

# THE PRINCIPLES OF INSECT PHYSIOLOGY

*by*

V. B. WIGGLESWORTH

M.A., M.D., F.R.S.

READER IN ENTOMOLOGY IN THE LONDON SCHOOL OF  
HYGIENE AND TROPICAL MEDICINE

*With 316 illustrations*

THIRD EDITION.

1947

|                        |   |   |   |   |                        |
|------------------------|---|---|---|---|------------------------|
| <i>First Published</i> | . | . | . | . | <i>June 29th 1939.</i> |
| <i>Second Edition</i>  | . | . | . | . | <i>February 1944</i>   |
| <i>Third Edition</i>   | . | . | . | . | <i>1947</i>            |

## PREFACE

INSECTS PROVIDE an ideal medium in which to study all the problems of physiology. But if this medium is to be used to the best advantage, the principles and peculiarities of the insect's organization must be first appreciated. It is the purpose of this book to set forth these principles so far as they are understood at the present day. There exist already many excellent text-books of general entomology; notably those of Imms, Weber and Snodgrass, to mention only the more recent. But these authors have necessarily been preoccupied chiefly with describing the diversity of form among insects; discussions on function being correspondingly condensed. In the present work the emphasis is reversed. Structure is described only to an extent sufficient to make the physiological argument intelligible. Every anatomical peculiarity, every ecological specialization, has indeed its physiological counterpart. In that sense, anatomy, physiology and ecology are not separable. But regarded from the standpoint from which the present work is written, the endless modifications that are met with among insects are but illustrations of the general principles of their physiology, which it is the aim of this book to set forth. Completeness in such a work is not possible, or desirable; but an endeavour has been made to illustrate each physiological characteristic by a few concrete examples, and to include sufficient references to guide the student to the more important sources.

The physiology of insects is to some the handmaid of Economic Entomology. For although it is not the purpose of physiology to furnish directly the means of controlling insect pests, yet the rational application of measures of control—whether these be insecticides of one sort or another, or artificial interferences with the insect's environment—is often dependent on a knowledge of the physiology of the insect in question. Physiology may thus serve to rationalize existing procedures, or to discover the weak spots in the ecological armour of a species. A knowledge of the ecology of a species is always necessary to its effective control; its ecology can be properly understood only when its physiology is known.

# CONTENTS

| CHAP.   | PAGE |
|---|------|
| PREFACE   | v    |
| I DEVELOPMENT IN THE EGG  | 1    |
| References  |      |
| II THE INTEGUMENT   | 16   |
| Properties of the cuticle. Formation and shedding of the cuticle.   |      |
| References  |      |
| III GROWTH  | 34   |
| Moulting. Metamorphosis. Determination of characters during post-embryonic development. Regeneration. Diapause. References  |      |
| IV MUSCULAR SYSTEM AND LOCOMOTION   | 77   |
| Anatomy and histology. Physiological properties of insect muscles. Locomotion. References   |      |
| V THE NERVOUS SYSTEM  | 93   |
| Nervous system. Visceral nervous system and associated glands. References   |      |
| VI SENSE ORGANS : VISION  | 108  |
| Compound eye. Simple eyes. References   |      |
| VII SENSE ORGANS : MECHANICAL AND CHEMICAL SENSES   | 131  |
| Mechanical senses. Hearing. Chemical senses. Temperature and humidity. References   |      |
| VIII BEHAVIOUR  | 157  |
| Kinesis and related phenomena. Orientation. Co-ordinated behaviour. References  |      |
| IX RESPIRATION  | 182  |
| Tracheal system. Development of the tracheal system. Transport of oxygen to the tracheal endings. Elimination of carbon dioxide. Respiration of aquatic insects. Respiration of endoparasitic insects. Respiratory function of the blood. Regulation of respiratory movements. References |      |
| X THE CIRCULATORY SYSTEM AND ASSOCIATED TISSUES   | 218  |
| Circulatory system. Haemolymph. Haemocytes. Pericardial cells and so-called 'nephrocytes'. Fat body. Oenocytes. Light-producing organs. References  |      |
| XI DIGESTION AND NUTRITION  | 254  |
| Fore-gut. Peritrophic membrane. Mid-gut. Hind-gut. Secretions of the alimentary canal. Digestion of some skeletal and other substances of plants and animals. The rôle of lower organisms in digestion. Nutrition. References   |      |

