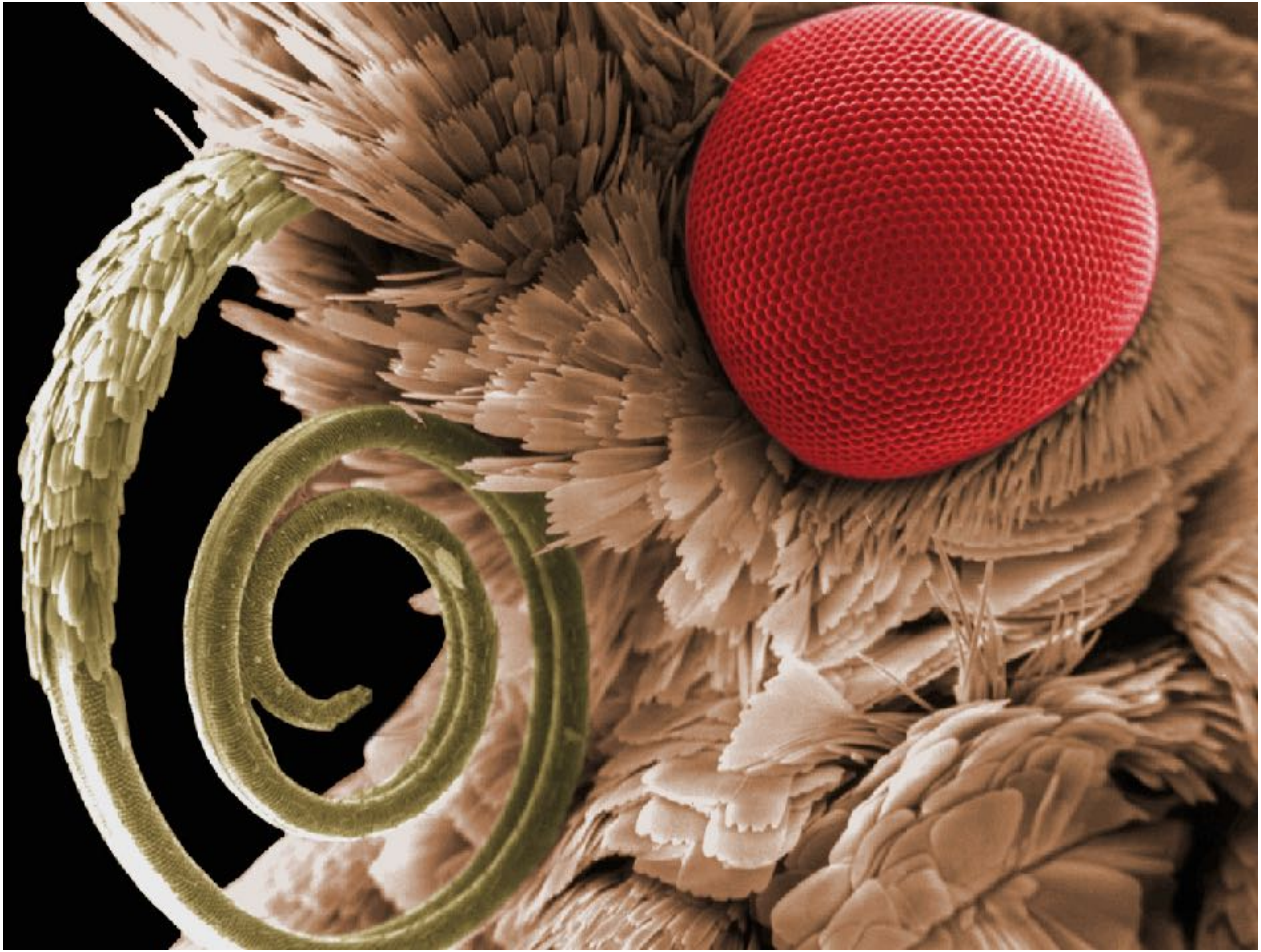
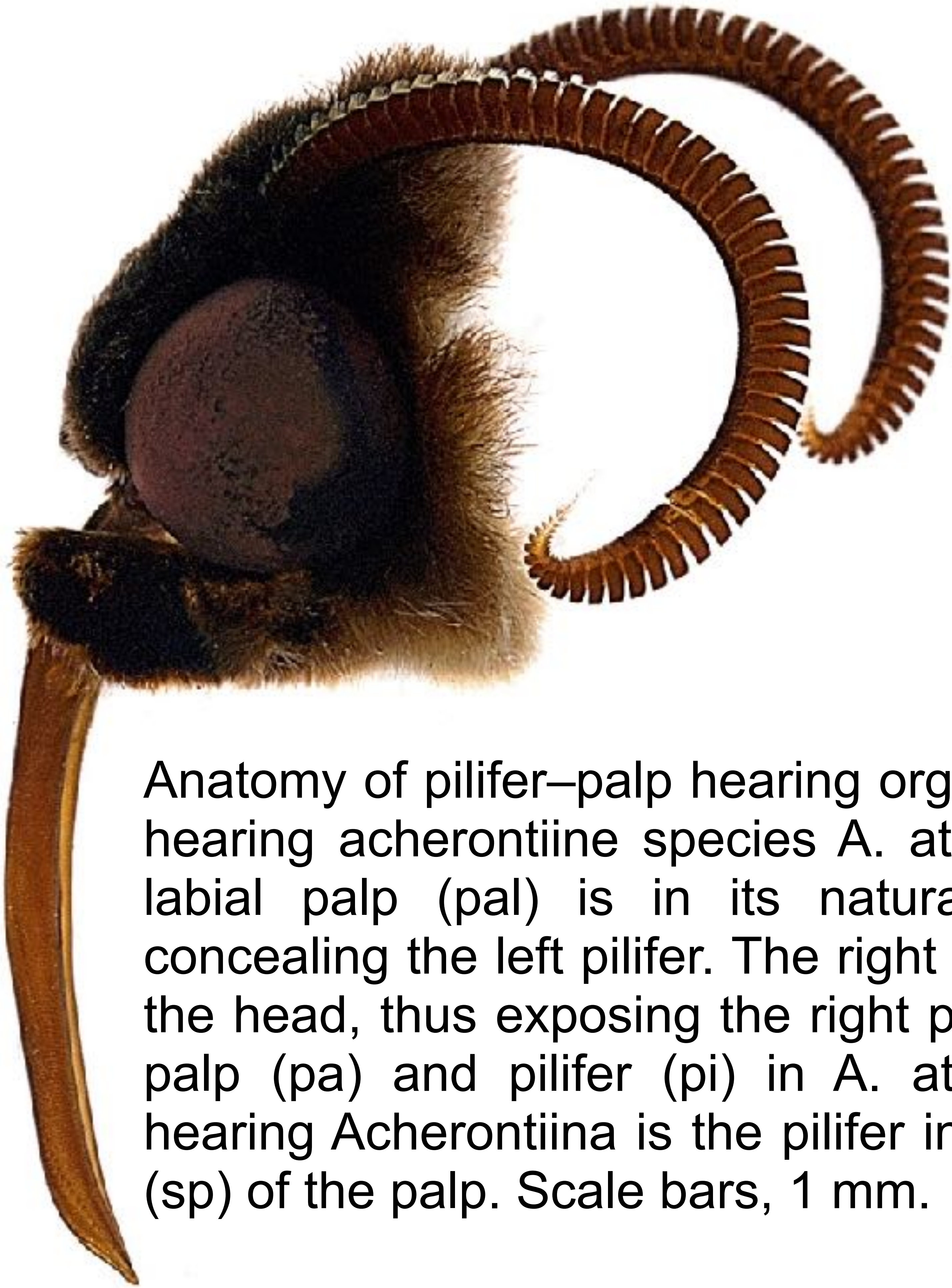
