INSECT PHYSIOLOGY

V. B. Wigglesworth

EIGHTH EDITION

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INTRODUCTION

To the insect, order and disorder are exposed to sight
and so we think to see the little emmets confer
and locking their antennae immediately transmit
the instinctive calls which each and all can feel; whereas
the mutual fellowship of distributed cells
hath so confounded thought that explanation is fetch'd
from chemic agency; because in that science
the reaction of unknown forces is described and summ'd
in mathematic formulae pregnant of truth,
and of such universal scope that, being call'd laws,
their mere description passeth for Efficient Cause.

ROBERT BRIDGES

The fundamental processes of vital activity, the ordered series of physical and chemical changes which liberate energy and maintain the 'immanent movement' of life, are probably the same wherever 'living matter' exists. The description of these changes is the ultimate goal of physiology, of whatever group of organisms; but in this book we shall be concerned only with physiology on a humbler plane: with the grosser functions of the organs and tissues, and with the mechanisms by which these functions are co-ordinated to serve the purpose of the insect as a whole.

Of all the zoological classes, the insects are the most numerous in species and the most varied in structure; the general physiology of the group is therefore only too apt to be obscured by the endless specializations of particular forms; and the main difficulty of a work like the present is the exclusion of all that is special and non-essential, and the retention of only that material which best illustrates the general theme. There are, indeed, certain common factors which condition the physiological make-up of the insects, and these factors serve, to some extent, to link them all together into one system. They are essentially terrestrial animals. This circumstance determines the characters of their cuticle, and this, in turn, conditions their respiratory mechanism and the physiology of their growth. The respiratory mechanism and the cuticular skeleton are among the factors which restrict the size of insects. Their small size and terrestrial habit render them very prone to lose water; and the urgent need for the conservation of water influences the integument, the respiratory, excretory and digestive systems. All these systems show special changes when the insect reverts to an aquatic life.

Yet, although the interaction of these factors results in some uniformity of principle in the physiology of insects, their diversity in habit, food and environment causes such endless variation in detail, that, quite apart from the conspicuous gaps in our present knowledge, any limited treatment of the subject must in any case be more or less arbitrary in presentation; and, were there space to insert them, nearly all the generalizations that are attempted should have qualifying instances.

The history of insect physiology is peculiar. The early microscopists, Hooke, Malpighi, Leuwenhoek, made many observations on the structure of insects, and many accurate inferences about their physiology. More was added by the great naturalists, Swammerdam, Réaumur, de Geer. But, with such conspicuous exceptions as Newport, Graber, Lubbock, Plateau, and others of more modern times, the majority of entomologists, until recent years, have been so fully occupied with the morphology and taxonomy of their colossal group that such advances in physiology as have been made have commonly been mere by-products of morphological study. From time to time we find the physiologists of the last century, Dutrochet, Treviranus, Marshall Hall, von Kölliker, Claude Bernard, turning to the insects to illuminate their theme; but their concern was not with the insect as such.

Within recent years, interest in the physiology of insects has arisen in a new quarter. The applied entomologist, confronted with the ravages of insects in the spheres of agriculture and of public health, has wanted to know something about their nutrition, about the laws governing their responses to sensory stimuli, about their reactions to parasites, about the precise way in which their bodies are adapted to diverse climatic conditions, and about the action upon them of toxic sprays and gases. With this demand for increased knowledge has come a realization of our present ignorance.

Since the first edition of this book was published fifty years ago extensive advances have been made in all parts of the subject. The interested and attentive reader will find statements in almost every sentence which excite curiosity or demand expansion. The most simple way of obtaining such information may be to refer in the first instance to the corresponding topics in *The Principles of Insect Physiology* by the present author. More recent and far deeper coverage will be found in the thirteen-volume *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, Editors G. A. Kerkut and L. I. Gilbert. Articles describing the most recent advances in the physiology and biochemistry of insects appear in the *Annual Review of Entomology*, in *Advances in Insect Physiology* and elsewhere. The bibliographies at the end of each chapter indicate a few papers which provide useful starting-points for further reading.