| CHAP. |  | PAGE |
|-------|--|------|
| XII   | EXCRETION  | 299  |
|       | Urine. Intermediary nitrogen metabolism. Malpighian tubes. Histophysiology of the Malpighian tubes. Accessory functions of Malpighian tubes. Malpighian tubes during moulting and metamorphosis. Cephalic excretory organs and intestinal excretion. Storage excretion. References |      |
| XIII  | METABOLISM   | 325  |
|       | Chemical transformations. Some chemical products of insects. Pigment metabolism. Respiratory metabolism. References  |      |
| XIV   | WATER AND TEMPERATURE  | 354  |
|       | Water relations. Temperature relations. References   |      |
| XV    | REPRODUCTIVE SYSTEM  | 376  |
|       | Female reproductive system. Male reproductive system. Mating, impregnation and fertilization. Some factors controlling fertility and fecundity. Special modes of reproduction. Sex determination. Transmission of symbiotic micro-organisms. References                            |      |
|       | INDEX  | 413  |

## Chapter I

### Development in the Egg

**Cuticular membranes of the egg: the chorion**—Most insects begin their independent life within an egg. When the egg is laid it is enclosed by two envelopes, the chorion and the vitelline membrane. The egg-shell or chorion is the product of the follicular cells in the ovary of the mother (p. 380). It consists typically of two layers; a relatively thick endochorion, composed of a scleroprotein, 'chorionin' <sup>43</sup> and a very thin outer layer, the exochorion, applied like a varnish over the surface. Sometimes the exochorion is perhaps the final product of the follicular cells, but often it is indistinguishable from the secretion applied to the eggs by the accessory or colleterial glands in the oviducts. This secretion secures the eggs to the surface on which they are laid; or it may serve to bind them together into a compact capsule or oötheca, as in Blattidae and Mantidae (p. 381).

The chorion may be thin and flexible, as in the eggs of such insects as *Tenebrio*, which are laid in protected situations; usually it is more or less rigid, as in the exposed eggs of Lepidoptera, Hemiptera, &c. In Phasmidae, and likely enough in other groups, it is strengthened by the incorporation of lime in its substance.<sup>28</sup> In most insects it protects the egg from loss of water by evaporation; but it is not completely impermeable to water, for insect eggs kept under too dry conditions may fail to hatch, in some cases because the embryo within is desiccated, in others because the chorion itself becomes too hard for the young insect to compass its escape.<sup>8, 12</sup>

Respiration may take place through the general surface of the egg when the chorion is thin; but some eggs show structural adaptations which combine rigidity with the needs of respiration. In many Diptera the chorion is made up of little vertical columns, with the intervening spaces occupied at first by fluid, but later by air; or extensive air-filled crypts may develop in the shell, widely spread or restricted to some limited area.<sup>27</sup> Similarly, in Locustids, respiration may take place through the general surface by means of superficial alveoli containing air, or at some region excavated to form a large reservoir.<sup>9</sup> The air sacs in the cap of Anoplura eggs, and the thin-walled evaginations of the chorion in Hemiptera, are likewise regarded as respiratory structures.<sup>47</sup>

**The vitelline membrane** originates from the cell wall of the ovum. In grasshoppers <sup>40</sup> and many other insects it remains a delicate structure and disappears as soon as development begins. In Tachinidae and other Diptera it is possibly of twofold origin—an inner oöplasmic zone, and an outer chorial zone, which is at first thick and viscous but later condenses to form a tough membrane <sup>27</sup>; muscid eggs in moist conditions will continue their development within this sheath after the chorion has been stripped off.<sup>48</sup> In *Dytiscus*, also, the vitelline membrane is a very definite structure.<sup>4</sup>

