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Insect Morphology and Phylogeny

De Gruyter Graduate

Rolf G. Beutel, Frank Friedrich, Si-Qin Ge,
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Insect Morphology and Phylogeny



A textbook for students of entomology

DE GRUYTER

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The carpet makers of Isfahan deliberately knot tiny flaws into their rugs,
because perfection is an attribute reserved for God.

We dedicate this book to Niels-Peder Kristensen who has set a shining example
in insect morphology and phylogeny.

Foreword

This book emerged from a close cooperation between scientists from the Institute of Zoology of the Chinese Academy of Sciences (CAS) and two German institutions, the Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum of the Friedrich-Schiller-Universität Jena and the Biozentrum Grindel & Zoologisches Museum of the University of Hamburg. Between these institutions, joint research projects have focused on insect anatomy and innovative morphological techniques and on the phylogeny and evolutionary history of different hexapod lineages. Our progress and interest in these topics are reflected in the contents of this work.

The tremendous importance of Hexapoda was highlighted in numerous contributions and will not be treated in detail here. However, the most outstanding feature of this clade is its unparalleled diversity. With approximately 1,000,000 described species, they comprise more than half of the known total species diversity on this planet. However, what is presently known is apparently only the tip of the iceberg. Estimates of the real diversity range between 2 million species and a staggering number of 30 million. Hexapod species often occur in extremely dense local populations and can form an immense biomass. Up to 100,000 springtails in only one m³ of forest topsoil or millions of mosquitos forming gigantic swarms are only two examples of such incredible population density, among many others. Hexapods are largely and primarily missing in marine habitats, but they play a crucial role in nearly all terrestrial ecosystems and occur in a broad variety of limnic habitats. They have a huge impact on human health as vectors of many diseases (e.g., malaria, sleeping sickness), and many species are important plant pests or pests of stored products. Positive aspects of hexapods include their role as predators or parasitoids of pest species (mostly pest insects) and as pollinators of plants including important crops. Insects are an important food source for numerous animal species and traditionally also for humans in many parts of the world. Last but not least, the production of silk and honey have been important economic factors going back several thousand years. The combination of unusually complex morphology, fascinating biology, remarkable species attractiveness and charisma, economic and medical impact, and various other aspects have made hexapods a highly attractive group for researchers and dedicated amateurs for centuries. Moreover, the grave threat posed by an unparalleled biodiversity crisis to the seemingly inexhaustible hexapod diversity presents one more very serious reason to intensify the study and detailed documentation of this fascinating group of organisms.

Insect morphology was a flourishing discipline in the first two thirds of the 20th century, with outstanding researchers such as J. Chaudonneret and H. Weber in European countries, but also excellent entomologists in other parts of the world. Morphology based systematic entomology arguably reached a peak with the publication of Willi Hennig's groundbreaking work "Die Stammesgeschichte der Insekten" in 1969. Towards the end of the 20th century, the detailed anatomical study of insects became

less and less popular, a development apparently linked to the rise of molecular systematics. However, in the last ten years innovative techniques and new theoretical concepts (e.g., “evolutionary morphology”) have led to a remarkable renaissance of the investigation of structures and functions of Hexapoda.

Molecular systematics has “evolved” with breathtaking momentum in the last ten years (see e.g., 1KITE.org). Robust “molecular phylogenies” will likely be available for Hexapoda and other groups of organisms in the very near future. Nevertheless, morphology will continue to play a vital role for different reasons. First of all, it provides an independent source of information for critically evaluating molecular trees (and vice versa), a procedure referred to as the “model of reciprocal enlightenment” by W. Hennig. Organisms cope with their environment using their morphological structures, which are the main target of natural selection. Body functions cannot be understood without solid morphological data, and detailed and meaningful evolutionary scenarios cannot be developed without knowing the changes on the phenotypic level. Another obvious reason is that morphology is the only source of information regarding fossils. To reconstruct the evolution of Hexapoda in its historical dimension is only possible using morphological data for the placement of extinct taxa.

The primary purpose of this book is to provide a comprehensive overview of hexapod morphology, mainly, but not exclusively, for investigations in an evolutionary context. On one hand an overwhelming richness of available data is made easily accessible here, including also extensive and highly valuable sources in non-anglophone languages (see below). On the other hand, extensive results of our own morphological investigations are integrated in this volume, including comprehensive tables of muscles with recently introduced nomenclatures, high quality SEM micrographs, and computer-based 3D reconstructions. The second main aim is to outline the state of the art in hexapod phylogenetics. The almost unprecedented progress in hexapod systematics in the last years, arguably comparable to Hennig’s “Stammesgeschichte der Insekten”, provides an almost ideal background. Long disputed questions, such as the position of Strepsiptera (“the Strepsiptera problem”), are now settled, and it is probably not overoptimistic to assume that a more or less completely resolved hexapod phylogeny (on the interordinal level) will be available in the very near future. In this context it should be emphasized that this is not only owed to the immense progress in molecular systematics, but also to several coordinated morphology-based projects, including phylogenetic studies of Polyneoptera and Holometabola.

The first main part of this book covers general hexapod morphology (**1. Morphology**) which is followed by a concise treatment of the development and immature stages (**2. Reproduction, development and immature stages**) and an extensive glossary (**3. Glossary of hexapod morphology**). A broad spectrum of traditional and innovative morphological techniques is described briefly in the next chapter (**4. Traditional and modern morphological techniques**) followed by a brief introduction into morphology-based phylogenetics (**5. Phylogenetic reconstruction based on morphology**). The second main part (**6. The hexapod orders**) covers all currently

recognized hexapod orders and their systematic relationships. The main focus in the ordinal chapters is on the morphology, but these chapters also contain shorter sections on the distribution and diversity, taxonomy, biology, reproduction, fossil record, and economic importance of the different orders.

The information presented in this volume is based on numerous sources (see **7. Literature**). Works extensively used are Snodgrass' classical "Principles of Insect Morphology", the German "Handbook of Zoology" series (De Gruyter), the "Traité de Zoologie" (edited by P.P. Grassé), some textbooks in German language (e.g., "Entomologisches Praktikum", G. Seifert), and last but not least "Evolution of the Insects" by D. Grimaldi and M. Engel. It should be emphasized that numerous specialists have made valuable contributions to this volume by carefully reviewing chapters (see Acknowledgements). Few chapters were written by invited specialists Assoc. Prof. Dr. M. Bai (Chinese Academy of Sciences), Dr. B. Wipfler, and Dipl. Biol. K. Schneeberg (Institut für Spezielle Zoologie und Evolutionsbiologie, University Jena).

This book addresses students of entomology, especially those interested in morphology, phylogeny and evolution, but also researches dealing with hexapod systematics or other aspects of entomology. A slightly modified Chinese version of this book is presently in preparation. We hope that this contribution will not only promote the study and investigation of insect morphology and evolution but also stimulate international exchange and joint research projects in systematic entomology and related disciplines.

Rolf G. Beutel
Frank Friedrich

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1 Morphology

1.1 Integument

1.1.1 Cuticle and epidermis

Like other euarthropods (Chelicerata, Myriapoda, crustaceans [probably paraphyletic]) Hexapoda (=insects in the widest sense)¹ are characterized by a differentiated exoskeleton formed by the external cuticle. It is composed of **sclerites**, **membranes**² and semimembranous areas. The cuticle is a biological composite material containing chitin, proteins, lipids and catecholamines (e.g., N-acetyl-dopamine). Catecholamines cross-link proteins and chitin filaments, which results in specific mechanical properties. The exoskeleton is usually robust in most areas and results in an improved mechanical protection of the body, but it also provides differentiated attachment areas for a complex muscular system. It is a precondition for the formation of a complex locomotor apparatus with true articulations and complex appendages (arthropodia), which was a key evolutionary innovation of Euarthropoda. Protection against desiccation is another function in most terrestrial arthropods, usually linked with the presence of an external wax layer (see below).

The cuticle does not only cover the surface. Endoskeletal structures are formed as ingrowths, referred to as **apodemes** if they are solid and as **apophyses** (or entapophyses) if they are hollow. They play an important role in most hexapods, especially as muscle attachment areas, but also increase the mechanical stability of certain body parts, such as the **tentorium** or **postoccipital ridge** in the head, or the **furcae** and **pleural ridges** in the thoracic segments. Internal organs such as the tracheae and fore- and hindgut are also covered by a very thin cuticle, the **intima**.

The cuticle is secreted by the single-layered epidermis, which is also referred to as **hypodermis** due to its position below the cuticle (Fig. 1.1.1.1). It is mainly formed by cubic or more or less strongly flattened cells with a basal lamina (0.2–0.5 µm), but contains also different types of gland cells (see **1.1.6 Integumental gland cells**), cells forming setae (**tormogen** and **trichogen cells**, see **1.1.4 Cuticular sensilla**), sensorial cells and **oenocytes**. The basal lamina is formed by epidermal cells but also by **plasmatocytes**. Its main components are collagen, glycoproteins and glycosaminoglycans (Chapman 1998). In contrast to most other cells of the hypodermis, the oenocytes have no contact with the cuticle. They are often large (more than 100 µm

1 Insects is the commonly used name for the entire Hexapoda (see title). In the text of the book we use consistently Hexapoda/hexapods for all insects including the entognathous orders (Collembola, Protura, Diplura) and Insecta/insects for Ectognatha, i.e. Archaeognatha, Zygentoma and Pterygota.

2 Terms in bold face in the parts 1 and 2 (Morphology and Development) are covered in the glossary (part 3).

in diameter) and characterized by a large nucleus, an extensive endoplasmatic reticulum, a low number of mitochondria, and crystalline inclusions. Oenocytes synthesize hydrocarbons that contribute to the epicuticle (Chapman 1998).

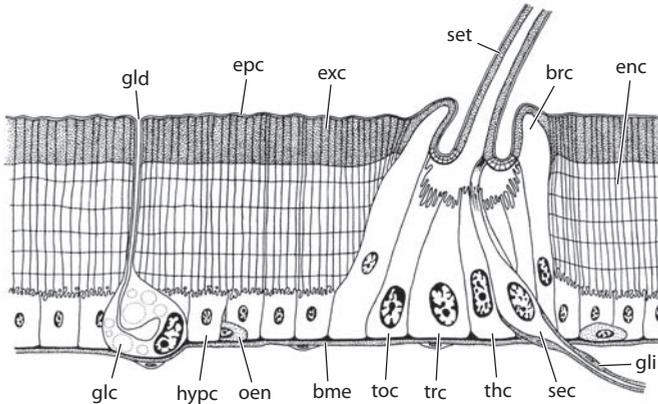


Fig. 1.1.1.1: Integument. Abbr.: bme – basement membrane, brc – basal ring cell, enc – endocuticle, epc – epicuticle, exc – exocuticle, glc – gland cell, gli – glia cell, hyc – hypodermal cell, oen – oenocyte, set – seta, sec – sensory cell, thc – thecogen cell, toc – tormogen cell, trc – trichogen cell. Redrawn from Seifert (1995).

The unmodified epidermal cells are held together by zonulae adherens near their apical regions and connected by septate junctions more basally. Desmosomes, hemidesmosomes and septate junctions also occur (Seifert 1995; Chapman 1998). The apical membrane forms a series of short ridges or projections (resembling microvilli) which are flattened apically. These plasma membrane plaques are the sites of the secretion of the **epicuticle** and chitin fibers (Chapman 1998). All epidermal cells have a glandular function as they secrete cuticle and also enzymes involved in its production and digestion.

The cuticle is composed of three layers, the external **epicuticle**, the **exocuticle**, and the internal **endocuticle** (Fig. 1.1.1.1). The two inner layers are initially secreted as a soft and more or less homogenous **procuticle** by the epidermis. It contains chains of alpha-chitin (poly-N-acetylglucosamine: $[C_8H_{13}NO_5]_x$) connected by hydrogen bonds as larger units with a parallel arrangement, the micelles or microfibrils (2.5–3 nm). These are embedded in a matrix of silk-like and globular proteins. The micelles lie parallel to each other in each plane, but the arrangement differs in successive layers of the cuticle. A regular helicoidal arrangement in a series of lamellae is a typical pattern.

The poly-N-acetylglucosamine molecules form the main component of the procuticle. The matrix protein of the procuticle and endocuticle is the flexible and water-soluble **arthropodin**. In the outer layer a hardening process takes place involving

dehydration and tanning mediated by phenoloxidases. This transforms the arthropodin into the rigid, brownish and water-resistant **sclerotin** of the exocuticle. A specialized matrix material is the rubber-like, highly elastic protein **resilin**. It occurs in sockets of true hairs (**setae**), in wings, and in mechanically highly active areas such as for instance the wing articulations.

