IMMS' OUTLINES OF ENTOMOLOGY

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AND
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SIXTH EDITION

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SIXTH EDITION

First published 1942
by Methuen and Co Ltd
Second edition 1944
Third edition 1947
Fourth edition 1949
Fifth edition revised by
O. W. Richards & R. G. Davies 1959
Reprinted 1961
Reprinted with corrections 1967
Reprinted 1970
Reprinted 1973

Sixth edition published 1978
by Chapman and Hall Ltd
11 New Fetter Lane, London EC4P 4EE

Printed in Great Britain by
Fletcher & Son Ltd, Norwich

ISBN 0 412 21660 4 (cased edition)
ISBN 0 412 21670 1 (paperback edition).

Distributed in the U.S.A
by Halsted Press, a division of
John Wiley & Sons, Inc., New York

Library of Congress Cataloging in Publication Data

Imms, Augustus Daniel, 1880–1949.
Imms' Outlines of entomology.

Bibliography: p.
Includes index.
1. Insects. I. Richards, Owain Westmacott, 1901–
II. Davies, Richard Gareth. III. Title.
IV. Title: Outlines of entomology.
QL463.159 1978 595.7 78-8413
ISBN 0-470-26409-8
ISBN 0-470-26412-8 pbk.

Contents

Preface to the Sixth Edition

In his preface to early editions of this book, the late Dr. A. D. Imms said that he intended it to be an elementary account of entomology as a branch of general biology. He had especially in mind the needs of university students of zoology and agriculture, as well as those intending later to specialize in entomology, and he suggested that the book might also interest teachers of advanced biology in schools.

These general aims and the balance between the different aspects of the subject have changed little in this and in our previous revision. We have, however, tried to bring the present edition up to date on the lines of our revised tenth edition of *Imms' General Textbook of Entomology*, published in 1977. The text has been entirely re-set and eleven illustrations have been replaced by new figures. The same orders of insects are recognized as in the last edition, but the sequence in which the Endopterygote groups appear has been changed to reflect more accurately their probable evolutionary relationships. Many small changes and some additions have been made in the physiological sections, the chapter on the origin and phylogeny of insects has been rewritten, and a new bibliography provides a selection of modern references for the intending specialist. It has been our object to make these alterations without materially increasing the length of the book or its level of difficulty.

We are greatly indebted to the authors on whose illustrations some of our diagrams are based; their names will be found in the legends to the figures concerned.

September, 1977

O.W.R.
R.G.D.

I

Introduction

Insects are segmented animals with a relatively tough integument and jointed limbs. They breathe by means of air-tubes or tracheae and the body is divided into head, thorax and abdomen. The head is the sensory and feeding centre, bearing the mouthparts and a single pair of antennae, perhaps homologous with the antennules of the Crustacea; compound eyes are usually present and often simple eyes or ocelli. The thorax is the locomotor centre, carrying three pairs of legs and usually two pairs of wings. The abdomen is the metabolic and reproductive centre; it contains the gonads and organs of digestion and excretion and usually bears special structures used in copulation and egg-laying. When it leaves the egg, the young insect differs more or less extensively from the adult form and its development therefore involves some degree of metamorphosis.

The number of known kinds, or species, of insects is difficult to estimate but certainly exceeds that of all other animals together. That approximately 800 000 different insects have been named and described is probably a conservative estimate. Usually several thousand new species are described in a single year, but notwithstanding this rate of discovery there is no doubt that the numbers yet to be brought to light exceed those of all the known kinds. The single order Coleoptera, or beetles, alone comprises over 330 000 named species. Even the one family Curculionidae, or weevils, includes more than 60 000 known species, while the Carabidae, or ground beetles, number about 25 000 kinds.

This remarkable capacity for differentiation shown by insects does not lend itself to exact analysis. It is, however, a matter of interest to consider some attributes which have most likely helped the members of this class to attain their dominant position in the animal kingdom.

(*a*) *Capacity for Flight*. The majority of insects are not wholly confined to the ground and vegetation but are also able to fly. The possession of wings provides unique means of dispersal, of discovering their mates, of seeking food and of escaping from their enemies. Such a combination of advantages is not to be found elsewhere among invertebrate animals.