**The serosal cuticle**—Later in development a layer of epithelium, the serosa, is formed beneath the vitelline

membrane; and this may lay down another cuticle. In *Dytiscus* it is a stout laminated structure which has been called the 'secondary vitelline membrane'.<sup>4</sup> In the grasshopper *Melanoplus* it closely resembles the ordinary integument of the insect (p. 16); consisting of two layers, (i) a thin 'yellow cuticle', responsible for the impermeability of the egg membranes for salt ions,<sup>28</sup> secreted at 6 or 7 days after laying (at 25° C.), and (ii) a laminated white cuticle, composed largely of chitin (p. 19), apparently free from protein, secreted during the next week (Fig. 1). When complete this inner layer is generally thicker than the chorion and is responsible for the toughness of the grasshopper's egg.<sup>40</sup>

**Absorption of water**—Eggs laid in moist surroundings may absorb water through their cuticular membranes. This was first noted by Rathke (1844) in the eggs of *Grylotalpa* from damp soil, and in the aquatic Trichoptera; it has since been observed in many other insects.<sup>8, 32</sup> In *Dytiscus* the egg, at first easily deformed by pressure, becomes tense and hard, increasing in length from 1.2 to 2.25 mm.; the chorion splits and falls away and the egg is enclosed only in the vitelline membrane and serosal cuticle.<sup>4</sup> The egg of *Locusta migratoria*, which will develop normally only in moist soil, increases in weight from 6.3 mg. to 14 mg., the water content increasing from 52 to 82 per cent.<sup>32</sup> As the egg swells the chorion usually cracks and peels away; but if kept moist it stretches and remains intact until hatching.<sup>40</sup> In the Capsid *Notostira*, water is absorbed from the tissues of the plant in which the egg is laid. Absorption begins about 55 hours after laying, at the same time as the formation of tissue becomes visible, and it reaches its maximum (a 75 per cent. increase) in about 160 hours (Fig. 2). In this case the chorion is

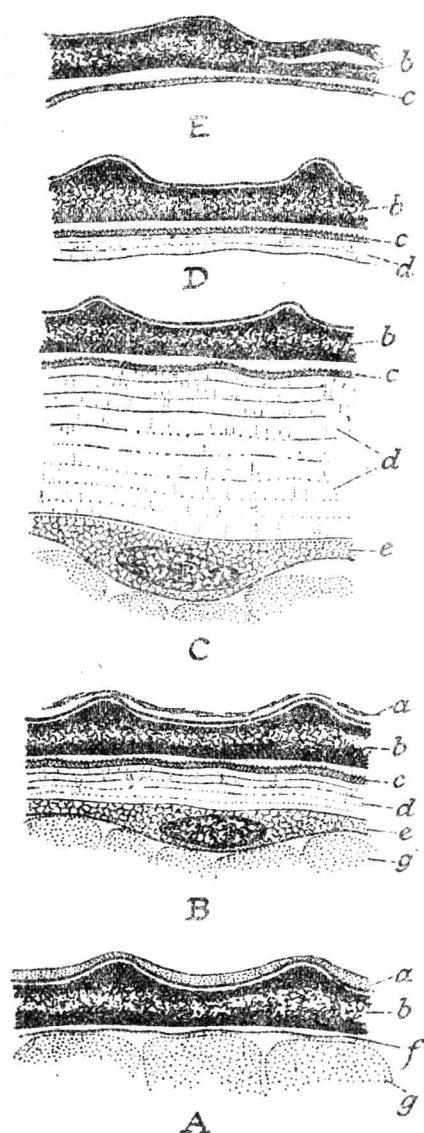


FIG. 1.—Egg membranes in *Melanoplus differentialis* (after SLIFER)

A, egg newly laid; B, egg incubated 11 days at 25° C. (serosa has laid down the yellow cuticle and part of white cuticle); C, egg incubated 21 days (serosal cuticle fully formed); D, egg 3 days before hatching (serosal cuticle much reduced); E, egg ready to hatch (nothing remains but chorion and the yellow part of the serosal cuticle); a, temporary secretory layer over chorion; b, chorion; c, yellow cuticle; d, white cuticle; e, serosa; f, vitelline membrane; g, yolk.

resistant to distension; the swelling

egg is prevented from bursting only by the formation over the yolk of a cuticular plug laid down by the serosa and probably comparable with the serosal cuticle of other insects.<sup>34</sup> The eggs of Aleurodids are implanted into the leaves of plants by a stalk which bears a thin-walled terminal bladder; this is able to extract water from the plant and so make up for loss of water from the egg surface<sup>46</sup> (Fig. 3).

