IMMS' GENERAL TEXTBOOK OF ENTOMOLOGY

TENTH EDITION

Volume 1: Structure, Physiology and Development

O. W. RICHARDS

and

R. G. DAVIES

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PREFACE TO THE TENTH EDITION

In the twenty years that have elapsed since our last complete revision of this textbook, entomology has developed greatly, both in extent and depth. There are now over 8000 publications on the subject each year (excluding the applied literature) and the difficulty of incorporating even a fraction of the more important new results has occupied us considerably. We have nevertheless retained the original plan of the book, especially as it has the merit of familiarity for many readers, but we have made a number of appreciable changes in the text as well as innumerable smaller alterations. We have decided, with some reluctance, to dispense with the keys to families that were formerly given for most of the orders of insects. These are increasingly difficult to construct because specialists tend to recognize ever larger numbers of families, often based on regional revisions and therefore applicable with difficulty, if at all, to the world fauna. Our revision of the text has also entailed extensive changes in the bibliographies, which have been brought more or less up to date. In doing this we have had to be rigorously selective and we have tended to give some emphasis to review articles or recent papers at the expense of older works. We recognize that this has sometimes done less than justice to the contributions of earlier authorities, but the immense volume of literature left little alternative and we apologize to those who feel our choice of references has sometimes been almost arbitrary.

Every chapter has been revised in detail, many of them include new sections, and some have been extensively rewritten. In a few groups such as the Plecoptera and Heteroptera the higher classification has been recast; more often we have made smaller amendments in the number and arrangement of families so as to bring the scheme into broad but conservative agreement with modern views. The general chapters now include some information on ultrastructure and we have retained and tried to modernize the physiological sections; as non-specialists in this field we owe a great debt to the textbooks of Wigglesworth and of Rockstein. Inevitably the book has grown in size with the development of the subject. It may, indeed, be argued that the day of the general textbook has passed and that it must be replaced by a series of special monographs. We believe, however, that there are some advantages in a more unified viewpoint and it is our hope that the new balance we have reached between the various aspects of entomology will seem as appropriate now as the original balance was when Dr A. D. Imms' textbook was first published over fifty years ago.

There are 35 new figures, all based on published illustrations, the sources of which are acknowledged in the captions. We are grateful to the authors concerned and also to Miss K. Priest of Messrs Chapman & Hall, who saved us from many errors and omissions, and to Mrs R. G. Davies for substantial help in preparing the bibliographies and checking references.

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Part I

ANATOMY AND PHYSIOLOGY

Chapter 1

INTRODUCTION

Definition of the Insecta (Hexapoda)

The insects are tracheate arthropods in which the body is divided into head, thorax and abdomen. A single pair of antennae (homologous with the antennules of the Crustacea) is present and the head also bears a pair of mandibles and two pairs of maxillae, the second pair fused medially to form the labium. The thorax carries three pairs of legs and usually one or two pairs of wings. The abdomen is devoid of ambulatory appendages, and the genital opening is situated near the posterior end of the body. Postembryonic development is rarely direct and a metamorphosis usually occurs.

Relationships with Other Arthropods

The arthropods (Snodgrass, 1952; Clark, 1972) include animals differing widely in structure but agreeing in certain fundamental characters, some of which probably evolved convergently. The body is segmented and invested with a chitinous exoskeleton. A variable number of the segments carry paired jointed appendages exhibiting functional modifications in different regions of the body. The heart is dorsal and is provided with paired ostia, a pericardium is present and the body-cavity is a haemocoele. The central nervous system consists of a supra-oesophageal centre or brain connected with a ganglionated ventral nerve-cord. The muscles are composed almost entirely of striated fibres and there is a general absence of ciliated epithelium. No animals other than arthropods exhibit the above combination of characters. Apart from the Insecta, the various major divisions are as follows.

The Trilobita (trilobites) are an extinct group of Palaeozoic marine forms with the body moulded longitudinally into three lobes. They possess a single pair of antennae followed by a variable number of pairs of biramous limbs little differentiated among themselves. Four pairs of these appendages belong to the head and the remainder to the trunk region.