(*b*) *Adaptability*. No other single class of animals has so thoroughly invaded and colonized the globe as the Insecta. Their distribution ranges from the poles to the equator; every species of flowering plant provides food for one or more kinds of insect, while decomposing organic materials attract and support many thousands of different species. Very many are parasites on or within the bodies of other insects or of some very different animals, including vertebrates. The soil and fresh waters support their own extensive insect fauna. Great heat and cold are not impassable barriers since some species can withstand temperatures of about $-50°$ C, while others live in hot springs at over 40° C or in deserts where the midday surface temperature may be twenty degrees higher. A few species live in what seem almost impossible environments; the larva of an Ephydrid fly inhabits pools of crude petroleum in California while some beetles have been reported from argol (containing 80% potassium bitartrate), opium, Cayenne pepper, sal ammoniac and strychnine.

(*c*) *Size*. The relatively small size of most insects has many advantages. Each individual requires little food so that large populations may occupy small habitats, which often also offer security from enemies. Thus, several leaf-mining larvae may develop in the tissues between the upper and lower epidermal layers of a single small leaf, a weevil will complete its life cycle in one small gorse seed, while a moderate-sized fungus will support very many beetles and fly larvae.

Insects, in fact, vary greatly in size, from minute Hymenopterus parasites about 0·2 mm long to forms like the bulky Goliath Beetle with a length of up to 120 mm. These, however, are extremes and both very large and very small insects suffer disadvantages which do not apply to the more numerous species of an intermediate size. If a very small insect is wetted, the weight and surface tension of the encompassing water film soon exhaust its efforts to free itself. Very large species, on the other hand, are subject to a limitation imposed by their characteristic method of tracheal respiration. Oxygen passes along these breathing tubes by gaseous diffusion and the physical law which this process follows is such that an increase in the size of an insect is not accompanied by a proportional increase in the rate at which oxygen can reach the tissues (p. 84). When an insect reaches a diameter of about 2 cm, therefore, its method of respiration is liable to incommode it and make it sluggish – further increase in bulk would soon make it too inert to survive competition with other organisms. For such reasons the relatively gigantic forms which do occur, as among beetles, grasshoppers, water-bugs and fossil dragonflies, form a very small proportion of their own groups. Furthermore, even among large insects, very few have a diameter of more than about half an inch, though there may be a great extension in the length of the body or the area of flat, plate-like projections from it. Thus the giant stick insect *Pharnacia serratipes* measures up to 260 mm long but retains a proportionately attenuated form. Some of the great fossil dragonflies of Carboniferous times had wings exceeding 2 feet in expanse but with typically slender bodies. The giant Noctuid moth *Erebus agrippina* has a wing spread of 280 mm, but its slender body is no more than 55 mm long, and the same applies to the giant Atlas moths and to Oriental butterflies of the genus *Troides*.

(*d*) *The skeleton*. The skeleton of insects, like that of other arthropods, is an exoskeleton and has many features of great significance. It consists of hard regions or *sclerites* separated by soft membranous zones and therefore combines strength and rigidity with flexibility. It protects the insect mechanically, provides firm sites for the attachment of the muscles which move the body, acts sometimes as a mechanism for storing energy, and is invaginated in various ways to support some internal organs and to line the tracheae and a few other structures.

Its construction in the form of a series of jointed tubes surrounding the body and appendages gives it a much greater power of resistance to bending than the endoskeleton of a vertebrate. The two cases have been contrasted by the Russian writer Chetverikov. In Fig. 1, A represents a cross-section of an insect limb with its tubular exoskeleton while B and C are cross-sections through two vertebrate limbs, each with its axial endoskeleton. It is known from physical principles that the modulus of resistance to bending in a solid cylinder and in a hollow one is given by the two formulae:

$$M = \frac{\pi D}{32} \quad \text{and} \quad M_1 = \frac{\pi(D_1^4 - d^4)}{32 D_1}$$

where M and M_1 are the respective moduli and D is the diameter of the endoskeleton, while d and D_1 are the internal and external diameters of the exoskeleton. If, for the sake of argument, we take the case of $d = \frac{4}{5} D_1$ and compare figures A and B, the cross-sectional areas of skeleton and muscle being the same in the two cases, then the formulae show that the limb with the solid axial endoskeleton will be nearly three times weaker than the one with the hollow exoskeleton. Further, it may be shown that to have the same strength as the exoskeleton of Fig. 1 A, an axial endoskeleton would take up 84% of the total diameter of the limb (Fig. 1 C); under such conditions there would be little space left for musculature.