Special structures for the absorption of water probably occur in other insects also. Thus at the posterior pole of the egg of the grasshopper *Melanoplus* there is a small circular area in the 'yellow cuticle' secreted by a group of enlarged and modified serosal cells. The chorion over this region is more permeable than elsewhere. The whole structure is termed the 'hydropyle', since it is responsible for the uptake of water which begins as soon as the yellow cuticle is formed.<sup>40</sup> In all cases the absorption of water is probably an active process, and not due simply to osmosis<sup>8</sup>; in *Melanoplus*, for example, the uptake varies with metabolic activity irrespective of the membranes present.<sup>42</sup>

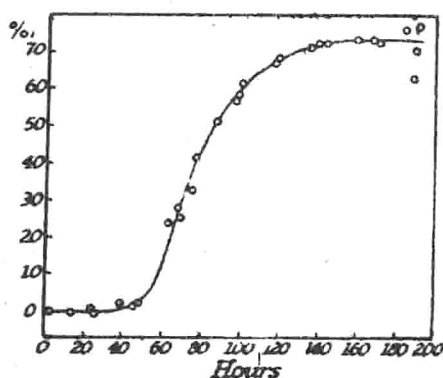


FIG. 2.—Increase of weight in eggs of *Notostira erratica* at 28° C. in contact with neutral water (after JOHNSON)

Ordinate: percentage increase in wet weight. Abscissa: hours after oviposition.

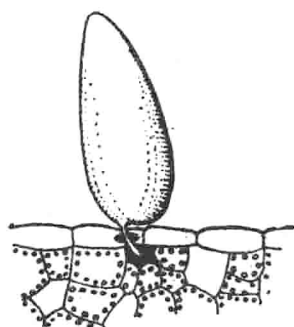


FIG. 3.—Egg of *Trialeurodes vaporariorum* with the process, through which water is absorbed, inserted into a leaf and surrounded by cement (after WEBER)

In the eggs of endoparasitic Hymenoptera, laid in the body fluids of other insects, the egg-shell is reduced to an excessively delicate envelope which must be permeable to many substances in the blood of its host.

**Early development**—Fertilization of the egg takes place about the time of laying (p. 388). The fertilized nucleus lies embedded in the yolk, surrounded by cytoplasm which ramifies throughout the egg enclosing in its meshes the yolk spheres. At the surface of the egg there is a zone where the cytoplasm is rather denser and is free from yolk; this is the cortical layer, the 'Keimhautblastem' of Weismann.<sup>48</sup> The nucleus divides without segmentation of the plasma; the daughter nuclei are surrounded by islands of cytoplasm connected to one another and to the cortical layer by cytoplasmic strands. At first these cleavage divisions take place simultaneously throughout the egg; but after a definite number of mitoses, peculiar to each species, the nuclei begin to divide independently. The cleavage nuclei arrange themselves in a single layer enclosing a spherical or pyriform space in the centre of the egg (Fig. 4, A). As they divide they move towards the periphery of the egg and



the space which they surround expands and changes its form and becomes poorer in cytoplasm than the yolk elsewhere in the egg (Fig. 4, B). The advancing cells leave behind some of their number to form vitellophags or yolk nuclei. Ultimately the nuclei reach the cortical layer (Fig. 4, C). The cytoplasm, previously trailing like a tail behind each nucleus, is drawn in; the lateral divisions between the cells now appear; then their inner limits are formed, a basement membrane is laid down, and the formation of the blastoderm is complete. In a limited ventral region of the egg the cells of the blastoderm become higher and form a cylindrical epithelium; this is the germ band which is later differentiated to form the embryo; the remainder of the blastoderm, made up of flattened cells, forms the serosa.<sup>14, 51</sup>