The Chelicerata include three classes, the Merostomata (king crabs), the Pycnogonida (sea-spiders) and the numerous Arachnida (spiders, scorpions, mites, ticks, etc.). The body is usually divided into cephalothorax and abdomen; the legs consist of four pairs and there are no antennae. The primitive forms respire by means of branchiae which, in the higher forms, are replaced by lung-books or tracheae. Spiracles when present are generally abdominal and consist at most of four pairs. The gonads open near the base of the abdomen and the excretory organs are usually Malpighian tubules. The presence of chelicerae, in place of sensory antennae, and the general characters of the remaining appendages mark off the Chelicerata very definitely from all other arthropods.

The Crustacea (lobsters, shrimps, crabs, barnacles, etc.) are characterized by the possession of two pairs of antennae and at least five pairs of legs. In the higher forms the body segments are definite in number and arranged into two regions – the cephalothorax and abdomen. Respiration almost always takes place by means of gills, and the excretory organs are, at least in part, modified coelomoducts usually represented by green glands or shell glands. The genital apertures are situated anteriorly, i.e. on the 9th postoral segment in some cases, up to the 14th in others.

The Onychophora (*Peripatus* and its allies) are in some respects annectent between the annelida and arthropods, and the reasons for their inclusion in the latter are not evident from superficial examination. They are probably to be derived from primitive Annelid ancestors which had forsaken a marine habitat and become terrestrial. The appendages are lobe-like structures (lobopodia) that have become modified for locomotion on land without having acquired the jointed arthropod character. The integument is soft, though it contains chitin, and the excretory organs take the form of metamerically repeated coelomoducts. Arthropodan features are exhibited in the possession of tracheae, salivary glands, and the terminal claws to the appendages. The presence of jaws of an appendicular nature, the paired ostia to the heart, the pericardium, the haemocoelic body-cavity and the reduced coelom are further important characters allying them with other arthropod groups.

The Myriapoda comprise four classes, whose members are characterized by the presence of a single pair of antennae and the absence of any differentiation of the trunk into thorax and abdomen; each segment usually bears appendages. The Diplopoda (millipedes) have the greater number of the body segments so grouped that each apparent somite carries two pairs of legs and two pairs of spiracles. The gonads open behind the 2nd pair of legs. The Pauropoda are characterized by the legs being arranged in single pairs although the terga are mostly fused in couples. The antennae are biramous and there are only twelve postcephalic segments, nine of which bear legs. The gonads open on the 3rd segment. The Symphyla have long antennae and most of the body segments bear a single pair of legs. The gonads open on the 4th postcephalic segment and there is a single pair of spiracles which are situated on the head. The Chilopoda (centipedes) are usually provided with a single pair of appendages and a pair of spiracles to each of the postcephalic segments. The first pair of legs is modified to form poison claws and the gonads open on the penultimate segment of the abdomen.

Two further small groups of animals, the **Tardigrada** and the **Pentastomida**, are placed in or near the arthropods. The Tardigrada (bear animalcules) are minute animals with a cuticle that is moulted and with four pairs of unjointed legs but devoid of antennae, mouth-appendages or respiratory organs. The gonads open into the intestine. The parasitic Pentastomida are worm-like and devoid of appendages except two pairs of hooks near the mouth. Their arthropodan affinities are mainly suggested by the larvae, which possess two pairs of clawed, leg-like processes.