The thickness of the epicuticle, which forms a multilayered external barrier, varies strongly (ca. 30 nm in culicid larvae, maximum ca. 4,000 nm). It is always free of chitin. In pterygote insects it is covered by a wax layer secreted by oenocytes. It is composed of paraffins and esters, which reduce water loss via evaporation. Its thickness varies between 10 nm and 1,000 nm and different surface modifications can occur (e.g., as whitish dust in Aleyrodoidea [white flies] and Coniopterygidae [dusty-wings]). An additional external cement layer occurs in some groups of insects (e.g., Blattaria), in some cases as an open meshwork. The very thin intermediate lamina of the epicuticle (ca. 15 nm) is mainly formed by the hardened protein **cuticulin**, which is similar to the sclerotin of the exocuticle. The homogenous inner layer is called the **dense lamina**. It is highly robust mechanically.

The exocuticle is strongly developed in the sclerites of the exoskeleton and can be half as thick as the entire cuticle in some cases. It is very strong under compressive forces, but comparatively weak under tension. It is very thin in the membranous areas, which are mainly formed by the endocuticle, which is flexible and able to resist tensile forces. Membranous areas occur at articulations but also on other body regions in most groups, notably between the segments (intersegmental membranes), in the pleurotergal (thorax) or pleural regions (abdomen), and on the ventral sides of the thoracic segments. The flexible parts have a higher proportion of chitin.

The hardening process transforming arthropodin into sclerotin takes place in several steps. **Prosclerotin** is an intermediate product. A cuticle where the tanning process terminates at an intermediate stage is referred to as **mesocuticle**. It is hardened but not fully pigmented, and can be stained with acid fuchsin (Chapman 1998). This type occurs in transition areas between sclerites and membranes (semimembranous areas).

1.1.2 Canals and pores

The endo-, meso- and exocuticle are perforated by **pore canals**. Very thin cellular processes of the hypodermis are involved in their formation during the secretion of the cuticle. They are usually withdrawn after the process is complete. The shape of the canals is often helical, following the arrangement of the chitin micelles in different layers. Single epidermal cells can form numerous pore canals, up to 200 in *Periplaneta americana* (Seifert 1995), which is equivalent to more than a million per mm². The lumen can vary between ca. 15 nm (*Periplaneta americana*) and 100 nm. The hypodermal cytoplasmic processes are maintained in the proximal parts of the channels

in some groups, but usually very fine chitin filaments are formed in the lumen. In the exocuticle of sclerites they are often filled with chitin-free sclerotin, which increases the mechanical stability in the vertical direction (Seifert 1995). At the base of the epicuticle each pore canal divides into several branches, which are filled with wax and perforate the dense lamina and the cuticulin layer (Seifert 1995).

1.1.3 Surface structures, microtrichia and setae

The cuticle is usually characterized by fine surface patterns reflecting the arrangement of subtending hypodermal cells. A multitude of surface structures and modifications occur in different lineages. Minute spines or tubercles can be formed by the epicuticle alone, but the exocuticle is usually involved in the formation of surface structures. Simple surface modifications are the solid **microtrichia** (=trichomes), which are not articulated and not in contact with the hypodermis after their formation. They are never associated with sensory cells and are referred to as **acanthae** when they are formed by a single cell. Specialized microtrichia, usually with a soft, flexible cuticle and a spatulate apical part, form attachment devices of the hairy type (e.g., hairy soles of **tarsomeres**; see 1.3.5 Attachment structures).

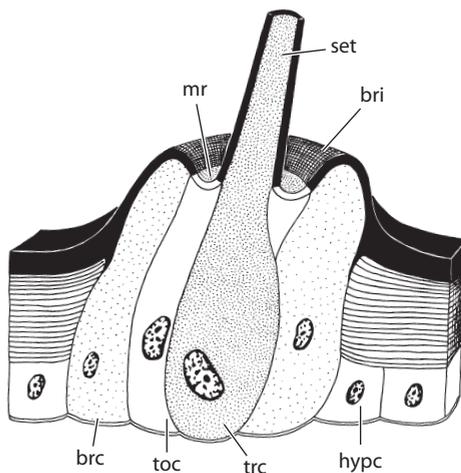


Fig. 1.1.3.1: Seta and associated cells, schematized. Abbr.: brc – basal ring cell, bri – basal ring, hycp – hypodermal cell, mr – membrane ring, set – seta, toc – tormogen cell, trc – trichogen cell. Redrawn from Seifert (1995).

Setae or true hairs articulate in a flexible socket or diaphragm permitting movement (Figs 1.1.1.1, 1.1.3.1). They are formed by a specific hypodermal cell, the **trichogene cell**,

and are always in contact with the hypodermis. The socket is formed by the **tormogene cell** and has usually three layers, the external joint membrane, a ring of suspensory fibers, and the thin and fibrous socket septum. The joint membrane is enclosed by the cuticular basal ring. Setae are primarily hair-like but can be modified in many different ways, especially in the context of sensorial functions (see **1.1.4 Cuticular sensilla**). Cuticular scales occur in Collembola, Diplura, Archaeognatha and Zygentoma, and are possibly an apomorphic groundplan feature of Hexapoda. The scales of Lepidoptera and Archostemata (Coleoptera) are neof ormations derived from hair-like setae. Club-shaped setae occur in 1st instar nymphs of Orthoptera and spear-shaped defensive hairs are present in larvae of Dermestidae (Coleoptera). Long and flexible swimming hairs occur in different lineages of aquatic beetles (e.g., Dytiscidae, Hydrophilidae) and also in aquatic groups of Heteroptera (e.g., Corixidae, Notonectidae).

1.1.4 Cuticular sensilla

Sensilla are the basal functional and structural units of cuticular mechanoreceptors and chemoreceptors. They include the cuticular component (e.g., the cuticle of a seta), the sensory neuron (or neurons), the associated sheath cells with the cavities they enclose and the structures they produce (Figs 1.1.1.1, 1.1.4.1) (Chapman 1998).

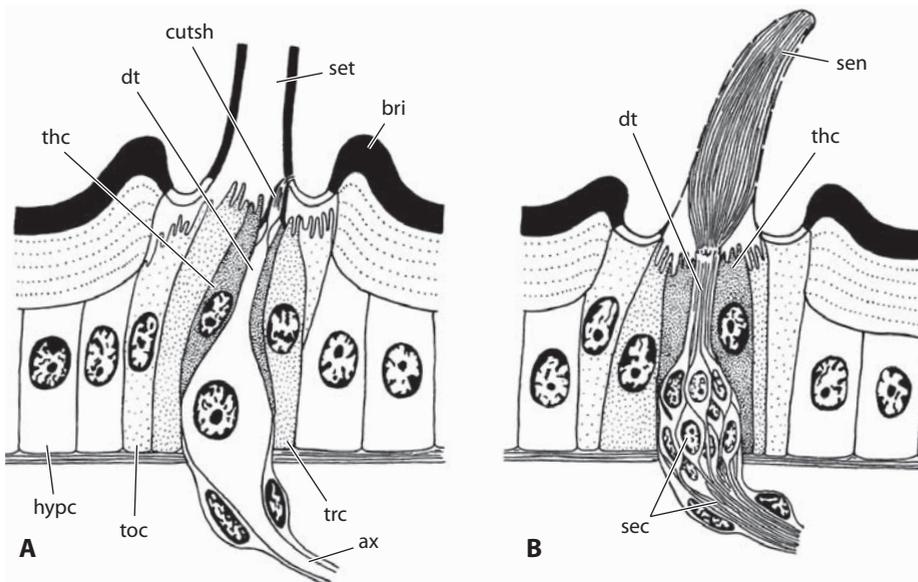


Fig. 1.1.4.1: Cuticular sensilla, schematized. A, mechanoreceptive seta; B, chemoreceptive sensillum. Abbr.: ax – axon, bri – basal ring, cutsh – cuticular sheath, dt – denrite, hyc – hypodermal cell, sec – sensory cell, sen – chemoreceptive modified seta, set – mechanoreceptive seta, thc – thecogen cell, toc – tormogen cell, trc – trichogen cell. Redrawn from Seifert (1995).

The least modified type is the **sensillum trichodeum** (hair sensillum). It is composed of a primary sensory neuron and a hair-like seta with a wall consisting of exocuticle and epicuticle (Figs 1.1.1.1, 1.1.4.1). The typical mechanoreceptive seta tapers from the base towards its apex. The displacement of the hair in the socket results in the neural stimulus (Chapman 1998). **Sensilla chaetica** are shorter and thick-walled hair-like mechanoreceptors. Very long and thin sensilla not tapering apically are sometimes referred to as **trichobothria**. They are not homologous with the true trichobothria occurring in Arachnida.

The cells involved in the formation of a sensillum are derived from the same hypodermal cell (sense organ precursor cell, sense organ mother cell). In addition to the **tormogen** and **trichogen cells**, a small **thecogen cell** is present between the latter and the neuron. It secretes a cuticular layer around the distal dendrite, the dendrite sheath, which usually ends at the base of the hair.

Modified types of cuticular sensilla are the apically rounded **sensillum basiconicum**, and the **sensillum campaniformium**, which scarcely protrudes beyond the basal ring enclosing it (Fig. 1.1.4.2). The **sensillum placodeum** is entirely flat and the **sensilla coeloconica** and **ampullacea** are sunk below the external cuticular surface to different degrees. The shape of the outer cuticular element of the sensillum does not necessarily indicate its function. Larger hair-like sensilla are in most cases mechanoreceptors, but can also function as contact chemoreceptors. A function as olfactory chemoreceptor is indicated by fine pores in the wall of the sensillum. Pores (apart from the molting pore) are always absent from sensilla solely functioning as mechanoreceptors (e.g., Chapman 1998). Therefore they are also referred to as aporous sensilla.

The sensorial neurons associated with sensilla trichodea are usually of the bipolar type (Figs 1.1.1.1, 1.1.4.1). Basally they are enclosed by the **neurilemma** (glial sheath). The distal dendrite is ensheathed by the thecogen cell and is strongly narrowed where it enters the base of the seta. Its distal part is characterized by one or two concentric rings of microtubule doublets ($9 \times 2 + 0$ pattern) and is consequently called the sensorial cilium. The receptive element is the membrane of its apical part, the tubular body, which comprises a bundle of numerous microtubules (between 30 and up to 1,000) connected by an electron-dense substance. The apical part of the tubular body is firmly embedded in the cuticle of the base of the sensillum trichodeum. The sensorial cilium (including the tubular body) is enclosed in the cuticular dendritic sheath, which is secreted by the thecogen cell. In contrast to mechanoreceptors, the distal dendrites of chemoreceptive cells do not insert into the cuticle at the base of the sensillum by way of a tubular body. Chemoreceptors are often equipped with several sensorial cells of different modality. Each individual dendrite can be enclosed in a tubular sheath but often all dendrites are enclosed within a multilocular dendritic sheath with one in each loculus. The dendrites usually branch after entering thin-walled olfactory sensilla, which are characterized by pores arranged in hexagonal groups. The diameter usually ranges between 15 and 20 nm. Each pore widens within the cuticle and forms a pocket.

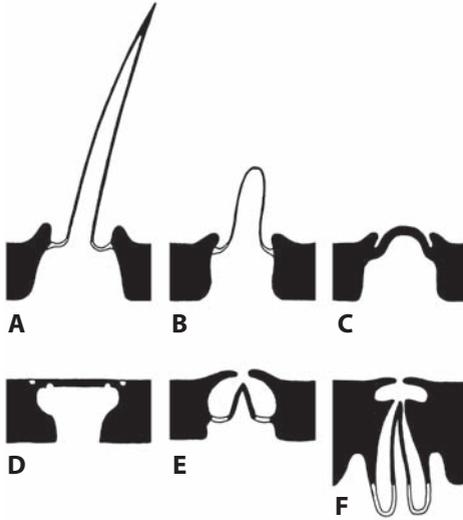


Fig. 1.1.4.2: Different types of cuticular sensilla. A, sensillum trichodeum; B, *s. basiconicum*; C, *s. campaniformium*; D, *s. placodeum*; E, *s. coeloconicum*; F, *s. ampullaceum*. Redrawn from Seifert (1995).

Extremely fine pore tubules (5–6 nm) originate from the pockets and end in the liquor of the sensillum adjacent to the dendritic membrane (Seifert 1995).

1.1.5 Scolopidia

Scolopidia are specialized internal (subcuticular) mechanoreceptors (Fig. 1.1.5.1) and probably derived from sensilla trichodea. They consist of the scolopale cell which is homologous to the thecogen cell, the scolopale cap cell which is equivalent to the trichogen cell (enclosed by a tormogen cell), and one or several bipolar sensory neurons. Scolopidia often function as proprioceptors or are sensitive to vibrations of air or substrates.