It is not known what mechanism ensures the simultaneous mitosis of the nuclei in the early stages of segmentation; we shall see the same phenomenon

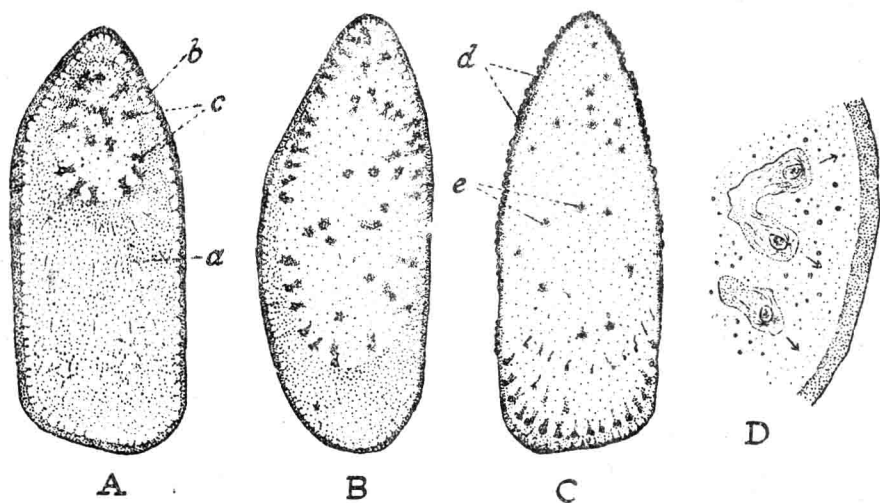


FIG. 4

A, B, and C, longitudinal sections of eggs of *Pieris*, showing migration of cleavage nuclei into the cortical layer (after EASTHAM). A, 6 hours after laying; B, 8 hours; C, 10 hours, nuclei of anterior pole have entered the cortical layer to form the blastoderm. a, yolk; b, cortical layer; c, cleavage nuclei; d, blastoderm; e, yolk cells. D, cleavage nuclei in *Calliphora* approaching the cortical layer (after STRASSBURGER).

in the healing of wounds (p. 63). Nor is it known whether the nuclei migrate actively towards the surface or whether they are carried along passively by an outward streaming of the plasma.<sup>51</sup> In *Calliphora* the nuclei are always orientated so that the centriole is directed towards the surface of the egg, and after each cell division the inner daughter nucleus swings round so that the centriole looks outwards (Fig. 4, D); here the cells or nuclei are actively concerned.<sup>41</sup> But there is also evidence of an outward movement of the cytoplasm independent of the nuclei. In *Pieris* there are elongated flecks radiating in the untraversed regions of the yolk<sup>14</sup>; and in *Tenebrio*, granules in the yolk plasma wander through the reticulum ahead of the nuclei to reach the cortical layer. During the first four hours after the egg of *Tenebrio* is laid there is an outward movement of the plasma which causes a gradual thickening of the cortical layer, especially in the region of the presumptive germ band,

ventrally and laterally at the posterior pole; so that in this insect the future position of the germ band can be made visible by staining *before* the entry of nuclei.<sup>17</sup>

**Organization**—The nuclei in the egg contain the chromosomes bearing the genes which are responsible for many of the hereditary characters (p. 53); but the general form and organization of the embryo is controlled by agents located in the plasma at the periphery of the egg, quite remote from the dividing nuclei. The organism seems from the outset to be something to which the constituent nuclei are subservient, their function determined by their position in relation to the whole.

Two centres control the beginnings of organization in the insect egg.