The phylogenetic relationships of the various arthropod groups have been much discussed and widely different theories of insect origins have been proposed. The very incomplete fossil record makes it impossible to substantiate these theories palaeontologically and they are based mainly on inferences from the morphology of recent forms. In an authoritative review, Tiegs and Manton (1958) gave reasons for believing that arthropod features evolved independently in more than one phyletic line. This interpretation is now supported by a large array of data from comparative and functional morphology (Manton, 1964, 1966, 1972, 1973, etc.) and from embryology (Anderson, 1973). One group which they regard as monophyletic, however, consists of the Onychophora, Myriapoda and insects (Hexapoda). These animals have in common primitively uniramous appendages, mandibles formed from the whole limb and biting with the tips, a long mid gut either without or with only a few simple diverticula, as well as distinctive embryonic features. The group – which Manton (1972) treats as an arthropod phylum Uniramia – may be contrasted with the Chelicerata, Trilobita and Crustacea, in which there are gnathobasic mandibles, primitively biramous appendages of various kinds, and a mid gut that is usually shorter and with elaborate diverticula. The ancestral stock in the Uniramian line probably comprised soft-bodied animals with many pairs of unsegmented, lobopodial appendages. The Onychophora retained these features and evolved simple sclerotized jaws on the second cephalic segment though they did not acquire a sclerotized head capsule. Insects and Myriapoda, on the other hand, seem to have arisen from ancestral forms in which the mandibles evolved on the fourth segment and which thereafter separated into two lines, each acquiring independently a sclerotized head capsule, trunk and jointed limbs. In the Myriapodan lines of evolution the mandibles are jointed structures, biting in the transverse plane, and the many pairs of limbs are associated with the trunk by coxo-sternal articulations. In the insect lineages, the mandibles are unjointed structures in which the primitive movement is a rolling action, and there has been independent evolution of the hexapod condition (with accompanying elaboration of thoracic segments), the legs being attached and moved in various ways.

The above views imply not only the parallel development of arthropod features in the Uniramian line and among the Chelicerata, Trilobita and Crustacea, but also involve the independent separation at a relatively early stage in evolution of five major groups of insects – the primitively wingless Thysanura, Diplura, Collembola and Protura as well as the winged Pterygota, all now deserving the status of separate classes. It follows also that none of these have a particularly close relationship with any of the recent Myriapodan classes, so that theories deriving the insects from a Symphylan-like stock (Imms, 1936; Tiegs, 1945) must be given up in favour of more remote connections through unknown, extinct groups. A further corollary is that the independent evolution of the hexapod condition nullifies many attempts to trace common patterns in the thoracic structures of the five insect groups listed above or in the highly modified entognathous mouthparts of the Diplura, Collembola and Protura.

The degree of convergence involved in this view of arthropod evolution is greater than can be accepted by some zoologists, e.g. Lauterbach (1973), Hennig (1969) and Siewing (1960), who find it impossible to regard the compound eye, the jointed cuticular exoskeleton, the extensive cephalization and the specialized anterior ganglia of the central nervous system as having evolved convergently. Less radical theories therefore tend to assume a monophyletic Arthropoda, within which the Myriapoda and insects are allied with the Crustacea to form a subphylum Mandibulata, which may be contrasted with the Chelicerata and Trilobita (Snodgrass, 1938–58). The insects moreover are still widely – if incorrectly – regarded as a natural, monophyletic group. Some of the problems involved will be discussed in connection with the apterygote groups (pp. 433 ff.) but it must be stressed that the detailed morphological and embryological evidence now available – mainly through Manton's work – renders some of the other phylogenetic and morphological discussions (including even relatively recent ones such as Sharov, 1966) subject to serious qualification and correction.

General Organization of a Winged Insect

Examination of the structure and development of the more primitive groups enables one to reconstruct a generalized winged insect. The characters of this hypothetical form show various secondary modifications in different orders of the Pterygota but its more important features are as follows.

The head is formed by the fusion of six embryonic segments of which the 2nd and 4th to 6th carry appendages in the adult. These appendages are the antennae, mandibles, maxillae and labium (2nd maxillae). The head also carries a pair of compound eyes and three dorsal ocelli.

The thorax consists of three segments each of which bears a pair of legs, while the 2nd and 3rd segments carry a pair of dorsolateral membranous outgrowths or wings. The two pairs of wings are similar, and each is supported by a system of longitudinal cuticular ribs or veins which are formed around the pre-existing tracheae of the externally developing wing-pad. There are no true cross-veins but only an irregular network (archedictyon) formed by thickenings of the wing-membrane.