An external hair-like element is not present. The cell body of the sensorial cell is sunk below the hypodermis. It is connected with it by the external **scolopale cap cell (=attachment cell)**, which is placed on top of the **scolopale cell** and the dendrite, which is proximally covered by a sheath cell and apically narrows to a cilium-like process containing a peripheral ring of nine microtubule doublets with proximally extending roots. The doublets are often (or perhaps always) connected with the cell membrane near their origin at the basal body by a structure called the ciliary necklace (Chapman 1998). The cuticular scolops is secreted by the scolopale cell and rests on the apical part of the dendrite like a cap. The scolopale cell contains the **scolopale**, which consists of fibrous material containing actin

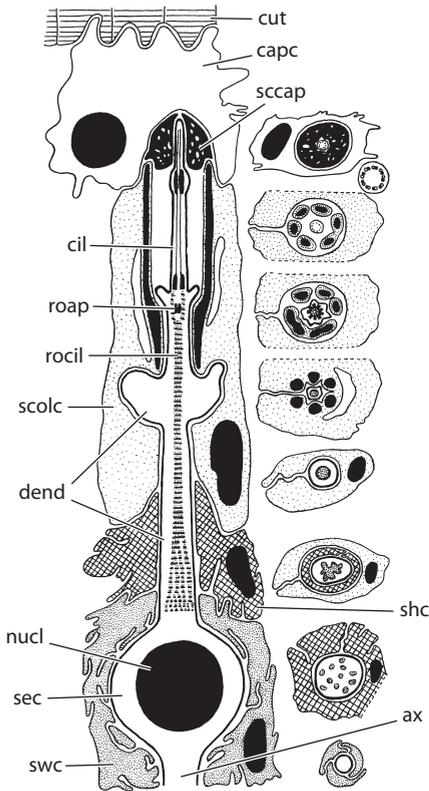


Fig. 1.1.5.1: Scolopidium. Abbr.: ax – axon, capc – cap cell, cil – cilium, cut – cuticle, dend – dendrite, nucl – nucleus, roap – root apparatus, rocil – root of cilium, sccap – scolopale cap, scolc – scolopale cell, sec – sensory neuron, shc – sheath cell, swc – Swann cell. Redrawn from Seifert (1995), after Gray (1960).

arranged in ring or a series of rods (scolopale rods) (Chapman 1998). In scolopidia of the subintegumental (=mononematic) type the distal end of the cap lies completely below the body surface. In integumental (=amphinematic) scolopidia the scolops is attached to the external cuticle by a thin cuticular terminal extending through a narrow fold of the scolopale cap cell.

Chordotonal (or scolopophorous) organs (Fig. 1.1.5.2) are formed by scoloparia, groups of scolopidia stretching between two movably connected sclerites. They are specialized mechanoreceptive organs (either proprioceptive or exteroceptive). Examples are Johnston's organ in the second antennomere (pedicel) of Insecta, or the subgenual organs in the distal parts of the legs which perceive substrate vibrations.

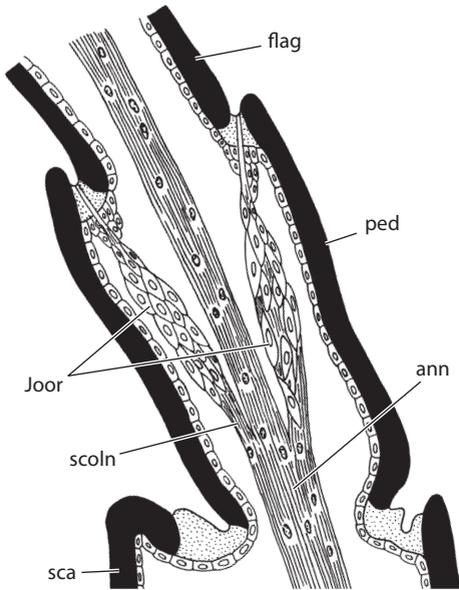


Fig. 1.1.5.2: Chordotonal organ, Johnston's organ of the pedicellus, *Melolontha vulgaris* (Coleoptera, Scarabaeidae).

Abbr.: ann – antennal nerve, flag – 1st flagellomere, Joor – Johnston's organ, ped – pedicellus, sca – scapus, scoln – scolopale nerve. Redrawn from Seifert (1995), after Snodgrass (1935).

1.1.6 Integumental gland cells

Gland cells associated with the integument are embedded in the hypodermis (Fig. 1.1.1.1: 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 by Noirot & Quennedey (1974). 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 (Chapman 1998). The duct is an invagination of the external cuticular layer (Seifert 1995). Microvilli are absent from class 2 cells (Noirot & Quennedey 1974).

1.1.7 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 (see **1.9 Digestive tract**). 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 (see **1.1.1 Cuticle and epidermis**). 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 (Dettner & Peters 2003).

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 (Dettner & Peters 2003). 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.

[Snodgrass (1935); Gray (1960); Noirot & Quenedey (1974); Seifert (1995); Chapman (1998); Dettner & Peters (2003)]

1.2 Head

1.2.1 Segmentation, sutures and cephalic regions

The head (Figs 1.2.1.1, 1.2.2.1) is a compact and complex **tagma** with a concentration of a broad array of structures and functions. It is equipped with sense organs such as the highly complex **compound eyes** (Fig. 1.6.2.1) and the **antennae**, an elaborate set of mouthparts (Fig. 1.2.4.1), and a complex muscle apparatus (see **Table I** for all cephalic muscles). It also contains central elements of the nervous system, the anterior part of the digestive tract including the **cibarium** (preoral cavity) and the **salivarium**, and also **neurohaemal organs** (Fig. 1.11.2). It is likely that the hexapod head is homologous to a six-segmented **cephalon** which may represent a groundplan apomorphy of Euarthropoda (Chelicerata, Myriapoda, Pancrustacea [=Tetraconata, crustaceans and Hexapoda]). A six-segmented head was likely present in the extinct †Trilobita and other fossil lineages, and is preserved in the extant Myriapoda and Pancrustacea (fused with thoracic segments in most crustacean subgroups: cephalothorax). In contrast to †Trilobita, the primary head segmentation in hexapods cannot be traced directly by external segmental borders, but it can be deduced from the tripartite **cer- ebrum** (brain) and tripartite **suboesophageal ganglion** (Figs 1.5.1.1–1.5.1.3) and the appendages, i.e. the antennae, **mandibles**, **maxillae** and **labium** (the segmental affiliation of the **labrum** is disputed). Territories of the head were identified by different authors, but it was pointed out by Denis & Bitsch (1973) that they do not exactly correspond with the primary segments. Unlike in crustaceans, the 3rd head segment (=intercalary segment) of hexapods, which is associated with the **tritocerebrum**, lacks appendages. The posterior three segments, associated with the three parts of the suboesophageal ganglion and the mouthparts, are sometimes referred to as **gnathencephalon**. The “**occipital ridge**” was postulated as a border separating the maxillary and labial segments. However, this line often depicted in schematic drawings is either absent or only present as a relatively short dorsolateral furrow, which does *not* delimit a primary “occipital segment”.

Different head regions separated by “**sutures**” can be distinguished in most hexapods (Fig. 1.2.1.1). However, it has to be noted that what is generally addressed as “sutures” comprises two very distinctly different structural modifications of the external cuticle (e.g., Wipfler et al. 2011):

- a) Molting lines (**frontal** and **coronal sutures** [=epicranial lines or sutures]). In the following only these will be addressed as sutures.
- b) Internal strengthening **ridges** (e.g., clypeofrontal “suture”). In the following they will be addressed as ridges or strengthening ridges. They are not lines of fusion or molting lines.

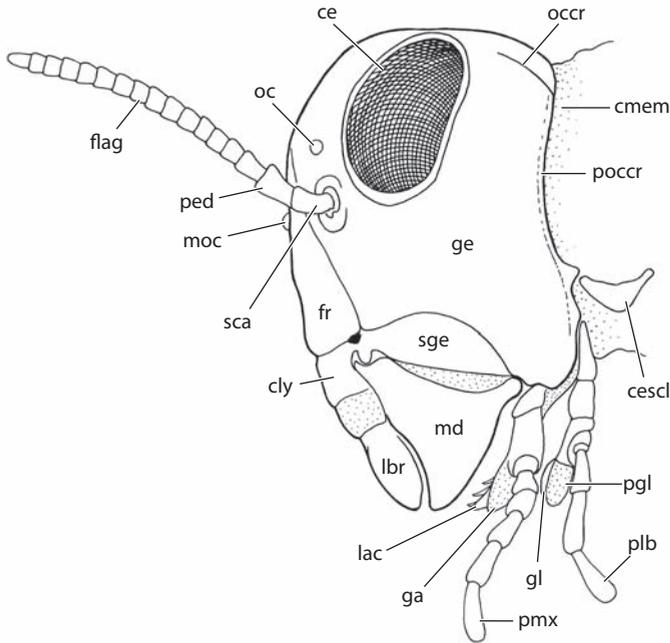


Fig. 1.2.1.1: Generalized hexapod head, lateral view. Abbr.: ce – compound eye, cescl – cervical sclerite, cly – clypeus, cmem – cervical membrane, flag – flagellum, fr – frons, ga – galea, ge – gena, gl – glossa, lac – lacinia, lbr – labrum, md – mandible, moc – median ocellus, oc – ocellus, occr – occipital ridge, ped – pedicellus, pgl – paraglossa, plb – palpus labialis, pmx – palpus maxillaris, poccr – postoccipital ridge, sca – scapus, sge – subgena. Redrawn from v. Kéler (1963).

1.2.2 Head capsule

The head capsule is almost always a rigid, well sclerotized structural unit, equipped with a defined set of appendages (Fig. 1.2.1.1). It is reinforced by strengthening ridges and the endoskeletal **tentorium** (Fig. 1.2.2.1). The shape is varying from more or less globular (e.g., Orthoptera) (Fig. 6.12.1) to strongly flattened and elongated (e.g., Raphidioptera) (Fig. 6.28.1A). It is connected with the prothorax by a more or less wide **cervical membrane**, often reinforced by articular **cervical sclerites**. The posterior head region can be fully exposed (e.g., Zoraptera, Hymenoptera, Diptera) or more or less strongly retracted into the prothorax (e.g., Blattodea, Coleoptera) (Fig. 6.29.1). The **foramen occipitale** can be very narrow (e.g., Diptera), moderately wide (most Coleoptera), or very wide (e.g., Orthoptera). It is usually divided by the **tentorial bridge** into a larger upper part (**alaforamen**) and a smaller lower part (**neuroforamen**), and strengthened by the more or less wide **postoccipital ridge**, which also serves as a muscle attachment area (Fig. 1.2.1.1).

In hexapods with an **orthognathous head** (e.g., Orthoptera, Zoraptera, Hymenoptera) (Figs 6.12.1, 6.13.1, 6.25.1) the mouthparts are ventrally directed, whereas they are anteriorly directed in those with a **prognathous head** (e.g., Grylloblattodea, Raphidioptera) (Fig. 6.14.2). A prognathous head is usually but not always found in predacious hexapods. Subprognathism is an intermediate condition, with a slightly to moderately inclined head. In the **hypognathous head** the mouthparts are posteriorly directed (e.g., Auchenorrhyncha, Sternorrhyncha) (Figs 6.24.1, 6.24.4). Hyperprognathism with dorsally directed mouthparts is an unusual condition occurring in larvae of Hydrophilidae (Coleoptera).

The different head regions usually bear a characteristic vestiture of setae (articulated hairs) (Figs 6.13.2, 6.25.1). The distribution pattern of setae and pores (chaetotaxy) is taxonomically informative in some groups, especially in larvae (e.g., Lepidoptera). The coloration and surface structure of the cuticle can differ strongly in different groups.

The compound eyes (see **1.6 Photoreceptor organs**) are usually well-developed and more or less strongly convex and round, oval or kidney-shaped. In some groups they are small and flat (Fig. 6.14.2) or even largely (e.g., Siphonaptera) or completely reduced (e.g., Protura, Diplura [=Nonoculata]). They are almost always placed laterally. A partial or complete subdivision occurs in few groups (e.g., males of Ephemeroptera, Gyrinidae). In Gyrinidae (Coleoptera) the upper and the lower parts are usually widely separated and differ in their fine structure. The transparent cuticle covering the **ommatidia** is thin, thus representing a zone of mechanical weakness of the head capsule. This is usually compensated for by the presence of a broad internal **circumocular ridge**. **Ocelli** (median eyes) (Fig. 1.6.2.3) are also present in most groups (e.g., Fig. 6.7.1). Three of them are usually arranged in a triangle on the frontal region. They are reduced in different groups (e.g., Dermaptera, Embioptera), often in correlation with flightlessness (e.g., Zoraptera [apterous morphs], Grylloblattodea).

The **frontal** and **coronal** (=epicranial) **sutures** are usually present (Figs 1.2.1.1, 1.2.2.1A). The former enclose a triangular **frons** in most groups (sometimes U-shaped). Both sutures split open during the molting process. The area laterad the coronal suture is referred to as **vertex** and the lateral head region as **gena**. However, both areas are not delimited by a suture or ridge. A lateral area above the lateral mandibular base, the **subgena**, is separated from the genal region by the **subgenal ridge**, which can be divided into an anterior **pleurostomal ridge** above the mandibular base and a posterior **hypostomal ridge**. The posterior part of the subgena, traditionally assigned as **postgena**, is usually not defined as a separate element. The antennal foramen is enclosed by a circumantennal ridge, which often bears a small articular process, the **antennifer**.