(i) At the posterior pole there is an *activation centre* (Bildungszentrum) which influences the peripheral zone of the egg in such a way that it can proceed to the subsequent stages of development. It does this probably by giving off a material substance which permeates the egg from behind forward. If this centre is eliminated at a very early stage by excision or exposure to ultra-violet light, cleavage and migration of nuclei occur as usual, but the resulting blastoderm is solely of the extra-embryonic type; no germ band is formed.<sup>36</sup> Elimination of other parts of the egg have not this effect; if the anterior parts are removed the embryo is merely smaller and the germ band displaced backwards (Fig. 6, B).<sup>30</sup> As the influence of this centre spreads forwards, during the early hours of development, increasingly large areas around the posterior pole must be excised or burned if the formation of the embryo is to be prevented. Within a few hours, although there is still no visible differentiation of any sort within the egg, the process of activation is complete (in *Tenebrio* there are at this time 64 cleavage nuclei<sup>17</sup>). A centre of this kind has been demonstrated in the dragon-fly *Platycnemis* (Fig. 5),<sup>36</sup> in the ant *Camponotus*,<sup>30</sup> in the weevil *Sitona*,<sup>30</sup> the bean beetle *Bruchus*,<sup>6</sup> and the mealworm *Tenebrio*.<sup>17</sup>

(ii) Towards the middle of the presumptive germ band, in a position corresponding with the future thorax of the embryo, there is a *differentiation centre*. As soon as this centre has been induced to begin its activity, under the influence of the activation centre, it provides the focus from which all subsequent processes of development spread forwards and backwards. It is a part of the cortical plasma zone with no visible difference from any other part. But when the cleavage nuclei reach the surface and form the blastoderm they accumulate first in the region of this centre. Later, the blastoderm is thickest here; cell divisions are most numerous; and differentiation of body segments and appendages extends forwards and backwards from this point. The differentiation centre is in fact the place where visible differentiation of form begins in point of time and at which, later, the degree of differentiation at any moment is greatest. A centre of this type, which determines the future function of the nuclei that come into its sphere of influence, has been demonstrated in Hemiptera (*Pyrrhocoris* <sup>36</sup>), Odonata (*Platycnemis* <sup>36</sup>) (Fig. 5), Hymenoptera (*Camponotus* <sup>30</sup> and *Apis* <sup>34</sup>), Lepidoptera (*Ephesia* <sup>35</sup>), and Coleoptera (*Tenebrio* <sup>17</sup>). It is said to act, not by giving out a diffusible substance, but by initiating a contraction wave in the yolk system, spreading forwards and backwards and forcing the blastoderm cells, hitherto distributed uniformly, to fill the space that is left. Indeed, artificial depressions in the

yolk system caused by heat or by ultra-violet rays will bring about this directed movement of blastoderm cells to any desired part of the egg.<sup>36</sup>

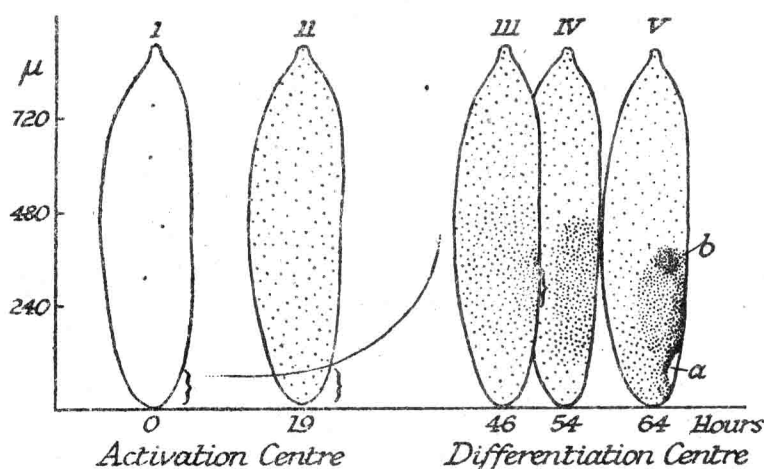


FIG. 5.—Organization in egg of *Platynemius pennipes* (Odonata) (after SEIDEL)

Ordinate: length of egg in  $\mu$ . Abscissa: time of development in hours at  $21.5^{\circ}\text{C}$ . (i) 0 hours, stage with 4 nuclei (position of activation centre indicated by bracket); (ii) 19 hours, stage with 236 nuclei. Influence from activation centre spreads forward as indicated by the curved line; (iii) 46 hours, cells accumulating first in region of differentiation centre indicated by bracket; (iv) 54 hours, germ band forming; (v) 64 hours, germ band fully formed: a, point where germ band sinks into the yolk; b, cephalic lobes forming.