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CONTENTS

Chapter One

THE INTEGUMENT

The key to much of the physiology of insects is to be found in the nature of the integument. The cuticle must be waterproof in order to protect these small animals from death by desiccation; it must be soft and flexible at the joints to allow movement; it must be extensible in places to allow for increase in bulk during feeding and during growth; and elsewhere it must be rigid to provide a firm foundation (an external skeleton) for attachment of the muscles; and it must furnish the material for horny tools such as mandibles and claws.

The cuticle, as was first shown by Haeckel, is the product of a single layer of epidermal cells; its substance is extracellular.

Cuticle structure

As seen in stained sections in the light microscope (Fig. 1.1) the cuticle consists of two primary layers: the *endocuticle* which makes up the greater part, and a thin refractile or pigmented *epicuticle* on the surface, usually not more than one micron (1 μm) in thickness. In the harder regions the outer part of the endocuticle is converted into a deep brown or amber-coloured layer, termed the *exocuticle*. The epicuticle and exocuticle usually appear homogeneous and structureless; the endocuticle shows more or less conspicuous horizontal lamellae.

But if the cuticle (e.g. in *Periplaneta* or *Tenebrio* larva) is cut in the fresh state with the freezing microtome, innumerable vertical threads are seen running right through the endocuticle from the

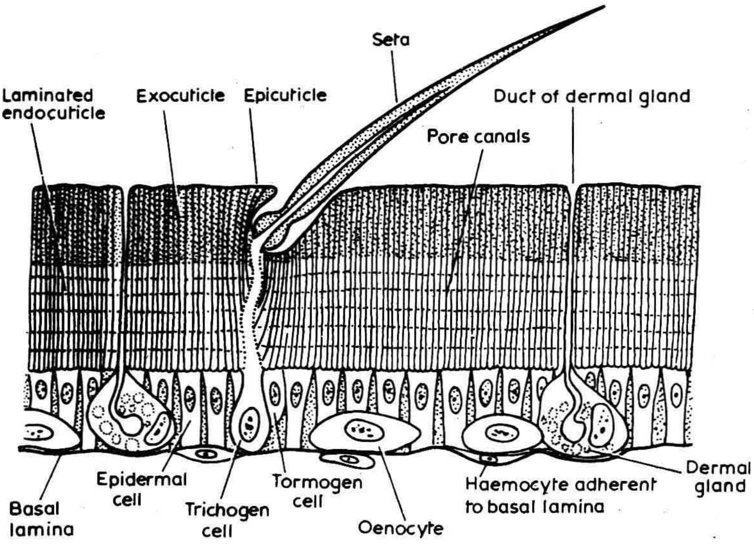

FIG. 1.1 Section of typical insect cuticle; the sense cell and nerve axon supplying the tactile seta are omitted (see Fig. 10.1).

epidermal cells and apparently ending below the epicuticle. These are fine channels called 'pore canals'. They are filled with fluid and serve to link the living cells with the epicuticle. By this route the epidermal cells can control the chemical changes in the cuticle, particularly at the time of its formation. Under the action of some humoral factor conveyed by the nerves it will become more pliable and extensible after feeding; and a hormone from the central nervous system may control its hardening and darkening at the time of moulting.

Composition and fine structure of the cuticle

Chitin and protein. The most familiar constituent of the cuticle is the nitrogenous polysaccharide chitin; but this rarely forms more than 50% of the substance of the cuticle. It is most abundant in the flexible and extensible endocuticle; it is not responsible for the hardness of the exocuticle, where it is reduced in amount, and it is entirely absent from the epicuticle.

Chitin, a polymer of acetylglucosamine, is closely related to cellulose, and like cellulose it exists in the form of sub-microscopic crystallites or micellae. In the endocuticle these tiny rodlets are aligned to form fibrils and these fibrils tend to be oriented all in one direction at one level in the cuticle. They may retain this 'preferred' direction in one lamina of the cuticle and then take up a new preferred direction in the succeeding lamina, at an angle of 60° or so to the first. This arrangement was observed in the cuticle of Coleoptera more than 150 years ago and the vertically flattened bundles of fibrils were termed 'Balken' or beams. In other cuticles the orientation of the fibrils changes systematically in each successive layer to form a regular spiral detectable only with the electron microscope. It is the changing orientation of the fibrils which is often responsible for the apparent lamination of the cuticle as seen in section. The fibrils of chitin are bound together by a protein matrix after the manner of fibre glass; indeed, the two may well be chemically united to form a mucopolysaccharide.