The **clypeus** is often trapezoid (Figs 1.2.1.1, 1.2.2.1A). Its broader posterior margin is primarily separated from the frontal region by a transverse **frontoclypeal strengthening ridge** (=frontoclypeal “suture”, epistomal “suture”). The clypeus is sometimes divided into an anterior, transparent **anteclypeus** without muscle attachment, and

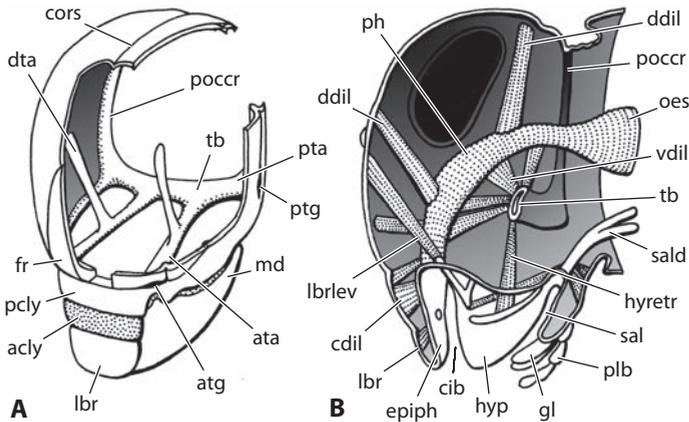


Fig. 1.2.2.1: Generalized hexapod head, internal structures. A, anterolateral view, frontal side of head capsule opened; B, sagittal section, brain and suboesophageal complex removed. Abbr.: ata – anterior tentorial arm, acly – anteclypeus, atg – anterior tentorial groove, cib – cibarium, cdil – cibarial 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*). Courtesy of H. Pohl, redrawn from Weber & Weidner (1974), with modifications.

a posterior sclerotized **postclypeus** (Fig. 1.2.2.1A), which serves as attachment area for epipharyngeal muscles (*M. clypeopalatalis*³). The dorsolateral clypeal margin is marked by the anterior tentorial pits or grooves, which represent the areas of invagination of the anterior tentorial arms.

The foramen occipitale may be narrowed by a sclerotized, unpaired **gula**, especially in prognathous forms (e.g., Coleoptera, Megaloptera, Raphidioptera). The gula is likely formed by a sclerotized ventromedian region of the cervical membrane and is usually distinctly separated from the laterally adjacent parts of the head capsule by internal **gular ridges**. The landmark between the gular region and the posterior labial (submental or postmental) margin is marked by the **posterior tentorial pits** or grooves, the posterior invagination sites of the tentorium, which are generally present in hexapods, with very few exceptions (e.g., Strepsiptera). An alternative partial closure

³ In the following names of Wipfler et al. (2011) are used for cephalic muscles. A muscle table (Table I) with the nomenclature for head muscles is presented at the end of the chapter **1.2 Head**.

of the foramen occipitale can be formed by a **hypostomal** (or **postgenal**) **bridge**, i.e. a mesally projecting duplicature of the posterolateral head capsule (e.g., Hymenoptera partim).

Muscles not associated with movable appendages or the digestive tract are largely or completely absent in hexapods. Exceptions are muscles linking the tentorium with the external wall of the head capsule and muscles associated with the **antennal hearts** (**pulsatile organs**).

1.2.3 Cephalic endoskeleton

The head endoskeleton (Fig. 1.2.2.1) comprises invaginated sclerotized elements and also mesodermal ligamentous structures in the most basal hexapod lineages (e.g., Archaeognatha, *Tricholepidion*). Ridges play an important role as muscle attachment areas and mechanical strengthening elements. The **postoccipital ridge** around the foramen occipitale is often an attachment area for bundles of the mandibular flexor and extensor and also for extrinsic head muscles. The **circumocular ridge** strengthens the zone of weakness resulting from the thin cuticle of the compound eyes and is sometimes an area of origin of bundles of the mandibular extensor. The transverse strengthening ridge separates the clypeus from the frons. Main elements of the tentorium of Insecta are the strongly developed **posterior arms**, which usually arise immediately anterad the foramen occipitale. The invagination sites are the posterior tentorial pits or grooves. The posterior arms are usually connected with each other by the **tentorial bridge** (= **corpotentorium**) and also fused with the **anterior tentorial arms** in Pterygota (connected by muscles in apterygote hexapod lineages). The tentorial bridge of Pterygota (and Maindroniidae [Zygentoma]) is a product of fusion of transverse connecting bars of the anterior and posterior arms, respectively (see **6 The hexapod orders [Dicondylia]**). In some groups an accessory bridge is formed by medially fused internally directed processes, the **laminatentoria**. This feature is sometimes erroneously referred to as “perforated corpotentorium”. It is likely an autapomorphy of Dictyoptera but does also occur in other groups (e.g., some groups of beetles). The **anterior tentorial pits** or grooves are the invagination sites of the anterior arms. They arise at the proximolateral edge of the clypeus, close to the secondary mandibular joint, almost always on the transverse frontoclypeal strengthening ridge (epistomal ridge) or on the subgenal ridge. The **dorsal tentorial arms** originate from the anterior arms (most groups of Polyneoptera) or at the junction area of the posterior and anterior arms. They are not invaginations of the head capsule but usually connected to it by fibrillar structures (fused with the wall of the head capsule in some cases).

In apterygote hexapods the tentorium is held in its position by several muscles that originate on the head capsule. Only one muscle (*M. tentoriofrontalis anterior*) is preserved in lower neopteran insects. Additionally, the posterior arms almost always serve as attachment areas of extrinsic maxillary, labial and hypopharyngeal muscles,

and the corpotentorium as an area of origin of ventral pharyngeal dilators. The dorsal and anterior arms are usually attachment sites of extrinsic antennal muscles, and the latter also of tentorial muscles of the mandibles.

Reductions and simplifications of the tentorium occur, especially but not only in groups with reduced or strongly modified mouthparts (e.g., Strepsiptera, Diptera).

1.2.4 Labrum and epipharynx

The **labrum** (Figs 1.2.1.1, 1.2.2.1, 1.2.4.1), is an unpaired anterior appendage of the head and forms the anterior closure of the **preoral cavity** between the paired mouthparts. It usually covers a considerable part of the mandibles. The preoral cavity or **cibarium** can be defined as the space between the inner labral wall (ventral⁴ **epipharynx**)

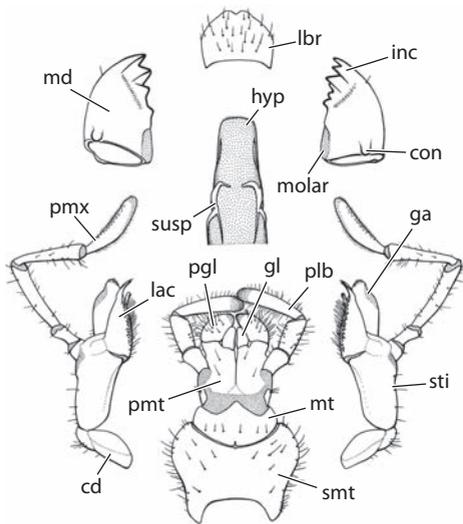


Fig. 1.2.4.1: Mouthparts of a generalized insect (*Periplaneta americana*, Blattodea), labrum (top), mandibles, hypopharynx (center), maxillae, labium (bottom). Abbr.: cd – cardo, con – condyle (primary mandibular joint), ga – galea, gl – glossa, hyp – hypopharynx, inc – mandibular incisivi, lbr – labrum, lac – lacinia, md – mandible, molar – molar region, mt – mentum, pgl – paraglossa, plb – palpus labialis, pmt – prementum, pmx – palpus maxillaris, smt – submentum, sti – stipes, susp – hypopharyngeal suspensorium. Courtesy of H. Pohl.

⁴ The terms referring to directions (e.g., anterior, ventral) apply to an orthognathous head here and in the following. The corresponding terms for a prognathous head are: anterior (orthognathous) = dorsal (prognathous); posterior = ventral; dorsal = posterodorsal; ventral = anterior.

(Figs 1.2.2.1A, 6.18.2B) and the inner surface of the clypeal region (dorsal epipharynx) on one hand, and the **hypopharynx** on the other (see below). A wider preoral space limited by the labrum and labium would also include the **salivarium** (see below). The proximal border of the epipharynx (and cibarium) is the **anatomical mouth**, the anterior opening of the **pharynx**.

The homology of the labrum is disputed. Its insertion below (or anterad in prognathous hexapods) the antennae suggests that it may belong to the first head segment, possibly homologous to the antennae of Onychophora and the “great appendages” of Cambrian fossils (e.g., †Anomalocarida). However, it was pointed out by Denis & Bitsch (1973) that a true preantennal segment (and the “acron”) is not traceable in Hexapoda. Moreover, the innervation from the tritocerebrum and embryological evidence suggest that it may rather belong to the intercalary (= 3rd) segment.

At its base the labrum is usually moveably connected with the ventral clypeal margin by an internal membranous fold. However, it is sometimes immobilized and more or less completely fused with the clypeus (e.g., predacious beetle larvae: Adephaga, Hydrophiloidea, Cleroidea etc.). The product of fusion is called **clypeolabrum** or **frontoclypeolabrum** if the frontoclypeal strengthening ridge is absent. The anterior labral wall is almost always sclerotized and equipped with setae. The ventral (anterior in prognathous insects) and lateral margins are usually rounded. A more or less deep ventromedian emargination is present in different groups (e.g., Orthoptera, Blattodea partim). Sensilla and/or microtrichia are often present along the ventral edge. Basolateral sclerotized rods, the **tormae**, reinforce the epipharynx and their distal part serves as attachment area of the lateral labral retractors (see below).

The inner labral wall, i.e. the ventral epipharynx (Figs 1.2.2.1B, 6.18.2B), is usually largely membranous or semimembranous. It often bears a vestiture of specifically arranged microtrichia (non-articulated hairs), which are usually posteriorly directed, thus facilitating the food transport towards the anatomical mouth. In some groups of insects the lateral margin of the dorsal (clypeal) epipharyngeal part is fused with the lateral margin of the dorsal hypopharynx, thus forming a more or less elongated **prepharyngeal tube**, which is continuous with the pharynx.

M. labroepipharyngalis, which is present in most lineages, connects the anterior and posterior labral wall. Its contraction widens the anterior region of the preoral cavity. Other intrinsic labral muscles can occur in apterygote hexapods, ephemeropterans and in members of Polyneoptera. The labrum is retracted by two pairs of extrinsic muscles in the groundplan of hexapods (reduced in different groups). *M. frontolabralis* (Figs 6.14.3, 6.18.2B) usually originates on the median frontal region and inserts medially on the external labral wall. *M. frontoepipharyngalis* originates laterad the former and inserts on the tormae. Reduction of labral muscles occur in different groups. *M. frontolabralis*, for instance, is always absent in Coleoptera.

In some groups the labrum is strongly modified. In some basal lineages of Diptera (e.g., Culicidae) and in Siphonaptera it forms a part of the piercing-sucking apparatus (Figs 6.35.1, 6.35.2) with a food channel on its ventral (epipharyngeal) side. The

labrum partly covers the labial rostrum in Hemiptera (Figs 6.21.2, 6.24.1, 6.24.4). It is almost always completely reduced in Strepsiptera but still present in the groundplan of the order.

1.2.5 Antennae

The **antennae** are the paired appendages of the 2nd segment and homologous to the 1st antennae (=antennulae) of crustaceans (Figs 6.1.1, 6.1.2, 6.4.1). The antennal nerve originates from the second part of the brain, the **deutocerebrum**. In Collembola and Diplura (and in Myriapoda and crustaceans) muscles are present in all antennomeres (often referred to as antennal segments) except for the apical one. This type of antenna (=“Gliederantenne” in German) belongs to the groundplan of Hexapoda (Figs 6.1.1, 6.3.3) An autapomorphy of Insecta is the antenna of the flagellar type (“Geißelantenne”) (Figs 6.4.1, 6.4.2), with muscles only in the basal antennomere, the **scapus** (Mm. scapopedicellares lateralis and medialis). A chordotonal organ is present in the **pedicellus** (2nd antennomere), which bears a more or less elongated **flagellum** without muscles, which is usually composed of many antennomeres (**flagellomeres**).

The antennae are inserted in the **antennal foramen** (see above), between or above the compound eyes in most groups (Fig. 1.2.1.1). They are almost always movable in all directions and more or less densely covered with setae and different sensilla, mostly chemo- and mechanoreceptors (Figs 4.4.1B, 4.9.1B). The scapus usually articulates with the **antennifer** and is moved by three or four extrinsic antennal muscles in most groups (Mm. tentorioscapales anterior, posterior, lateralis and medialis). The two intrinsic muscles (see above) are attached to the base of the pedicellus and move the remaining part of the antenna. The Johnston’s organ in the pedicellus of Insecta is a complex chordotonal organ composed of numerous scolopidial sensilla. It functions as a mechanoreceptor and registers movements of the flagellum. It also perceives acoustic signals in some groups (e.g., Culicidae, Chironomidae).