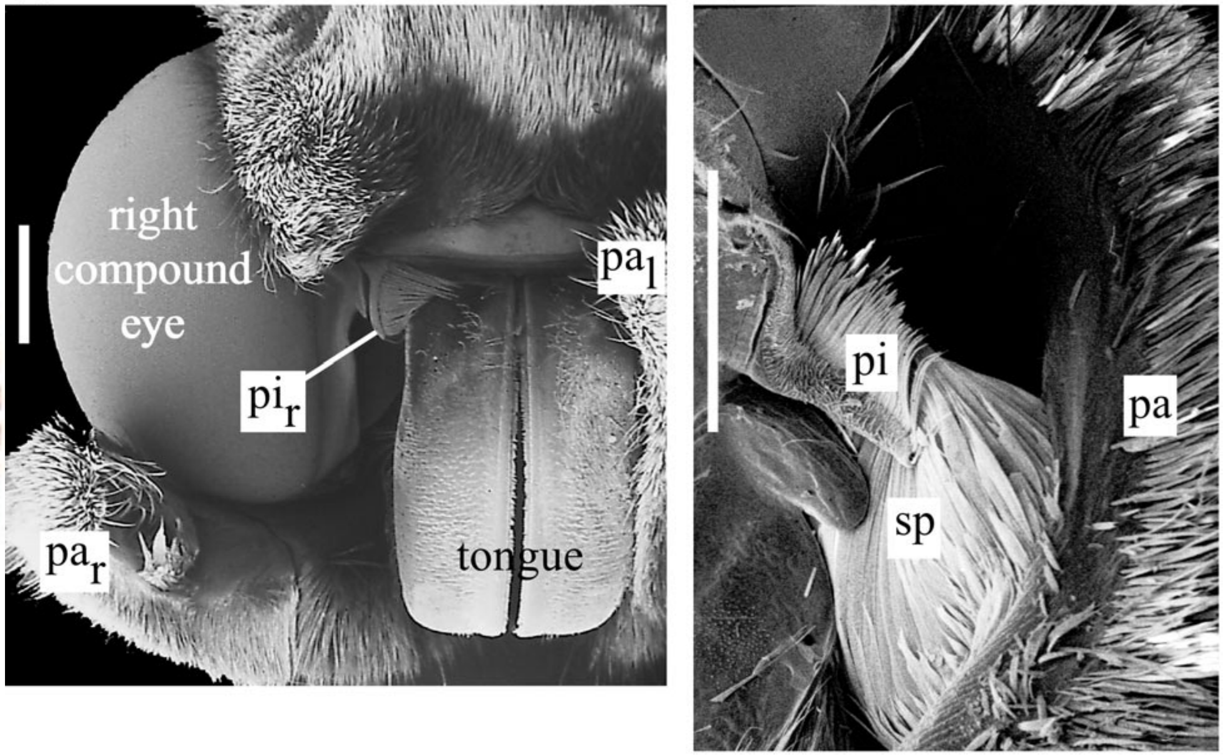