The best test for chitin is that of van Wisselingh, which consists in its conversion into chitosan by saturated caustic potash at a high temperature, and the recognition of chitosan by its solubility in acids and by the violet colour it gives with iodine.

The protein of the endocuticle is readily demonstrated by the protein colour tests: the biuret, Millon's and xanthoproteic reactions, all of which are strongly positive. Modern methods of protein separation, notably by electrophoresis, have revealed a score or more of different proteins in the cuticle. Some of these are enzymes or carriers of enzyme substrates, others are purely structural proteins associated with chitin.

Sclerotin. In the exocuticle the protein component has become converted into a horny substance termed 'sclerotin'. Sclerotin bears some resemblance to vertebrate horn or keratin; but whereas keratin is described as 'vulcanized protein', a substance in which adjacent protein chains are chemically bound together by means of sulphur linkages, sclerotin is described as 'tanned protein'. It is produced by the action of quinones which are formed in the cuticle from the oxidation of various diphenols. The quinones react with adjacent protein chains and bind these firmly together, converting a soft, white, extensible material into a hard and horny substance that may vary in colour from pale amber to deep brown. Gelatin tanned with benzoquinone gives rise to somewhat similar material. It was the invention of sclerotin and keratin which made possible a truly terrestrial existence for insects and vertebrates. It is these same materials which have made possible the development of wings.

Figure 1.2 summarizes the classical conception of sclerotin formation. But other, milder forms of polymerization, some involving the inclusion of lipids, occur in the cuticular proteins. For example there is good evidence that so-called β-sclerotin can be formed by the combination of the side-chain in acetyldopamine with protein without involving quinone production (see Fig. 1.2).

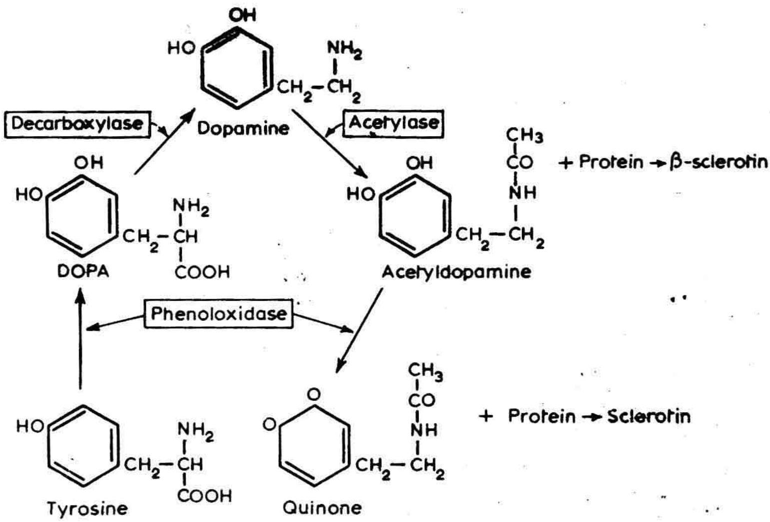

FIG. 1.2 The biochemistry of sclerotin formation in the larva of *Calliphora* (after Karlson and Sekeris) and β-sclerotin (after Andersen).

Resilin. Another protein which is always present in the endocuticle is called 'resilin'. This is an elastic substance in which the protein chains are bound together in a uniform three-dimensional network so as to yield a perfect rubber. Resilin may be deposited between the chitinous lamellae and provides the elasticity of the cuticle; or it may exist in the pure state to form elastic hinges at the base of the wings, and elastic tendons for muscles connected to the wings or elsewhere.

Lime. In a few aquatic larvae of Diptera there may be deposits of lime in the cuticle and in a few Diptera the puparium may be strengthened with a deposit of lime inside. But insects in general do not harden the cuticle as do many Crustacea by incorporating lime in the form of calcite. It is interesting to note, however, that sclerotin is actually harder than calcite, and that for their mandibles and claws which must be as hard as possible the Crustacea provide a covering of sclerotin. The sclerotized mandibles of some insects are so hard that they can readily bite through sheets of foil of lead, copper, tin, zinc or silver.