The antennae can be modified in many different ways (e.g., Fig. 6.35.4). They are completely absent in Protura (Figs 6.2.1, 6.2.2), largely reduced in larvae of some groups of Holometabola (e.g., Strepsiptera) (Fig. 6.30.1), and shortened and more or less bristle-like in Odonata (Fig. 6.7.1A), Ephemeroptera (Fig. 6.6.2) and Auchenorrhyncha (Fig. 6.21.2). The ancestral type (groundplan of Insecta) is the filiform antenna with a multisegmented, slender flagellum. In moniliform antennae the flagellomeres are more or less globular (e.g., Isoptera, Embioptera partim), whereas they are sawtooth-shaped in the serrate type (e.g., Elateridae [Coleoptera]). The flagellomeres of pectinate antennae bear elongate extensions either on one or on both sides (e.g., different groups of Lepidoptera, Tipulidae [Diptera]). In capitate or clubbed antennae one or several apical segments are symmetrically or asymmetrically widened (e.g., different groups of Lepidoptera and Coleoptera). Genuiculate antennae are hinged or bent (e.g., different groups of Hymenoptera [e.g., ants], Curculionidae [Coleoptera]). In “higher”

dipterans (Cyclorrhapha) the first flagellomere (postpedicellus) is strongly enlarged whereas the remaining flagellum forms a bristle-like **arista** (aristate type) (Fig. 6.35.4).

1.2.6 Mandibles

The **mandibles** are the paired appendages of the 4th head segment (Figs 1.2.1.1, 1.2.4.1) and receive their innervation from the anterior part of the suboesophageal ganglion. They play a dominant role in the mechanical processing of food. Unlike the **maxillae** (Fig. 1.2.4.1) they are primarily a compact, undivided and strongly sclerotized element without appendages. In Dicondylia (Zygentoma + Pterygota) they are connected with the head capsule by a posterior primary mandibular joint (condyle on the mandible) and an anterior secondary joint (condyle at the clypeal base). The movements of the dicondylous mandible are restricted to a single level perpendicular to the axis between these two articulations. The mandible is almost always distinctly curved inwards, especially at its outer margin, and it is usually broadest at its base. One or several apical or subapical teeth (**incisivi**) (Fig. 1.2.4.1) are used to perforate and crush food substrate. Often, especially in hexapods feeding on plant matter or fungi, a mesally directed prominence is present at the mandibular base, the **mola**; usually its surface is modified for efficient grinding, with parallel ridges or densely arranged tubercles. In predacious forms (e.g., Odonata, Mantophasmatodea) the mesal surfaces of the mandibles form distinct cutting edges. An articulated mesal appendage, the **lacinia mobilis** or prosthema, occurs in several groups. It can be sclerotized or largely membranous and is often equipped with microtrichia.

In neopteran insects with well-developed mandibles a pair of antagonistic muscles with a cranial origin move the mandibles, the very large *M. craniomandibularis internus* (flexor=adductor) and the distinctly smaller *M. craniomandibularis externus* (extensor=abductor) (Figs 6.14.3, 6.18.2B). Both insert on strongly developed tendons attached to the mandibular base. In the groundplan of Hexapoda strongly developed muscles arising from the hypopharynx (*M. hypopharyngomandibularis*) or the anterior tentorial arms (*Mm. tentoriomandibulares lateralis superior* and inferior, *Mm. tentoriomandibulares medialis superior* and inferior) are present, and also a transverse muscle medially connected by a ligament (e.g., *Zygentoma*). They insert on the internal surface of the mandible. The hypopharyngeal and tentorial muscles persisting in many pterygote groups are almost always very thin. One of them is usually accompanied by a nerve and functions as a proprioceptor.

Only the primary joint is present in Collembola, Protura and Archaeognatha and both joints are missing in Diplura. Mandibular sucking channels occur in larvae of some groups of beetles (e.g., Dytiscidae, Lampyridae). The mandibles are transformed into stylets in Hemiptera and biting flies (in addition to stylets formed by the laciniae, see below). The mandibles form a sucking apparatus together with the laciniae in neuropteran larvae.

1.2.7 Maxillae

The **maxilla** (Figs 1.2.4.1, 6.14.2, 6.27.3C), which is homologous to the maxillula (1st maxilla) of crustaceans, is usually composed of cardo, stipes, lacinia (=inner endite lobe), galea (=outer endite lobe), and palp. The relatively short **cardo** articulates with the head capsule, usually in a more or less deep maxillary groove (=fossa **maxillaris**). At its base it bears a lateral process for muscle attachment. The articulation point lies between the insertion of the extensor and the flexor, which originate on the lateral head capsule and the posterior tentorial arm, respectively. The **stipes** is connected with the cardo by a hinge. It is usually the largest part of the maxilla and bears the palp and endite lobes. The ventral and lateral sides are sclerotized and divided into a **basistipes** and **mediostipes** in some groups (e.g., Coleoptera). The **lacinia** is usually more or less firmly connected or fused with the stipes mesally. It is sclerotized and apically curved and pointed in most groups, and usually set with strong setae or spines along its mesal edge. In groups with sucking-piercing mouthparts (e.g., Anoplura, Hemiptera, biting flies) the lacinia is transformed into a piercing stylet (Figs 6.35.1, 6.35.2). The **galea** is usually less strongly sclerotized and equipped with chemoreceptors; it is composed of one or two segments. The maxillary **palp** is usually five-segmented and also equipped with chemoreceptive sensilla; its apex often bears a dense field of sensorial structures.

In most groups two extrinsic maxillary muscles originate from the head capsule (*M. craniocardinalis* and *M. craniolacinalis*) and three from the posterior tentorial arms (*M. tentoriocardinalis*, *Mm. tentoriostipitales anterior* and *posterior*). Additional muscles insert on the endite lobes, on the base of the palp, and on the base of the palpomeres.

1.2.8 Labium

The **labium** or lower lip (Figs 1.2.4.1, 6.14.2, 6.27.3C) forms the posterior (orthognathous head) or ventral (prognathous head) closure of the preoral space and of the salivarium. It is homologous to the maxilla (2nd maxilla) of crustaceans, but its proximal parts form a structural unit without a recognizable median line or suture. The proximal **postmentum** primarily forms the posterior closure of the head capsule and is adjacent with the foramen occipitale unless a gula or hypostomal bridge is present; it is often divided into a **mentum** and **submentum** (Fig. 1.2.4.1). The anterior element, the **prementum**, bears the appendages, i.e. the palps and the **para-glossae** and **glossae** (outer and inner endite lobes; serially homologous to the galea and lacinia); it may or may not be incised medially. The labial palp is usually three-segmented but otherwise very similar to the maxillary palp; it is either inserted on a more or less distinct **palpiger** or directly on the distolateral edge of the prementum. The musculature is similar to the muscle equipment of the maxilla. Three pairs of

premental retractors are usually present in Pterygota, one of them originating on the postlabium (*M. submentopraementalis*) and two on the posterior tentorial arms (*Mm. tentoriopraementales inferior* and *superior*). In addition intrinsic premental muscles are associated with the glossae and paraglossae, the palps, and the salivarium. Intrinsic palp muscles are also usually present.

The labium is transformed into a rostrum in Hemiptera (Figs 6.24.1, 6.24.4A). It forms a sheath for the stylet-like mandibles and laciniae. The outer and inner endite lobes of the labium are distinctly reduced or missing in holometabolous insects with the notable exception of Hymenoptera. In bees, the labium forms a complex with the maxillae. Both elements of this maxillolabial complex are connected by a small rod-like sclerite, the **lorum**. The frontally fused, strongly elongated and pubescent glossae serve as uptake apparatus of liquid food.

1.2.9 Hypopharynx

The **hypopharynx** is an unpaired tongue-like structure between the paired mouthparts (Figs 1.2.4.1, 6.18.2B). It is likely a derivative of several segments and not serially homologous to the primarily paired appendages (Denis & Bitsch 1973).

The hypopharynx is usually largely semimembranous, but almost always reinforced by sclerites (Fig. 1.2.4.1: susp). It forms the posterior floor of the cibarium and a ramp for transporting food towards the anatomical mouth (Fig. 6.18.2B). Its anterior surface is often at least partly sclerotized and bears a vestiture of posteriorly directed **spinulae** which facilitate this process (see epipharynx). Between the hypopharynx and the anterior side of the distal part of the labium lies the salivarium, a pocket where the salivary ducts open (see **1.2.10 Salivarium**) (Fig. 6.18.2B). **Superlinguae** are lateral lobes of the hypopharynx (Fig. 6.6.5), flanking the median **lingua**. They are likely a groundplan feature of Hexapoda (present in Collembola, Diplura and Archaeognatha) but they are missing in *Zygentoma* and distinctly reduced or absent in Pterygota (with the exception of Ephemeroptera: Fig. 6.6.5). Reduced superlinguae are usually represented by lateral sclerotizations, the basal sclerites or basal plates, which sometimes extend to the salivarium. They serve as attachment areas of the tentorial retractors of the hypopharynx, *M. tentoriohypopharyngalis*. The **suspensoria** (= **fulturae**) are paired sclerites or groups of sclerites embedded in the proximolateral hypopharyngeal wall (Fig. 1.2.4.1: susp). They form long anterior projections, the oral arms which end laterad the anatomical mouth and serve as attachment area of *M. oralis transversalis*, *M. frontooralis* and *M. tentoriooralis*. The last two muscles were addressed as retractors of the mouth angle by Snodgrass (1935). Their antagonist is *M. craniohypopharyngalis*, a retractor originating from the head capsule (apterygote lineages) or posterior tentorium (Pterygota). The muscle is missing in different groups, especially in correlation with a reduced salivarium (e.g., Coleoptera). Several other muscles linked with the hypopharynx occur in different lineages.

The hypopharynx can be distinctly modified or reduced in different groups of hexapods. It is greatly reduced in size in Hymenoptera and fused with the distal part of the labium in Coleoptera, which consequently lack a salivarium. It forms one of the stylets in basal dipteran groups (e.g., Culicidae). In Hemipterans it is perforated by the canal of the salivary pump and continuous with the food canal of the laciniae.

1.2.10 Salivarium

The **salivarium** is the pocket between the posterior side of the hypopharynx and the anterior (internal) side of the distal part of the labium (Figs 1.2.2.2B, 6.18.2B). It is part of the preoral cavity in the wider sense and receives the openings of the **salivary ducts**. The salivary glands (Fig. 1.2.10.1) are usually well developed and located in the anterior part of the thorax. In some groups they are connected with a large reservoir (Fig. 1.9.2). The salivarium is usually equipped with three pairs of short muscles originating from the hypopharynx (*M. hypopharyngosalivaris*) and the prementum (*M. praementosalivaris* anterior and posterior), respectively. In certain groups a small ring muscle (*M. annularis salivarii*) is present where the salivary duct opens into the salivarium. Reductions of the salivarium (including muscles and glands) occur in different groups, notably in Coleoptera (completely absent) and in Megaloptera (vestigial).

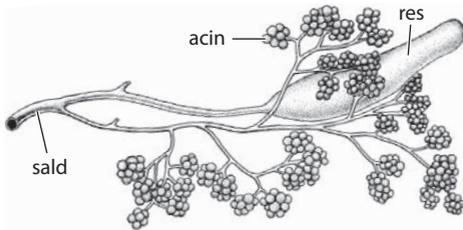


Fig. 1.2.10.1: Salivary gland. Abbr.: acin – acini (berry-like substructure) of salivary gland, res – reservoir, sald – salivary duct. Redrawn from Seifert (1995).

[Snodgrass (1935); Weber (1933, 1938); v. Kéler (1963); Matsuda (1965); Denis & Bitsch (1973); Weber & Weidner (1974); Chapman (1998); Wipfler et al. (2011)]

Table 1: Generalized nomenclature for cephalic muscles (based on Wipfler et al. [2011] and von Kéler [1963], modified). The terms used for the orientation of structures refer to a prognathous head. For orthognathous heads: dorsal = anterior, ventral = posterior, anterior = ventral, posterior = dorsal.