The abdomen consists of eleven segments together with a terminal region or telson: the 11th segment carries a pair of segmented appendages, the cerci.

The digestive system is divisible into the fore gut or stomodaeum, a simple sac-like mid gut or mesenteron and the hind gut or proctodaeum. A pair of salivary glands lies along the sides of the fore gut and their ducts pass forward to unite and form the main salivary duct which opens behind the hypopharynx. Six Malpighian tubules are present and arise at the junction of the mid and hind gut.

The central nervous system consists of two principal cephalic centres united with a ventral ganglionated nerve-cord. The supra-oesophageal centre or brain is formed by the fusion of the three preoral cephalic ganglia. It is

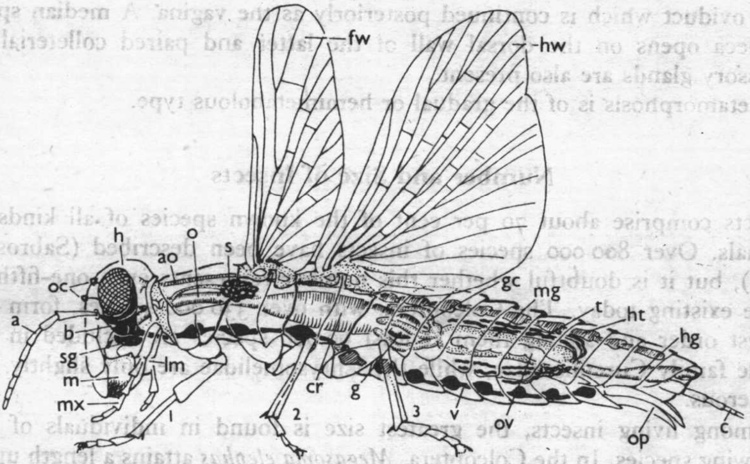

FIG. 1 General organization of a winged insect

a, antenna; *ao*, aorta; *b*, brain; *c*, cercus; *cr*, crop; *fw*, fore wing; *g*, gizzard; *gc*, gastric caeca; *h*, head; *hg*, hind gut; *ht*, heart; *hw*, hind wing; *lm*, labium; *m*, mandible; *mg*, mid gut; *mx*, maxilla; *o*, oesophagus; *oc*, ocelli; *op*, ovipositor; *ov*, ovary; *s*, salivary gland; *sg*, suboesophageal ganglion; *t*, Malpighian tubule; *v*, ventral nerve cord; *1*, *2*, *3*, fore, mid and hind legs

joined by a pair of para-oesophageal connectives with the sub-oesophageal centre. The latter is formed by the fusion of the three postoral cephalic ganglia. The ventral nerve-cord consists of three thoracic and nine abdominal ganglia united by paired longitudinal connectives. There is consequently one ganglion to each of the first twelve postcephalic segments.

The dorsal vessel consists of an abdominal portion or heart and a thoracic portion or aorta. The heart is metamerically divided into chambers, each of which is provided with paired lateral ostia. Beneath the heart is a transverse septum or pericardial diaphragm. The aorta is a narrow tubular extension arising from the first chamber of the heart and extending forwards through the thorax into the head, where it ends just behind the brain.

The respiratory system consists of segmentally repeated groups of tracheae linked by longitudinal and transverse trunks and communicating with the exterior by ten pairs of spiracles. These are situated on each of the two hinder thoracic and the first eight abdominal segments respectively.

The reproductive organs of the two sexes are very similar. In the male each testis consists of a small number of lobe-like follicles whose cavities communicate with the vas deferens. The vasa deferentia unite posteriorly and continue as a common ejaculatory duct which opens on the aedeagus. Vesiculae seminales are present as simple dilations of the vasa deferentia and paired accessory glands open into the proximal portion of the latter. In the female each ovary consists of several panoistic ovarioles comparable to the lobes of the testis. The lateral oviducts combine posteriorly to form a common oviduct which is continued posteriorly as the vagina. A median spermatheca opens on the dorsal wall of the latter and paired colleterial or accessory glands are also present.