The epicuticle

The endocuticle is responsible for the extensibility of the integument and for combining toughness with flexibility. The exocuticle provides the rigidity in the hard parts such as the head capsule, the segments of the limbs, and so forth. The epicuticle is responsible for the impermeability of the cuticle, and particularly its power of preventing the loss of water by evaporation.

When the epicuticle of the fully developed integument is examined microscopically it appears as a refractile amber-coloured layer, usually not more than 1 μm in thickness. It is inextensible; but where the cuticle is liable to bend or stretch it is deeply folded, as in recently moulted caterpillars or newly emerged termite queens. The epicuticle is a highly complex structure; the only way in which it has been possible to learn something of its composition has been to observe the stages in its development when a new cuticle is being formed.

The electron microscope has shown that the cuticle is an extracellular structure. The surface of each epidermal cell, when it becomes separated from the old cuticle before moulting, shows tongue-like projections or microvilli about 0.5 μm long. The tips of the microvilli contain a lipid-staining deposit (Fig. 1.3(a)). Then a cap of clear material forms over the tip of each microvillus (Fig. 1.3(b)). Gradually the caps fuse with their neighbours to form a continuous glassy membrane about 17 nm thick (Fig. 1.3(c)). This is the *outer epicuticle* which is of constant form in all insects. It takes up lipid stains and is perhaps composed of some unknown polymer of lipophilic material.

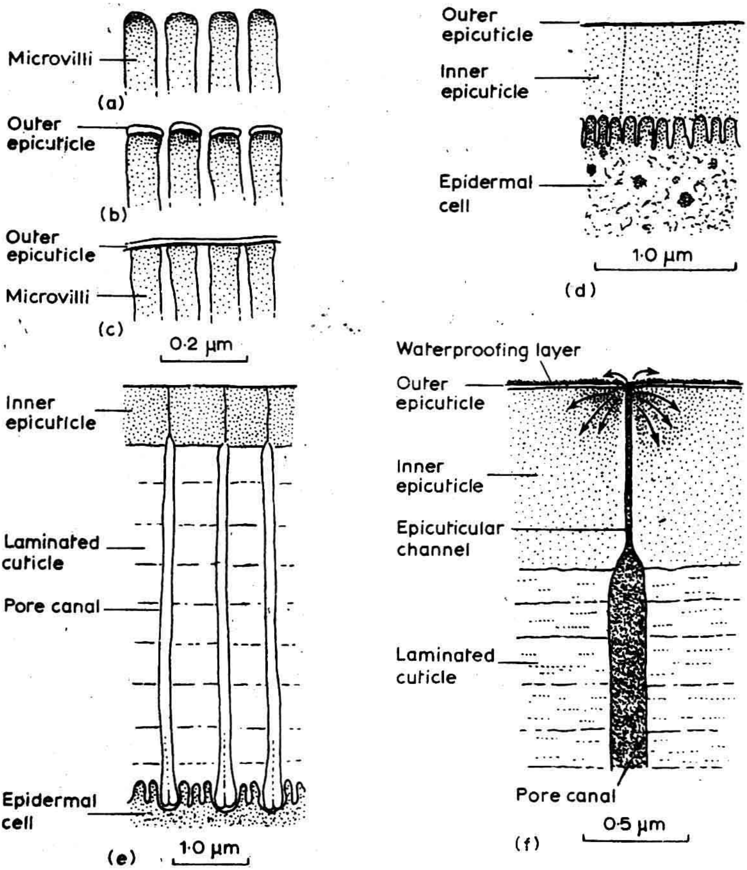

FIG. 1.3 Stages in formation of epicuticle and waterproof layer; (a), (b) and (c) deposition of outer epicuticle; (d) deposition of inner epicuticle; (e) three pore canals ending in epicuticular channels; (f) discharge of sclerotin and wax precursors from pore canal.

The epidermal cells now lay down the *inner epicuticle* which is composed of protein with lipid and reaches a thickness of 0.5 – 1 µm (about 25 – 50 times that of the outer epicuticle) (Fig. 1.3(d)).

Pore canals and epicuticular channels. During the next few days the endocuticle is laid down. Figure 1.3(e) shows three pore canals running vertically through the newly formed endocuticle.

They arise from pits in the surface of the epidermal cell, between the microvilli. The pore canals may have an 'axial filament' arising from the floor of the pit and often a bundle of lipid-rich filaments.