Abbrev. Name	Origin	Insertion
<i>Antennal muscles</i>		
0an1	M. tentorioscapalis anterior	anteriorly on base of scapus
0an2	M. tentorioscapalis posterior	posteriorly on base of scapus
0an3	M. tentorioscapalis lateralis	lateral margin of scapus
0an4	M. tentorioscapalis medialis	mesal margin of scapus
0an5	M. frontopedicellaris	lateral edge of pedicellus
0an6	M. scapopedicellaris lateralis	posteriorly or posterolaterally on base of pedicellus
0an7	M. scapopedicellaris medialis	mesal, anterior or anteromesal base of pedicellus
0an8	M. intraflagellaris	close to tip of flagellum
<i>Antennal heart muscles</i>		
0ah1	M. interampullaris	antennal ampulla of opposite side
0ah2	M. ampulloaortica	cephalic aorta
0ah3	M. ampullopharyngalis	anterior pharynx
0ah4	M. ampullofrontalis	frons
0ah5	M. frontopharyngalis	dorsolaterally on pharynx
0ah6	M. frontofrontalis	opposite side of frons
<i>Labral muscles</i>		
0lb1	M. frontolabralis	posterior labral margin
0lb2	M. frontoepipharyngalis	posterolateral edge of labrum (labro-epipharyngeal border) or tormae
0lb3	M. epistoeipharyngalis	posterolateral edge of labrum (labro-epipharyngeal border)
0lb4	M. labralis transversalis	opposite side of ventrolateral edge of labrum
0lb5	M. labroepipharyngalis	epipharynx
0lb6	M. labrolabralis	medially on apical labral area

<i>Mandibular muscles</i>		
Omd1	M. craniomandibularis internus	Ventral, posterior, lateral and/or dorsal parts of the head capsule and/or posterior and anterior tentorial arms adductor (mesal) tendon of mandible
Omd2	M. craniomandibularis externus anterior	base of mandible (behind anterior mandibular articulation)
Omd3	M. craniomandibularis externus posterior	abductor (lateral) tendon of mandible
Omd4	M. hypopharyngomandibularis	dorsolateral area of mandible (inside of mandible)
Omd5	M. tentoriomandibularis lateralis superior	laterally on mandibular base (between processus paratentorialis and posterior mandibular articulation)
Omd6	M. tentoriomandibularis lateralis inferior	ventrally on mandibular rim (inside of mandible)
Omd7	M. tentoriomandibularis medialis superior	dorsomesal area of mandible (inside of mandible)
Omd8	M. tentoriomandibularis medialis inferior	dorsal part of mandibular base (inside of mandible)
<i>Maxillary muscles</i>		
Omx1	M. craniocardinalis	proximal part of cardo (cardinal process)
Omx2	M. craniolacinalis	proximal edge of lacinia
Omx3	M. tentoriocardinalis	distal part of cardo (close to stipitocardinal suture)
Omx4	M. tentoriotipitalis anterior	stipital ridge
Omx5	M. tentoriotipitalis posterior	proximal rim of stipes (close to stipito-cardinal sulcus)
Omx6	M. stipitolacinalis	base of lacinia (in some cases common tendon with Omx4)
Omx7	M. stipitogalealis	base of galea
Omx8	M. stipitopalpalis externus	laterally on base of first maxillary palpomere
Omx9	M. stipitopalpalis medialis	posteriorly on base of first maxillary palpomere
Omx10	M. stipitopalpalis internus	mesally on base of first maxillary palpomere

Abbrev. Name	Origin	Insertion
Omx11	M. stiptitalis transversalis	stiptital ridge
Omx12	M. palpopalpalis maxillae primus	laterally on base of second maxillary palpomere
Omx13	M. palpopalpalis maxillae secundus	mesally on base of third maxillary palpomere
Omx14	M. palpopalpalis maxillae tertius	mesally on base of fourth maxillary palpomere
Omx15	M. palpopalpalis maxillae quartus	mesally on base of fifth maxillary palpomere
<i>Labial muscles</i>		
Ola1	M. postoccipitoglossalis medialis	glossa
Ola2	M. postoccipitoglossalis lateralis	dorsolaterally on base of glossa
Ola3	M. postoccipitoparaglossalis	base of paraglossa
Ola4	M. postoccipitopraementalis	posterolateral corner of prementum
Ola5	M. tentoriopraementalis	proximal rim of prementum
Ola6	M. tentorioparaglossalis	paraglossae (close to base of labial palp)
Ola7	M. tentorioglandularis	labial gland
Ola8	M. submentopraementalis	medially on proximal premental margin or distal part (close to galea)
Ola9	M. postmentomembranus	internal (ventral) membrane of labium
Ola10	M. submentomentalis	mentum
Ola11	M. praementoparaglossalis	proximolaterally on paraglossa
Ola12	M. praementoglossalis	mesal wall of glossa
Ola13	M. praementopalpalis internus	mesally on first palpomere
Ola14	M. praementopalpalis externus	laterally on first palpomere
Ola15	M. praementomembranus	internal (ventral) membrane of labium
Ola16	M. palpopalpalis labii primus	mesally on base of second labial palpomere
Ola17	M. palpopalpalis labii secundus	mesally on base of third labial palpomere

<i>Hypopharyngeal muscles</i>		
0hy1	M. frontooralis	oral arm of suspensorial sclerite
0hy2	M. tentoriooralis	oral arm of suspensorial sclerite
0hy3	M. craniohypopharyngalis	suprasalivariar sclerite
0hy4	M. postoccipitalohypopharyngalis	hypopharyngeal phragma
0hy5	M. tentoriosuspensorialis	hypopharyngeal suspensorial sclerite
0hy6	M. postmentoloralis	loral arm of suspensorial sclerite
0hy7	M. praementosalivariarialis anterior	laterally on salivarium
0hy8	M. praementosalivariarialis posterior	laterally on salivarium
0hy9	M. oralis transversalis	oral arm of suspensorial sclerite of opposite side
0hy10	M. loroloralis	oral arm of suspensorial sclerite of opposite side
0hy11	M. lorosalivariarialis	suprasalivariar sclerite
0hy12	M. hypopharyngosalivariarialis	salivary orifice
0hy13	M. annularis salivarii	ring muscle close to salivary orifice
<i>Tentorial muscles</i>		
0te1	M. tentoriofrontalis posterior	frons
0te2	M. tentoriofrontalis anterior	frons
0te3	M. tentoriofrontalis dorsalis	frons
0te4	M. posterotentorialis	external rim of tentorium
0te5	M. tentoriotentorialis longus	mesally on posterior tentorial part
0te6	M. tentoriotentorialis brevis	posterior part of tentorium
<i>Cibarial muscles</i>		
0ci1	M. clypeopalatalis	roof of cibarium
<i>Buccal muscles</i>		
0bu1	M. clypeobuccalis	roof of bucca (between anatomical mouth and frontal ganglion)
0bu2	M. frontobuccalis anterior	dorsal wall of bucca (directly behind frontal ganglion)
0bu3	M. frontobuccalis posterior	dorsal wall of bucca (directly in front of brain)

Abbrev.	Name	Origin	Insertion
Obu4	M. tentoriobuccalis lateralis	dorsal tentorial arm	lateral wall of bucca
Obu5	M. tentoriobuccalis anterior	anterior tentorial arm or corporotentorium	ventral wall of bucca (directly behind anatomical mouth)
Obu6	M. tentoriobuccalis posterior	posterior tentorial arm or corporotentorium	ventral wall of bucca (directly in front of brain, ventrally of Obu3)
Pharyngeal muscles			
Oph1	M. verticopharyngalis	vertex or occipitale	dorsally on postcerebral pharynx (directly posterad of brain)
Oph2	M. tentoriopharyngalis	posterior tentorial arm	ventrally on postcerebral pharynx (beneath Oph1)
Oph3	M. postoccipitopharyngalis	postocciput (close to median line)	posterior pharynx
Stomodaeal muscles			
Ost1	M. annularis stomadaei		ring muscle layer covering pharynx
Ost2	M. longitudinalis stomadaei		longitudinal muscles along pharynx

1.3 Thorax

1.3.1 Segmentation and composition of segments

The presence of a **thorax** composed of three clearly defined segments is arguably the most important autapomorphy of Hexapoda. It is usually the second largest tagma of the body and structures related to locomotion are concentrated in this region. On each of the three segments a pair of legs is inserted ventrolaterally. Two pairs of wings with a dorsolateral articulation area are present in most lineages of Pterygota (groundplan autapomorphy). The three segments are more or less similar and relatively simple in the apterygote lineages. In pterygote insects the **mesothorax** and **metathorax** (together forming the **pterothorax**) are strongly modified and much more complex than the **prothorax**, especially on the dorsal side (tergal region) and dorsolaterally (wing base).

All three segments are composed of dorsal, lateral and ventral elements, the **tergum**, **pleuron** and **sternum** (Figs 1.3.3.1, 6.13.3, 6.18.3). The individual regions of sclerotized cuticle (**tergites**, **pleurites** and **sternites**) are connected by membranes and semimembranous areas. The membranous areas are exposed to varying degrees in almost all groups (Fig. 6.13.3), especially on the ventral side (not in Coleoptera [Figs 6.29.4, 6.29.5] and some groups of Heteroptera). The unsclerotized regions ensure the necessary flexibility within the segments, especially at the articulation areas of the locomotor organs. The three segments are connected by intersegmental membranes, which are often more or less concealed. On the dorsal and ventral side the membranous connection does not correspond with the true segmental border (see below). Laterally the thoracic **spiracles** are embedded in the intersegmental membranes (Fig. 1.3.3.1A), in most groups two pairs belonging to the meso- and metathorax, each pair located in front of the respective segment. Thoracic spiracles are usually larger than their abdominal equivalents, which are serially homologous. The two pterothoracic segments often form a more or less rigid functional unit, whereas the flexibility between the pro- and mesothorax is usually relatively high. Posteriorly the metathorax is broadly connected with the abdomen in most groups. Different types of fusion of metathoracic and abdominal elements occur in various groups (e.g., Hymenoptera).

The prothoracic tergum or **pronotum** is usually a simple, plate-like structure, whereas the dorsal and dorsolateral regions of the pterothorax of pterygote insects are modified in a complex way in correlation with the flight function (see **1.3.3 pterothoracic segments**) (Figs 1.3.3.1, 6.13.3). Dorsolateral tergal duplicatures (**paranota**, **laterotergites**) probably belong to the groundplan of Insecta (preserved in the original form in Archaeognatha and Zygentoma). They are possibly precursors of the meso- and metathoracic wings of Pterygota. The lateral sclerotized element of the thoracic segments, the **pleurite**, is located between the tergum and sternum. It is possibly formed by the subcoxa, an element supposedly separating from the coxal primordium

in the embryonic development (Matsuda 1970), but this interpretation is uncertain. It is divided by a slanted dorsoventral **pleural ridge**, which is always present in the meso- and metathorax, but often reduced or absent in the prothorax (Figs 1.3.3.1A, 6.13.3). It stabilizes the lateral body wall and divides it in the anterior **episternum** and the posterior **epimeron**. It is also important in the functional context of the articulations of the coxae and wings. It connects the pleural wing joint with the pleurocoxal joint, the latter generally formed by a condyle at the posteroventral edge of the ridge and a corresponding coxal concavity. An additional coxal articulation is formed by the triangular anteroventral **trochantin** (Figs 1.3.3.1A, 6.13.3A), an additional pleural element below the episternum (small and crescent-shaped, reduced in some groups of Holometabola). The sternal region usually contains more extensive unsclerotized areas than the lateral and dorsal walls of the segments (Figs 1.3.3.1C, 6.13.3B). However, it is almost always reinforced by several sternites. A series of five elements is arguably present in the groundplan of Hexapoda, the short anterior **presternum**, the extensive **basisternum**, the **furcasternum** (or **sternellum**), the **spinasternum**, and the posterior **poststernite** (Matsuda 1970). In Pterygota, the presternum is almost generally absent (possibly represented by isolated sclerites in Plecoptera) and the spinasternum is reduced to varying degrees in many lineages. In Holometabola the true sternal elements are largely invaginated, mostly represented by an internal median longitudinal ridge (**discrimen**), and externally largely replaced by pleural elements (**preepisternum**, **katepisternum**).

More or less extensive ligamentous endoskeletal elements occur in the apterygote lineages. They are of subepidermal origin, usually branched, and serve as insertion points of muscles and tendons (Matsuda 1970). These structures are completely absent in most groups of Pterygota, at least in the adult stage. The pterygote endoskeletal elements are the **furcae** and the smaller **spinae** (Fig. 1.3.3.1D). The former arise from the furcasternum. Primarily their invagination sites are distinctly separated and connected by a transverse ridge, the **sternocosta**. In correlation with a narrowed or invaginated sternum (Holometabola) the furcal bases can be more or less closely adjacent or even arising from a common invagination site. The dorsolaterally extending furcal arms are often fused to the pleural ridge or connected with it by short muscles or fibrillae. They serve as muscle attachment area, especially for muscles attached to basal elements of the legs, the coxa and the trochanter, but also for the ventral intersegmental muscles. The spina is an unpaired invagination of the spinasternum and serves as attachment area of coxal and intersegmental muscles. It is partly or completely reduced in many groups, especially in the metathorax (distinctly developed in Grylloblattodea).