FIG. 169.—Mouth parts and sucking apparatus of adult Lepidoptera. A, *Synanthedon exitiosa*, labrum, epipharynx, and pilifers. B, same, base of maxilla. C, *Malacosoma americana*, showing rudimentary maxillae. D, *Hyphantria cunea*, head and proboscis. E, cross section of proboscis of *Danais archippus*. (*From Burgess*, 1880.) F, section of head of sphinx moth, showing sucking pump, diagrammatic. G, diagram of part of proboscis and its muscles.





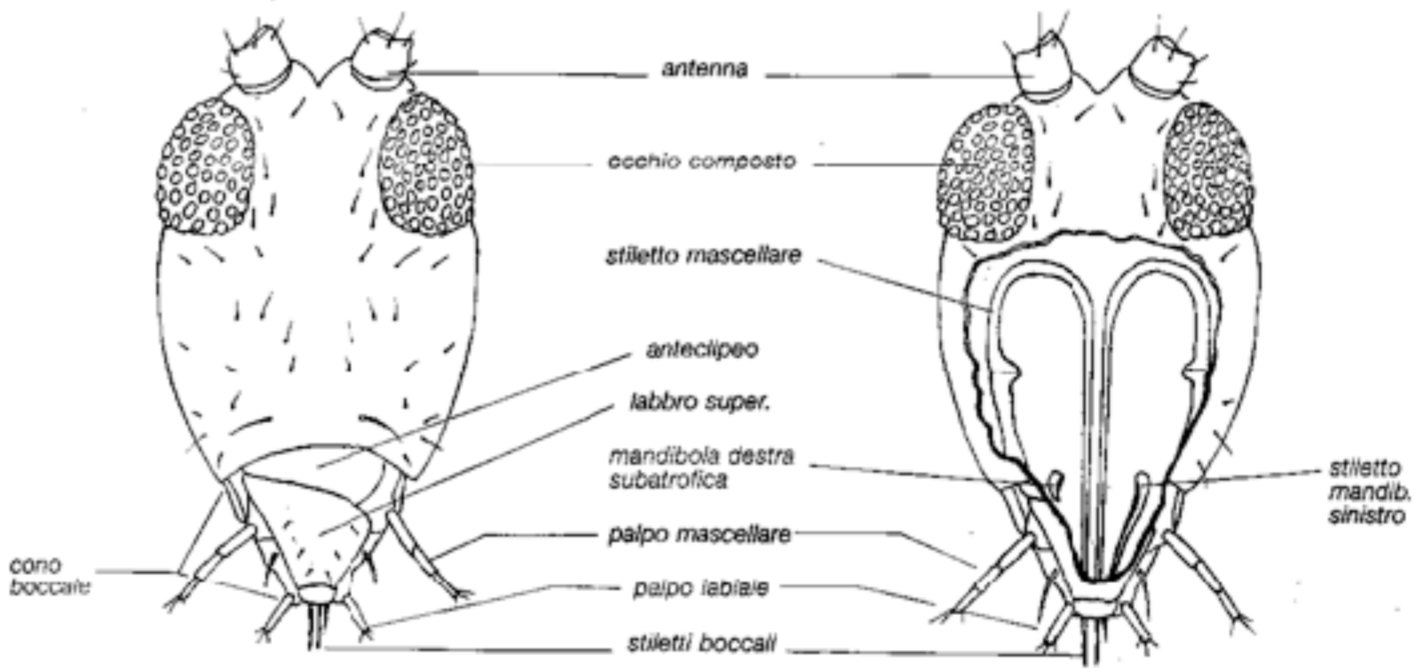




Anatomy of pilifer–palp hearing organs in hawkmoths. (a) Head of the hearing acherontiine species A. atropos (frontodorsal view). The left labial palp (pal) is in its natural, adducted position, completely concealing the left pilifer. The right palp (par) has been deflected from the head, thus exposing the right pilifer (pir). (b) Contact between the palp (pa) and pilifer (pi) in A. atropos. A characteristic feature of hearing Acherontiina is the pilifer in close contact with the scale-plate (sp) of the palp. Scale bars, 1 mm.