Where the pore canal reaches the base of the inner epicuticle it narrows abruptly from about 150 nm to form an epicuticular channel about 20 – 25 nm in diameter. By this route the epidermal cells control events in the cuticle. They discharge enzymes into the space below the old cuticle, which is digested (p. 11). They then discharge the precursors needed for sclerotin formation: notably protein and tyrosine and the necessary enzymes. These products will react with ammoniacal silver hydroxide. By stripping away the thin remnants of the old cuticle and immersing the insect in the silver solution it can be seen that the secretion is escaping from the fine epicuticular channels and spreading over the surface of the outer epicuticle (Fig. 1.3(f)). It also diffuses into the substance of the inner epicuticle, spreading inwards as far as the endocuticle. In regions where an exocuticle is to be formed it spreads further, for a varying distance into the substance of the lamellar endocuticle.

Waterproofing of the cuticle. The silver-binding contents of the pore canals and epicuticular channels are associated with the lipids that are the precursors for wax formation. Indeed the material which forms the thin layer on the surface of the outer epicuticle, when it first appears, will take up lipid stains, for example, Sudan B. But when the sclerotin begins to harden, and presumably the wax is formed, the surface layer no longer reacts with silver hydroxide nor does it take up lipid stains. The surface of the cuticle is now completely unwettable by water.

This inert surface layer appears to be the waterproof or 'wax layer' characteristic of all insects. It is only a fraction of a μm thick and is unstainable. But if the lipid is extracted with chloroform the sclerotin will react with silver and in this way it can be made visible.

In many insects (Orthoptera, Hemiptera, Coleoptera) there are abundant dermal glands that discharge their secretion, which appears to be a mucopolysaccharide, that dries on the surface of the wax layer, at the time of moulting or immediately afterwards. This tenuous secretion has been called the 'cement layer'. It becomes impregnated with wax but it is absent in Diptera and Hymenoptera which have no dermal glands, and its function is uncertain.

Cuticular waxes. The waxes of the epicuticle have the important function of protecting the insect from loss of water by transpiration. They vary in character from soft greasy materials as in *Periplaneta*, to hard crystalline substances, as in *Tenebrio* larva or the pupa of *Pieris*. If the insect, with its spiracles occluded, is exposed to an unduly high temperature the crystalline wax begins to loosen and the rate of water loss increases rapidly. The drier the conditions under which the insect has to live, the higher is this 'transition temperature' (Fig. 1.4). Thus the waterproofing of the insect resembles the former waterproofing of a packet of cereals, in which thin paper impregnated with wax took the place of the wax-impregnated sclerotin and cement layers of the insect.

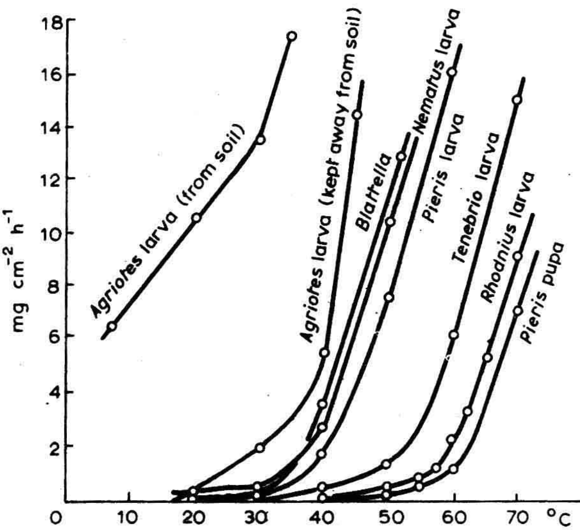

FIG. 1.4 Rate of transpiration from insects, with spiracles sealed, in relation to temperature (after Wigglesworth).

If the surface of the insect cuticle, notably the softer areas of the cuticle, are gently rubbed against an abrasive dust (such as fine Linde powder) the 'wax layer' is locally removed; the endings of the epicuticular channels are exposed, and the polyphenols in the epicuticle are again accessible to darkening in ammoniacal silver. In dry air the insect so treated rapidly loses water and dies. But if kept in a moist atmosphere a fresh layer of sclerotin and wax is secreted;