Because of its mechanical efficiency, therefore, the insect skeleton combines great strength with lightness. Composed as it is of an amazingly plastic material, it has lent itself to the most varied processes of evolutionary modification under the influence of natural selection. Increased deposition of cuticular substance has occurred in endless ways and in adaptation to manifold requirements. Especially to be noted are the immensely varied

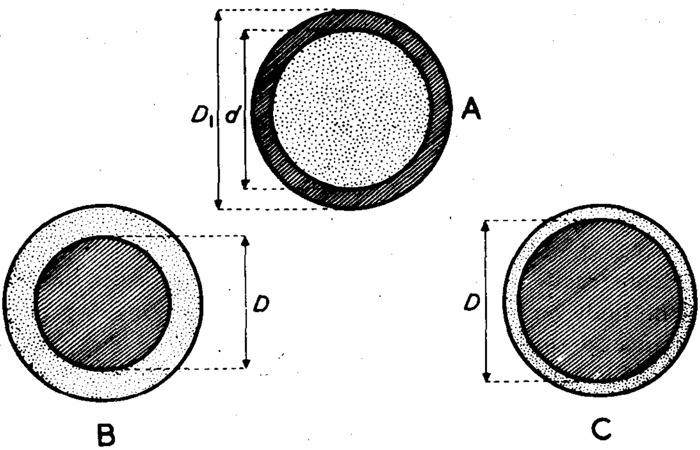

Fig. 1. Diagram of cross-sections of limbs; from Chetverikov

A, exoskeleton with internal diameter $d = \frac{4}{5}$ of the external diameter D_1. B and C, endoskeletons. (Skeleton cross-hatched: musculature, etc. stippled) developments of form and size in the head and jaws; the growth of horns, spines and other processes; of bristles and of scales; of membranous wings and horny elytra; of stout fossorial legs; of needle-like ovipositors, and so forth. It is, furthermore, the exoskeleton which displays many of the structural characters that distinguish the many species of insects.

Because it possesses a rigid exoskeleton, the growing insect must shed it periodically. During this process of moulting the insect is somewhat vulnerable, but this disadvantage may be less real than it seems for the sequence of moults is the basis on which have been evolved the elaborate changes of form which occur in the life cycles of the higher insects and which have allowed the immature and adult stages to become adapted each to its own conditions of life.

(*e*) *Resistance to Desiccation.* Though some insects are aquatic or inhabit moist environments, the success of the class has depended to a considerable extent on an ability to survive under the relatively dry conditions of terrestrial life. The insects' capacity for resisting desiccation and conserving water shows itself in many ways. The cuticle is provided with a thin layer of waxy material which greatly reduces transpiration from the surface of the body and the openings of the tracheal system, or spiracles, are provided with closing mechanisms or other devices which further reduce water loss, while permitting enough oxygen to enter. The principal excretory products of most insects are insoluble and therefore do not require a large volume of water for their removal from the body in solution, while the terminal part of the alimentary canal reabsorbs water which would otherwise be lost in the faeces. Some insects living under unusually dry conditions depend to a considerable extent on the water produced when foodstuffs are oxidized within their bodies – the so-called metabolic water. Finally, in their reproductive behaviour, with internal fertilization and the habit of laying eggs whose impervious shell protects the developing embryo from desiccation, the insects are well adapted to terrestrial conditions.