▽ CAPO CON PARTI BOCCALI VISIBILI DALL'ESTERNO

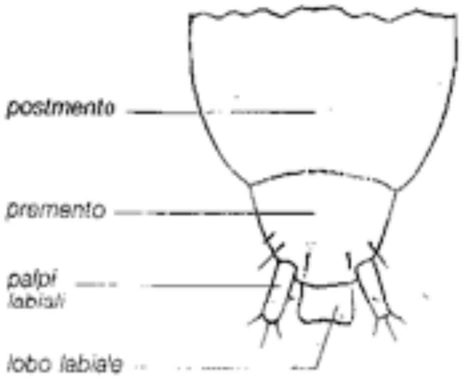
▽ CAPO APERTO AD ARTE PER MOSTRARE LE APPENDICI BOCCALI ENTOGNATE



▽ PARTI BOCCALI

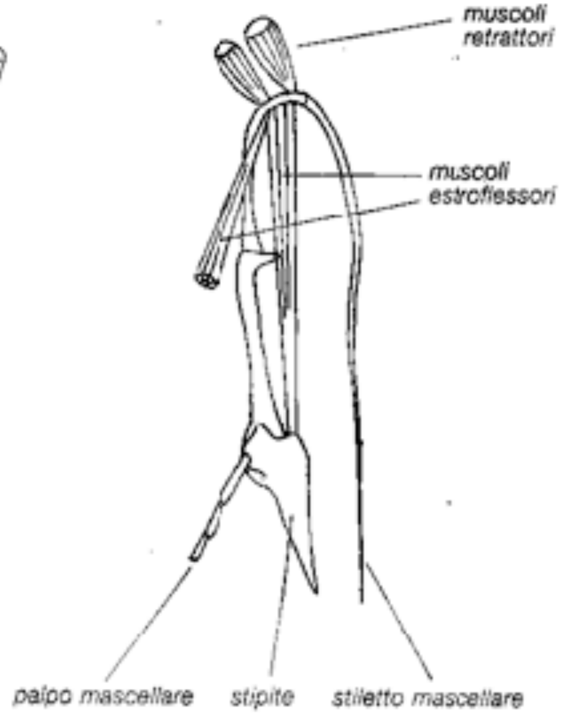
▽ labbro superiore

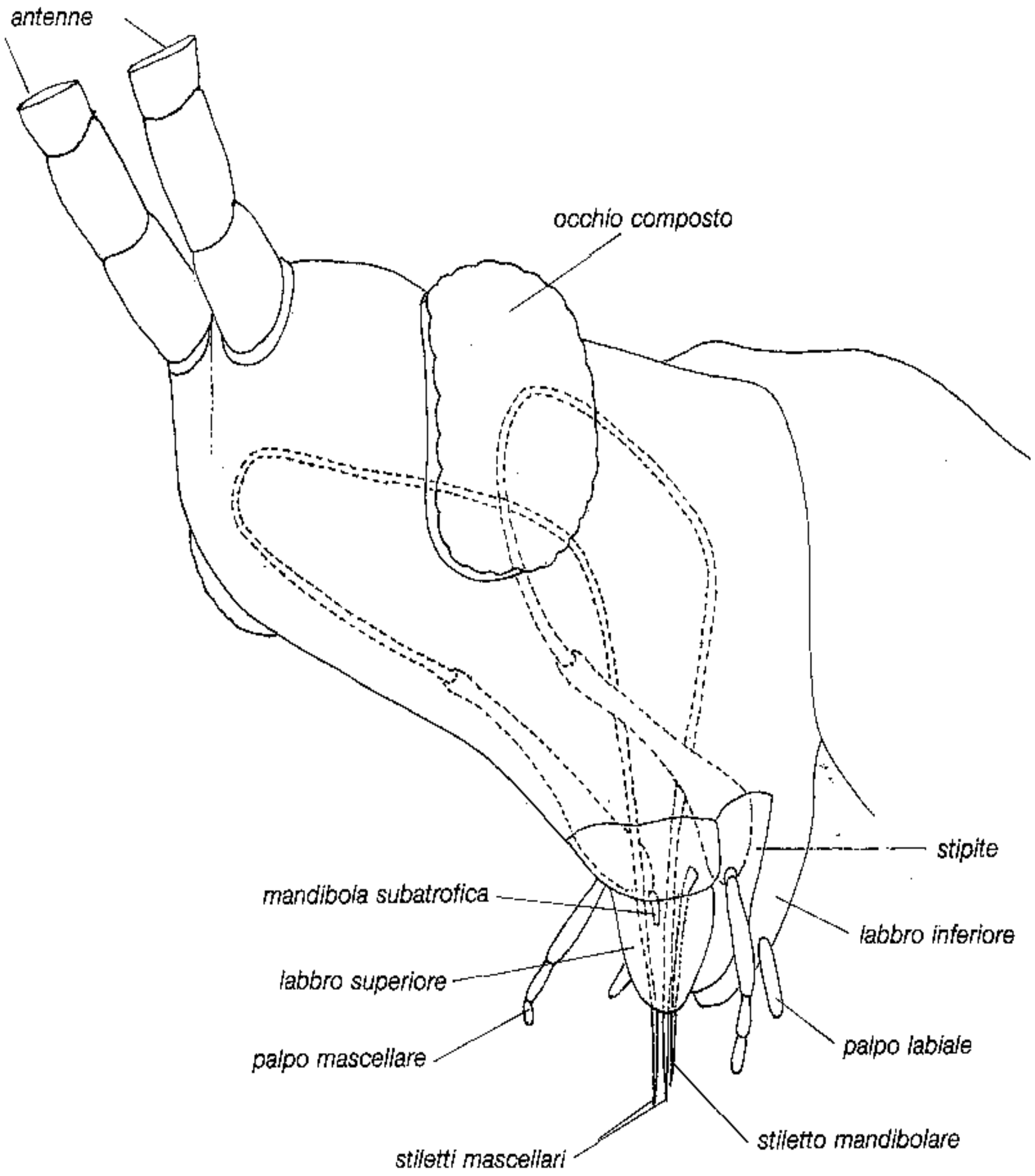