Metamorphosis is of the gradual or hemimetabolous type.

Number and Size of Insects

Insects comprise about 70 per cent of the known species of all kinds of animals. Over 800 000 species of insects have been described (Sabrosky, 1952), but it is doubtful whether this number represents even one-fifth of those existing today. The Coleoptera, with over 330 000 species, form the largest order and among them at least 60 000 species are included in the single family Curculionidae, while the Chrysomelidae are only slightly less numerous.

Among living insects, the greatest size is found in individuals of the following species. In the Coleoptera, *Megasoma elephas* attains a length up to 120 mm and *Macrodontia cervicornis* (including the mandibles) ranges up to 150 mm. Among Phasmida, *Pharnacia serratipes* may exceed 260 mm long and the Hemipteran *Belostoma grande* attains a length of 115 mm. For the Lepidoptera their size may, perhaps, be best gauged by the wing-span. The latter reaches its maximum in *Erebus agrippina*, whose outspread wings measure up to 280 mm from tip to tip and in large examples of *Attacus atlas* they measure 240 mm. None of these compare with the extinct dragonfly *Meganeura monyi*, which had a wing-span of up to 700 mm. With regard to the smallest insects certain Coleoptera (family Ptiliidae) do not exceed a length of 0·25 mm while egg-parasites belonging to the Hymenopteran family Mymaridae are, in some cases, even more minute. As Folsom has observed, some insects are smaller than the largest Protozoa and others are larger than the smallest vertebrates.

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Chapter 2

THE INTEGUMENT

Reviews of various general aspects of the insect integument have been given by Beament (1961, 1964), Hackman (1971, 1974), Hinton (1970), Lawrence (1967), Locke (1964, 1967), Neville (1967, 1970, 1975), Weis-Fogh (1970) and Wigglesworth (1959).

Structure, Composition and Functions

The integument consists of the following layers: (i) the cuticle, (ii) the epidermis, and (iii) the basement membrane (Fig. 2).

(1) **The Cuticle** is a complex, non-cellular layer secreted largely by the epidermis and though commonly considered non-living is actually the seat of complex biochemical changes, some at least under enzymatic control. It forms the outermost investment of the body and its appendages but is invaginated locally to form endoskeletal structures (p. 81) and also provides

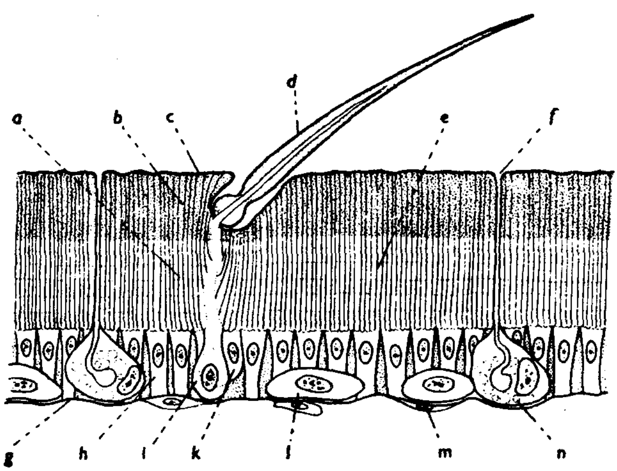

FIG. 2 Section of typical insect cuticle (*after* Wigglesworth)

a, laminated endocuticle; *b* exocuticle; *c*, epicuticle; *d*, bristle; *e*, pore-canals; *f*, duct of dermal gland; *g*, basement membrane; *h*, epidermal cell; *i*, trichogen cell; *k*, tormogen cell; *l*, oenocyte; *m*, haemocyte adherent to basement membrane; *n*, dermal gland. *From* Wigglesworth, *Principles of Insect Physiology*, 7th edn, p. 27, Fig. 19.