(*f*) *Tracheal Respiration.* The characteristic tracheal respiratory system of insects tends to limit their size and requires modifications to offset this disadvantage and to restrict water loss. In other respects, however, tracheal respiration is very efficient and the direct carriage of gaseous oxygen to within very short distances of the respiring tissues has enabled the insects to evolve the very high rates of metabolic activity needed to achieve rapid flight. Insect flight muscle is, in fact, the most actively respiring animal tissue known and the tracheal system shows several specially interesting adaptations to supply it with enough oxygen (e.g., p. 84). It is also worth emphasizing that though tracheal respiration probably arose and first evolved in terrestrial and aerial habitats, it has nevertheless been retained (though often with a closed tracheal system) in almost all the insects that have returned to colonize aquatic environments secondarily. Only a relatively few, very small insects are able to obtain enough oxygen by simple diffusion through their tissues.

(*g*) *Complete metamorphosis.* The more highly evolved types of insect life cycle entail a transition from the immature larval stages through a pupal phase into the winged, sexually mature adult (p. 121). This form of development, found for example in beetles, moths and flies, differs from the simpler, incomplete metamorphosis of, say, grasshoppers or cockroaches in that it allows the larva and adult to exploit different food resources and occupy different ecological niches. Such a transition from larva to adult involves extensive anatomical, histological and functional changes, which occur mainly during the apparently quiescent pupal stage. The latter therefore represents an evolutionary innovation of great importance, as can be seen from the fact that insect species with a complete metamorphosis outnumber those with an incomplete metamorphosis by about ten to one and have successfully invaded a much greater range of habitats.

This short preamble reviews the more obvious factors that may have contributed to the success of the insect type of organization. It also helps to explain why that type has persisted from pre-Carboniferous times, with increasing differentiation and expansion, beyond that of any other class of animals. In the pages that follow the elementary features of insect structure and functions are discussed. These are succeeded by a short account of development and metamorphosis, a brief discussion of the more important modes of life, and a section dealing with nomenclature, classification and biology. Some account of the essential features of each of the twenty-nine orders of insects is given, and finally the position of these animals in the arthropod series, their ancestry and their mutual relationships, are dealt with in an elementary way.

2

Anatomy and Physiology

THE INTEGUMENT AND ITS DERIVATIVES; COLORATION

The Integument (Fig. 2). This consists of a cellular layer, the *epidermis*, with an outer non-cellular *cuticle*. The epidermis secretes the greater part of the cuticle and is responsible for dissolving and absorbing most of the old cuticle when the insect moults (p. 119) as well as repairing wounds and differentiating so as to determine the form and surface appearance of the insect. The cuticle forms the outer exoskeleton and is also present as a lining to the fore and hind intestine, to the tracheae, and to other parts similarly formed by an ingrowth of the ectoderm. Typically, it is composed of three layers:

(i) The outermost layer or *epicuticle*, less than 4 μm thick, consists mostly of a hardened protein, but also contains the waxes which are largely responsible for reducing water-loss through the cuticle, as well as an outer 'cement layer'.

(ii) The *exocuticle* is a much thicker layer consisting mainly of chitin and proteins, the latter being 'tanned' by phenolic substances to produce a hard, brown material called *sclerotin* which gives the cuticle its rigidity. The exocuticle is absent or reduced in the more flexible regions of the integument and may be entirely absent from insects with a soft, thin cuticle.

(iii) The *endocuticle*, which is usually the thickest layer, also contains chitin and proteins but the latter are not tanned and this part of the cuticle is therefore soft and flexible.

Both endocuticle and exocuticle consist of numerous laminae arranged more or less parallel to the surface and are traversed by very numerous *pore canals*, each of which may contain a threadlike cytoplasmic extension of the epidermis. Chitin, which makes up 25–60% of the dry weight of the cuticle, is a nitrogenous polysaccharide consisting of many sugar-like residues joined end to end in long molecular chains. It is resistant to alkalis and dilute mineral acids and can be detected by the van Wisselingh test: heating with concentrated potassium hydroxide at 160° C for 20 minutes converts it to chitosan which gives a rose-violet colour with 0·2% iodine in 1% sulphuric acid. In the cuticle the chitin forms ultramicroscopic fibres embedded in a protein matrix.