▽ labbro inferiore



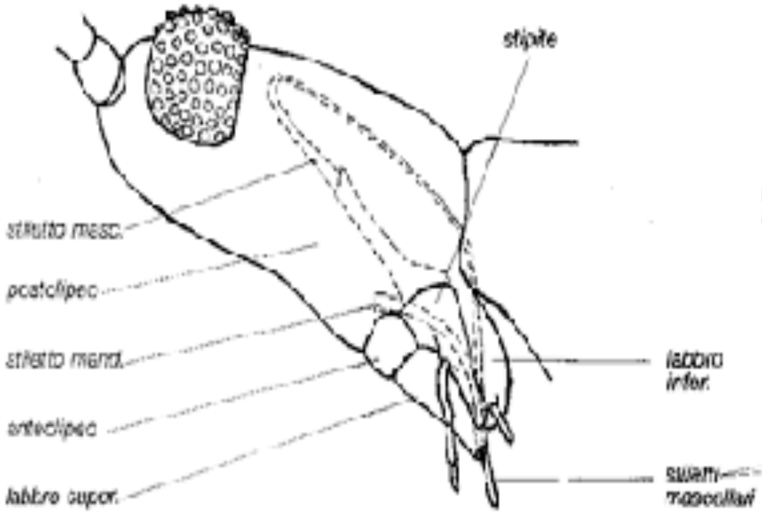
▽ mandibole

▽ mascella

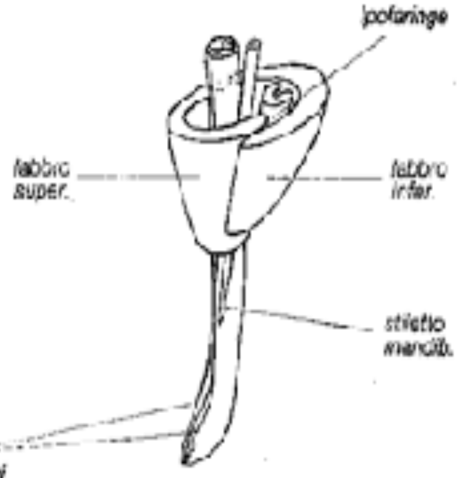



antenne
occhio composto
stipite
mandibola subatrofica
labbro inferiore
labbro superiore
palpo labiale
palpo mascellare
stiletto mandibolare
stiletti mascellari

