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INSECT MORPHOLOGY AND PHYLOGENY

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Insect Morphology and Phylogeny

A textbook for students of entomology

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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.

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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 m^3 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.

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Frank Friedrich
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Contents

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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

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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).

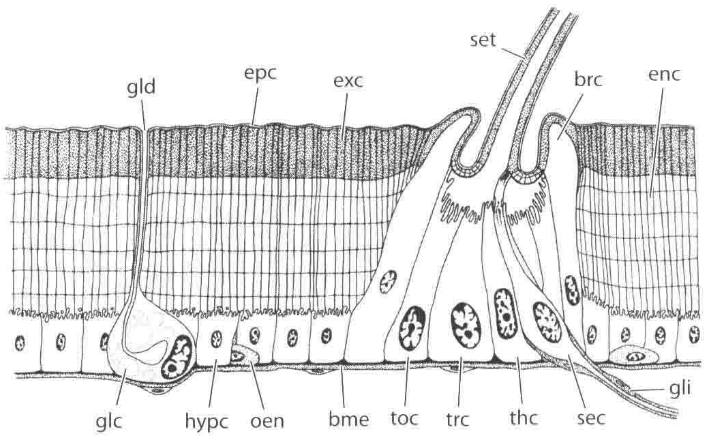

Fig. 1.1.1.1: Integument. Abbr.: bme – basement membrane, brc – basal ring cell, enc – endocuticle, epc – epicuticle, exc – exocuticle, glc – gland cell, gli – glia cell, hypc – hypodermal cell, oen – oenocyte, set – seta, sec – sensory cell, thc – thecogen cell, toc – tormogen cell, trc – trichogen 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 [dustywings]). 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 fuchsine (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 mm^2. 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

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