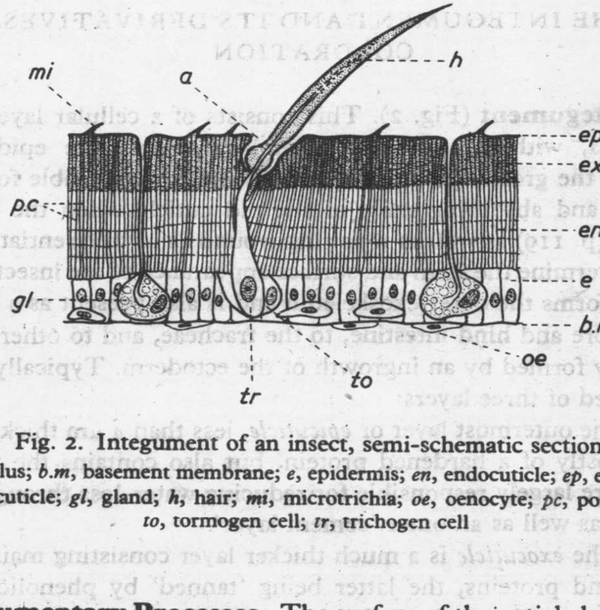

Fig. 2. Integument of an insect, semi-schematic section
a, alveolus; *b.m*, basement membrane; *e*, epidermis; *en*, endocuticle; *ep*, epicuticle; *ex*, exocuticle; *gl*, gland; *h*, hair; *mi*, microtrichia; *oe*, oenocyte; *pc*, pore canals; *to*, tormogen cell; *tr*, trichogen cell

Integumentary Processes. The surface of the cuticle bears two main types of outgrowths:

(i) Rigid non-articulated processes; these include the microtrichia and spines. *Microtrichia* are minute, non-cellular, hair-like structures (Fig. 2), formed entirely of cuticle and often occurring in very large numbers on the wings of certain insects. *Spines* are large, hollow, heavily sclerotized, thorn-like processes of multicellular origin; they are well seen on the legs of cockchafers and dor-beetles (Scarabaeidae).

(ii) Movable articulated processes attached to the cuticle by a ring of articular membrane which may be sunk into a cuticular socket or *alveolus* or elevated on a tubercle; they include macrotrichia and spurs. *Macrotrichia* or *setae* (Fig. 2) are hollow extensions of the exocuticle and epicuticle. Each is secreted by the cytoplasmic outgrowth of a single modified epidermal cell, the *trichogen cell*, while the socket from which the seta protrudes is produced by another specialized epidermal cell, the *tormogen cell*. The following specially modified setae are known: (*a*) *Clothing hairs* which cover the general surface of the body and appendages. They may be branched or *plumose*, as in the bees, or, when specially stiff, they form the bristles of, say, Tachinid flies. (*b*) *Scales*, such as occur in Lepidoptera and some Collembola, Diptera and Coleoptera. Essentially these are flattened setae, often with a striate surface and sometimes containing pigment. (*c*) *Glandular setae*, which serve as outlets for the secretions of epidermal glands; they include the silk-spinning hairs of Embioptera and the urticating hairs of some caterpillars, e.g., those of the Gold-tail moth (*Euproctis chrysorrhoea*). (*d*) *Sensory setae*, which are more or less specialized in structure and have one or more nerve cells at their base. They perceive various stimuli and are discussed further on p. 57. *Spurs* differ from setae in being thick-walled multicellular structures; they are often large and occur more especially on the tibiae of the legs.

Epidermal Glands. These comprise one or more cells specially modified for the secretion of such materials as wax, lac and a variety of substances known as *pheromones* (p. 62) which influence the behaviour or development of other members of the species.

Apodemes. These are sclerotized cuticular ingrowths which collectively form the *endoskeleton*, providing sites for the attachment of muscles and sometimes supporting other organs. They may be more or less tubular or flattened and though the mouths of the invaginations sometimes persist, the apodeme usually becomes solid as the cuticle is laid down. The endoskeleton of the head is known as the *tentorium* (Fig. 3). It consists of paired anterior and posterior arms whose origins are visible externally as slit-like pits; the inner ends of the arms amalgamate to form the body of the tentorium, from near which a third, dorsal pair of arms often arises. The tentorium gives rigidity to the head capsule,