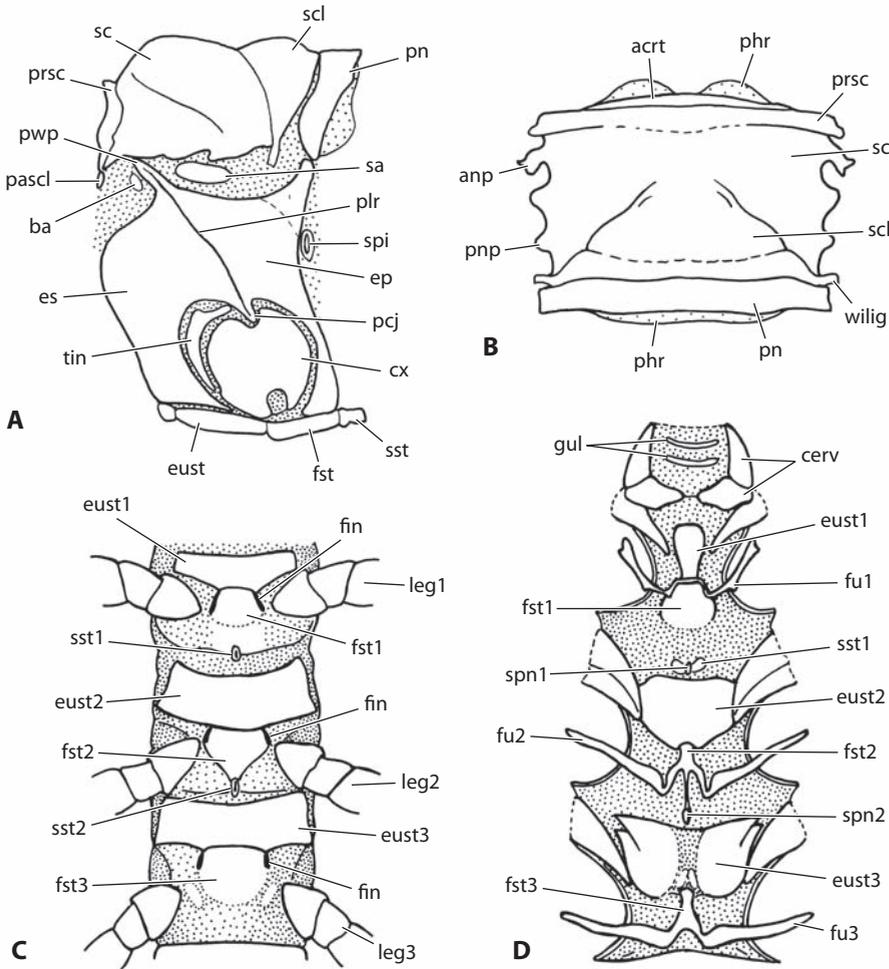


Fig. 1.3.3.1: Thoracic skeleton. A, pterothoracic segment, lateral view, schematized; B, pterothoracic tergal region, schematized; C, sternal region, ventral view *Isoperla* sp. (Plecoptera, Perlodidae); D, sternal region, internal view, *Periplaneta americana* (Blattodea, Blattidae). Abbr.: acrt – acrotergite, anp – anterior notal wing process, ba – basalare, cerv – cervical sclerite, cx – coxa, ep – epimeron, es – episternum, eust1–3 – pro-, meso-, metathoracic eusternum, fin – furcal invagination site, fst1–3 – pro-, meso-, metathoracic furcasternum (sternellum), fu1–3 – pro-/ meso-/ metafurca, gul – gularia, leg1–3 – fore-/ mid-/ hindleg, pascl – prealar sclerite, pcj – pleurocoxal joint, phr – phragma, plr – pleural ridge, pn – postnotum, pnp – posterior notal wing process, prsc – prescutum, pwp – pleural wing process, sa – subalare, sc – scutum, scl – scutellum, spi – spiracle, spn1/2 – pro-/ mesospina, sst1/2 – pro-, mesothoracic spinasternum, tin – trochantin, wilig – wing ligament. Redrawn from Seifert (1995).

1.3.2 Prothorax

The prothorax is anteriorly connected with the head by the cervical membrane, usually with embedded **cervical sclerites** (Figs 1.3.3.1D, 6.13.3A) forming articulations and serving as muscle attachment areas. One or two pairs of lateral cervical sclerites (**laterocervicalia**) are present in most groups. Unpaired ventral sclerites occurring occasionally are called **gularia**. Unpaired dorsal sclerites occur in several groups (e.g., Zoraptera, Coleoptera [Hydrophilidae]). Paired dorsal cervical sclerites are present in Dermaptera.

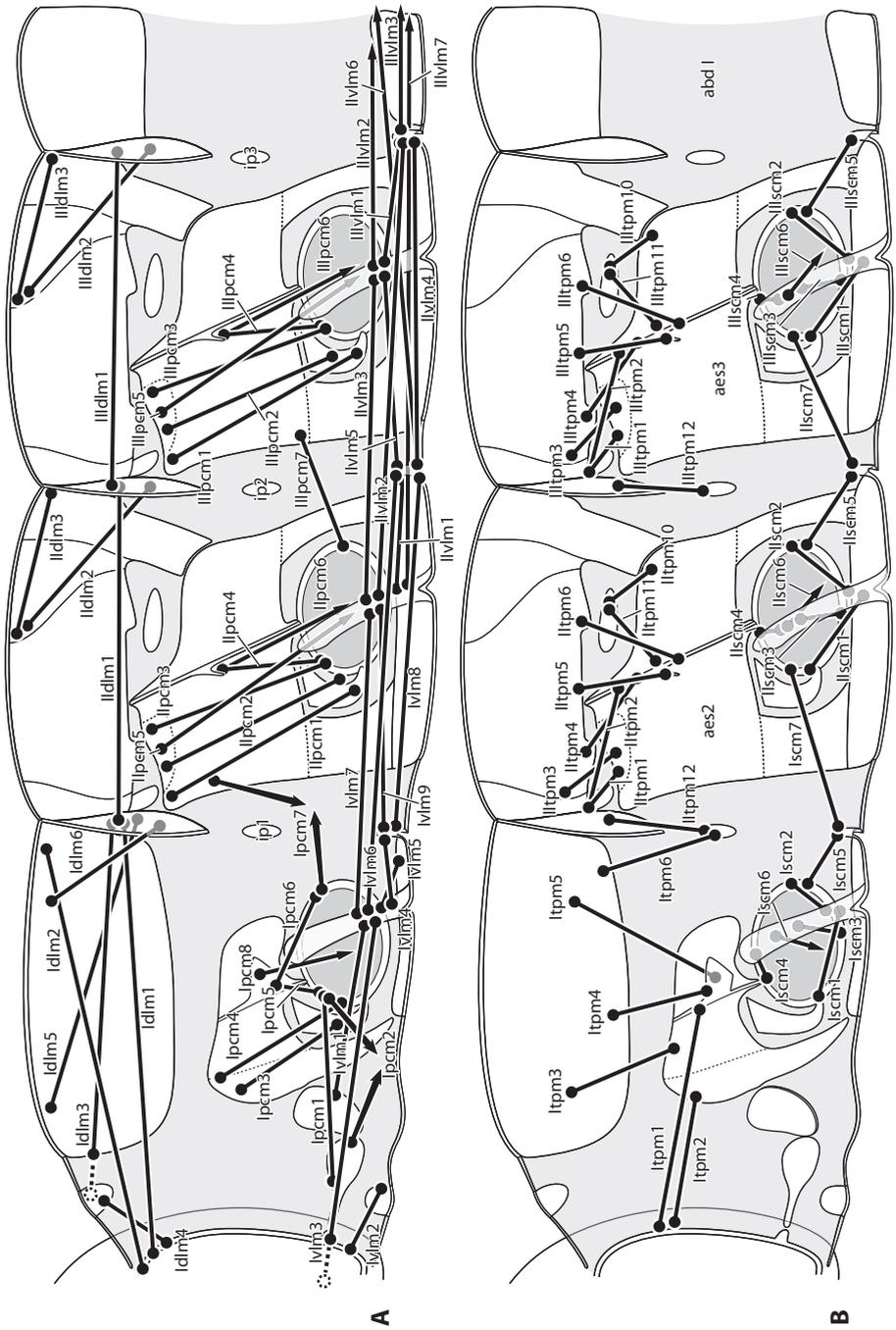
The pronotum is often divided by a median line or zone of weakness (ecdysial line in immatures) but otherwise forms a single, more or less plate-like structure, with or without a distinct lateral edge. It mainly serves as attachment area of large dorsoventral leg muscles and some of the extrinsic muscles of the head. The size of the pronotum varies greatly. It forms a conspicuous pronotal shield in Blattodea, Coleoptera and some other groups. In orthopterans it is saddle shaped and laterally covers extensive parts of the pleuron. Anteriorly the pronotum covers the posterior margin of the head in many groups. Posteriorly it often overlaps with the anterior region of the mesotergum. Distinctly developed lateral duplicatures are present in the primarily wingless Archaeognatha and Zygentoma (see above: paranota). Prothoracic winglets were present in some Paleozoic insects (e.g., †Palaeodictyoptera) but absent in all extant pterygote lineages. The prothoracic pleuron is generally less complex than the corresponding regions of the pterothoracic segments. All modifications or structures related to flight are lacking (e.g., **basalare** and **subalare**) (Fig. 6.13.3A). The pleural suture is often short, indistinct or lacking. In some groups more or less extensive propleural parts are invaginated below the pronotum, thus forming a **cryptopleuron** (e.g., Coleoptera, especially Polyphaga). Compared to the tergal and pleural elements, the prosternum differs less profoundly from its pterothoracic counterparts, as it is not directly connected to the flight organs. Modifications occur in different groups, for instance in relation with hypognathous heads or raptorial forelegs. The prosternum is often reduced in width in Holometabola but is broad in Megaloptera and Raphidioptera.

The prothoracic musculature differs distinctly from the pterothoracic muscle systems (Figs 1.3.3.2, 1.3.3.3, 6.13.4, see also **Table II**). A complex array of extrinsic head muscles (**cervical muscles, muscoli cranii**) is always present, whereas muscles related to the flight apparatus are absent for obvious reasons. The leg muscles are similar to those of the pterothorax (see below). The cervical muscles (Fig. 6.13.4; Matsuda 1970: fig. 19, 22; Friedrich & Beutel 2008) form a complex system of dorsal and ventral longitudinal retractors and of oblique muscles, thus guaranteeing the movability of the head in all directions (Figs 1.3.3.2, 1.3.3.3C). They originate on the prothoracic **phragma**, different regions of the pronotum, the propleuron, the prosternum, and the profurca. They insert on the cervical sclerites, the tentorium and on different regions of the posterior head capsule, especially on the postoccipital ridge.

1.3.3 Pterothoracic segments

The meso- and metathorax are largely unmodified and similar to the prothorax in the apterygote lineages (e.g., Fig. 6.1.1). Far-reaching modifications have resulted from the acquisition of wings and functions related to flight, especially of the tergal and pleural elements (Figs 1.3.3.1–1.3.3.3, 6.13.3, 6.13.4).

The meso- and metaterga of pterygote insects are complex and specifically subdivided structures (Fig. 1.3.3.1B). The main division is into the large anterior **notum** and the transverse posterior **postnotum**. The notum is primarily subdivided into the short **prescutum**, the extensive **scutum**, and a **scutellum**, which is usually triangular. The part of the notum connected with the wing base is called the **alinotum**. In apterygote hexapods an **acrotergite** is separated from the prescutum by the **antecosta**, an intersegmental furrow. The acrotergite and antecosta are equivalent with the postnotum of the preceding segment of Pterygota. The antecosta (or internal part of the postnotum) forms a **phragma** for attachment of the dorsal intersegmental muscles. In most groups of Pterygota it is an extensive attachment site of large dorsal indirect flight muscles and plays an important role in the flight apparatus. The transverse prescutum is strongly narrowed in some groups. Laterally it forms the **prealar** (or **prealar sclerite**), an attachment area of short direct flight muscles. In some groups a process of the prescutum is bent downwards and linked with the episternum, thus forming a **prealar bridge**. The scutum is the largest element of the notum and the area of origin of large dorsoventral and oblique indirect flight muscles, and also of muscles attached to the basal elements of the leg. Some smaller muscles associated with the flight apparatus originate from its lateral regions. Laterally the scutum bears the anterior, the postmedian and the posterior **wing processes** (=alar processes), and occasionally also an anteromedian process. These small projections, usually more or less triangular in shape, are directly connected with the wing base and interact with its **axillary sclerites** (see 1.3.6 Wings) (Fig. 1.3.3.1A, B). The scutal surface is subdivided into different regions partly corresponding with the sites of origin of the large dorsoventral muscles. The separating lines are frequently addressed as sutures (e.g., Matsuda 1970), but are in fact ridges locally increasing the rigidity of the sclerite. They also play a role in the context of the specific deformations resulting from alternating contractions of dorsal longitudinal and dorsoventral indirect flight muscles. A short anterolateral scutal line separates the area bearing the anterior alar process (occasionally also an additional anteromedian process) from the main scutal region. In a similar way, the oblique posterolateral scutal line delimits the area bearing the posterior alar process. The transverse transscutal line between the posterior margins of the anterior (or anteromedian) alar process divides the scutum in an anterior and a posterior half. Additional scutal lines can occur, such as the oblique notaulix on the anterior alinotum, or the more or less parallel-sided longitudinal “suturae parapsidiales” (Matsuda 1970). The anteromedially sinuate scutoscutellar line separates the scutum from the scutellum. Laterally it reaches the **axillary ligament** (Fig. 1.3.3.1A,