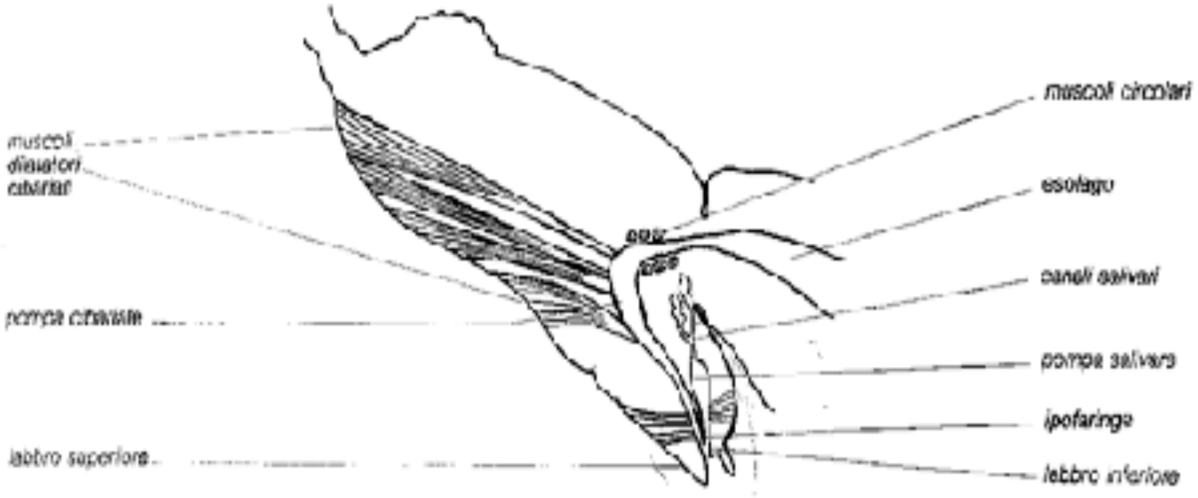
▽ CAPO DI PROFILO



▽ SPACCATO DEL CONO BOCCALE E STILETTI CON FUNZIONE PUNGENTE



▽ SEZIONE LONGITUDINALE - MEDIALE DEL CAPO



▽ MODALITÀ DI PENETRAZIONE E RETRAZIONE DEGLI STILETTI (RISPETTIVAMENTE A SINISTRA E AL CENTRO) E DI SUZIONE (A DESTRA)