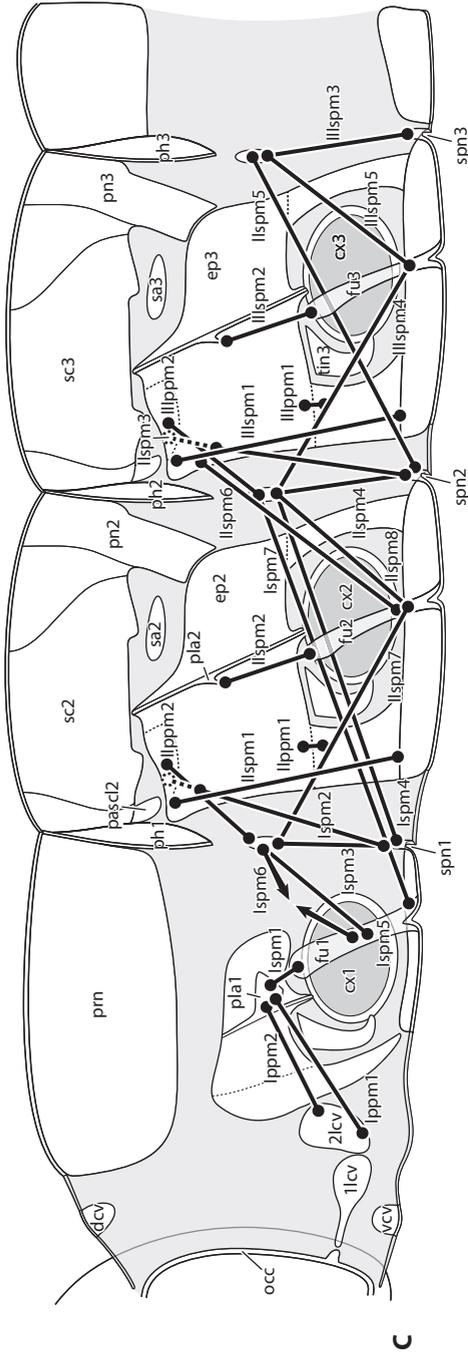


Fig. 1.3.2: Schematic drawings of thoracic muscle system. A, dorsal longitudinal (dlm), pleuro-coxal (pcm) and ventral longitudinal muscles; B, tergo-pleural (tpm) and sterno-coxal muscles (scm); C, pleuro-pleural (ppm) and sterno-pleural muscles (spm). Abbr.: 1/2lcv – 1st/2nd lateral cervical sclerite, abdl – abdominal segment I, aes2/3 – mes-/metanepisternum, cx1/2/3 – pro-/meso-/metacoxa, dcv – dorsal cervical sclerite, ep2/3 – mes-/metepimeron, fu1–3 – pro-, meso-, metafurca, ip1/2/3 – pro-/meso-/metathoracic interpleurite, occ – occipitale, pascl – prealar sclerite, ph1/2/3 – pro-/meso-/metaphragma, pla1/2 – pro-/mesothoracic pleural arm, pn2/3 – meso-/metapostnotum, prn – pronotum, sa2/3 – meso-/metathoracic subalare, sc2/3 – meso-/metascutum, spn1/2 – pro-/meso-/metaspina, tin3 – metatrochantin, vcv – ventral cervical sclerite. See Table II (end of 1.3) for detailed description of muscles. From Friedrich & Beutel (2008), modified.

B) which is continuous with the posterior margin of the wing base. The posteriormost part of the tergum is the postnotum (see above: antecosta and acrotergite). Similar to the prescutum it is bent downwards in some groups and connected with the epimeron, thus forming a **postalar bridge**.

The membranous region below the wing base is ventrally adjacent with the upper edge of the pleuron. The **epipleurites**, the anterior **basalare** and the posterior **subalare**, are embedded in this membrane (Figs 1.3.3.1A, 6.13.3A). They are likely small isolated elements of the anepisternum and epimeron, respectively (see below). Both are important attachment sites of direct flight muscles. The basalare is usually a small external sclerotisation connected with an extensive interior muscle disc by a tendon, whereas the subalare is a relatively extensive sclerotisation exposed at the surface of the membrane. In winged insects, the pleuron is always composed of an anterior episternum and a posterior epimeron. Both sclerites are separated by a very distinct oblique external line corresponding with the more or less extensive internal pleural ridge between the anterodorsal pleural wing joint and the posteroventral pleurocoxal articulation (see above and **1.3.4 Legs**). Its anterodorsal apex forms the **fulcrum** or **pleural wing process** in all winged insects. It articulates with the second axillary sclerite and plays a crucial role in the flight apparatus. An internal process of the pleural ridge is the pleural arm. It is almost always connected with the furcal arms by a muscle. The ventral end of the pleural ridge forms a ventromedially directed lower pleural arm in some groups (e.g., Orthoptera, Antliophora). The episternum is divided into several regions (Fig. 6.13.3A). The dorsal **anepisternum** is separated from the ventral **preepisternum** by the **anapleural cleft**. The paracoxal suture separates the katepisternum from the preepisternum. The relatively narrow **katepisternum** is adjacent with the **trochantin** and the coxa. The small, crescent-shaped trochantin articulates with the coxal base anterior to the pleurocoxal joint. The epimeron is usually undivided. In some groups a fairly indistinct horizontal suture incompletely divides the sclerite into a dorsal and a ventral part, the **anepimeron** and the **katepimeron** (Matsuda 1970). The meso- and metathoracic spiracles are usually embedded in the intersegmental membrane in front of the respective segment.

As pointed out above, the meso- and metasternal structures are primarily more or less similar to the corresponding elements of the prothorax (apterygotes and basal pterygote lineages) (e.g., Matsuda 1970: fig. 35). In most pterygote insects the entire sternal region is more extensive and often also the individual sternites (Figs 1.3.3.1C, D, 6.13.3B). The furcae (**mesendosternite**, **metendosternite**) are often extensive and stabilized by their lateral connection with the pleural arms (see above). The spina is often reduced in the mesothorax and almost always missing in the metathorax. Far-reaching modifications occur in acercarian lineages and a far-reaching internalization of the true sternal elements (**endosterny**) is an autapomorphy of Holometabola. The ventral body wall is then largely formed by the pleural preepisternum.

The pterothoracic muscle system is more complex than that of the prothorax (Figs 1.3.3.2, 1.3.3.3; see also **Table II**), except for the absence of extrinsic head muscles (cer-

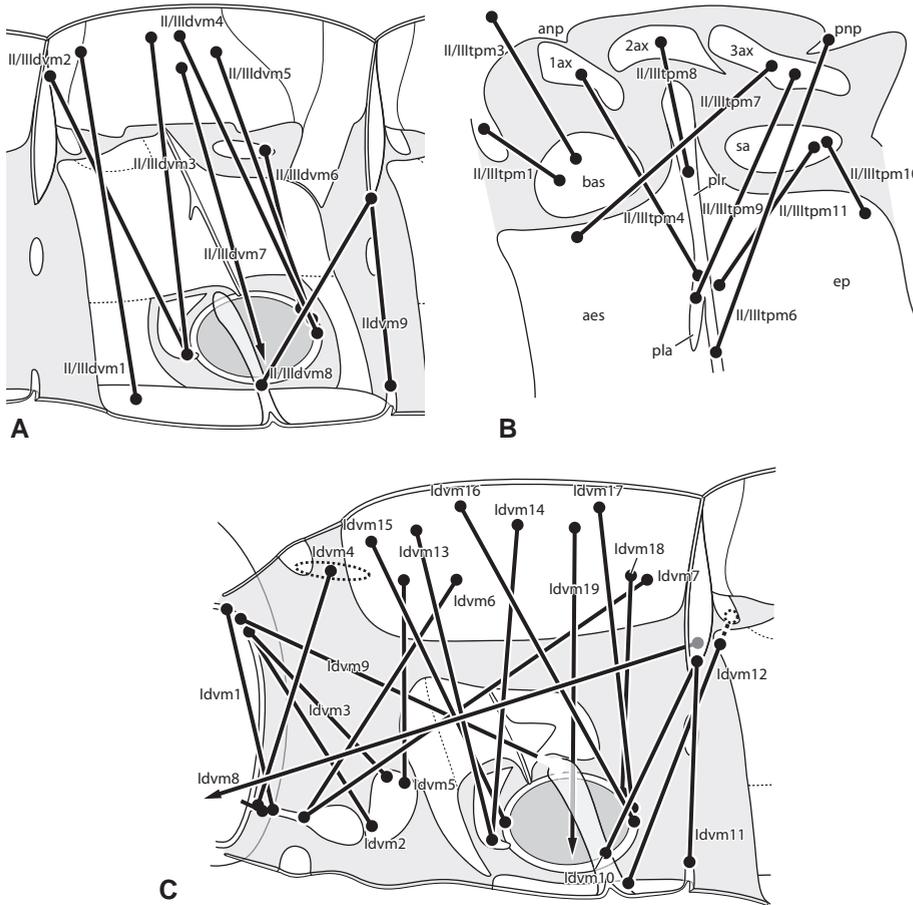


Fig. 1.3.3.3: Schematic drawings of thoracic muscle system. A, dorso-ventral muscles (dvm) of a pterothoracic segment; B, tergo-pleural wing base muscles (tpm); C, dorso-ventral muscles (dvm) of prothorax. Abbr.: 1/2/3ax – 1st / 2nd / 3rd axillary sclerite, aes – anepisternum anp – anterior notal process, bas – basalare, ep – epimeron, pla – pleural ridge, plr – pleural ridge, pnp – posterior notal process, sa – subalare. See Table II (end of 1.3) for detailed description of muscles. From Friedrich & Beutel (2008), modified.

vical muscles). Ventral longitudinal muscles are present and the full sets of extrinsic and intrinsic leg muscles (Fig. 1.3.3.2). Additional muscles are related to the flight apparatus. Direct flight muscles insert on sclerites at the wing base (Fig. 1.3.3.3B). Their function is the fine adjustment during flight. Other muscles already present in the hexapod groundplan (dorsal longitudinal muscles, noto-sternal muscles, noto-coxal muscles) play an important role as indirect flight muscles (Figs 1.3.3.2, 1.3.3.3A, 1.3.3.4) in almost all pterygote groups (not in Odonata). The dorsal longitudinal muscles and dorsoventral muscles alternatively deform the pterothoracic tergites.

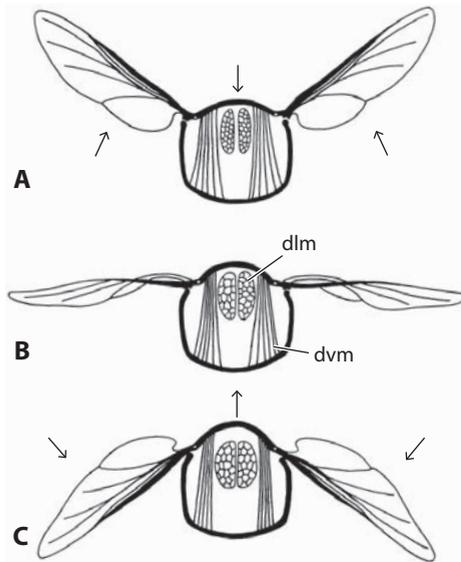


Fig. 1.3.3.4: Indirect flight muscle system. A, upstroke; B, intermediate position; C, downstroke.
 Abbr.: dlm – dorsal longitudinal muscles, dvm – dorsoventral muscles. Redrawn from Seifert (1995).

The resulting vibrations of the segments cause a rapid sequence of upstrokes and downstrokes of the wings (Fig. 1.3.3.4). Some muscles have alternative double functions, either as part of the flight apparatus or as leg muscles involved in the locomotion on the ground (e.g., *M. notocoxalis*, *M. nototrochanteralis*, *M. coxabasalaris*).

1.3.4 Legs

Three pairs of legs are present in the groundplan of Hexapoda. Reductions occur in very few specialized groups, for instance in parasitic females of Strepsiptera (Fig. 6.30.2) and semi-sessile females of Coccoidea. Different degrees of reduction occur in larvae of some holometabolan lineages (e.g., Mecoptera, Curculionidae [Coleoptera]), and the larval thoracic legs are completely absent in Diptera and Siphonaptera (Figs 6.34.4, 6.35.9, 6.35.10). Various kinds of abdominal appendages occur, especially in the apterygote lineages, but they are always distinctly modified and never function like thoracic walking legs. Secondarily evolved **abdominal prolegs** of holometabolan larvae may be involved in locomotion to a certain degree (e.g., symphytan larvae, lepidopteran caterpillars) (see **1.4 Abdomen**).

The uniramous thoracic legs of Hexapoda (Fig. 1.3.4.1) are likely derived from a biramous **arthropodium**, which is a groundplan autapomorphy of Euarthropoda