**Determination**—Until the differentiation centre has performed its function, the egg is capable of extensive 'regulation'; that is, complete formation

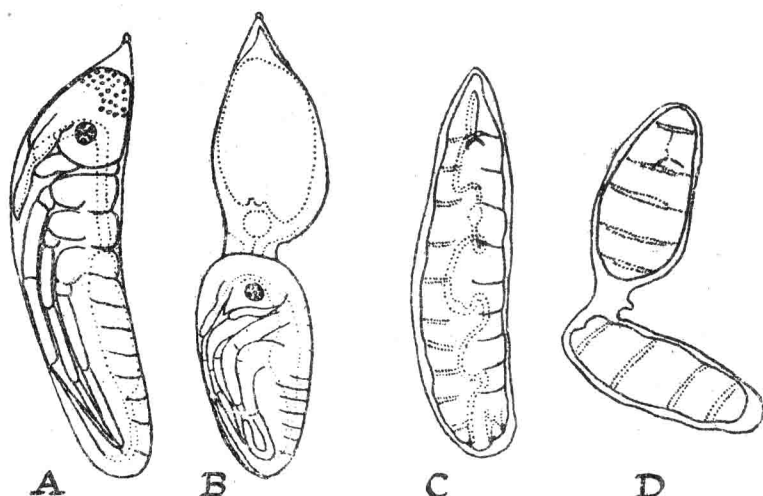


FIG. 6

A, *Platynemius pennipes*; normal embryo shortly before hatching; B, dwarf embryo of the same age produced by ligaturing the egg in the middle at the stage with 4 cleavage nuclei (after SEIDEL); C, Muscid larva, normal embryo shortly before hatching; D, embryo of *Calliphora* ligatured at the stage with 16 nuclei, showing mosaic development (from SEIDEL, after REITH and PAULI).

from reduced material. If the egg of *Platynemius* is ligated in the middle soon after laying, a differentiation centre appears in each half in a definite position in harmony with the diminished whole, so that double dwarfs are

developed.<sup>36</sup> In the egg of the honey-bee 12 hours after laying, the 'potency' to form all parts of the body is still so concentrated around the differentiation centre that about one-fifth of the entire egg can be removed at the anterior end and development of a complete dwarf embryo follows. As development proceeds, the 'potency' to form the different regions spreads outward over the egg; and in the bee, by 24 hours after laying, the prospective functions of all the main parts are finally determined.<sup>34</sup> The egg is then a 'mosaic' egg. If any part is eliminated, a corresponding region of the completed embryo is missing.

In the greenhouse cricket *Tachycines*, as in *Platynemis* (Fig. 7), the embryonic germ is still capable of well-marked regulation at the time the egg is laid; and if the germ band is divided with a needle, many types of doubling, at first of the whole body and later of individual organs, can be produced.<sup>25</sup> The converse process, the fusion of eggs to form a single embryo, is seen in Phasmids. Senile *Carausius* females will lay eggs containing anything up to 10 oöcytes which fuse to form a compound egg. If fusion takes place early in development, regulation occurs and a normal insect results; if fusion takes place later, double monsters are produced, doubling being most frequent at the anterior end where differentiation first occurs.<sup>10</sup> Other Phasmid eggs may have two micropyles; in them there is no fusion where the embryos come in contact; each develops as far as it is able in the space available.<sup>10</sup>

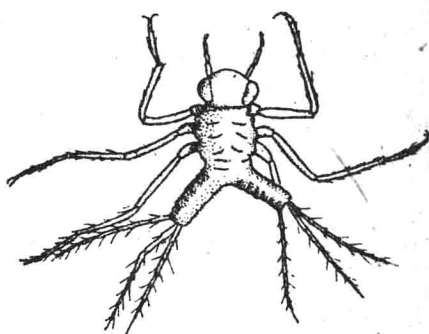


FIG. 7.—*Platynemis pennipes*, showing doubling of the posterior part of the body as the result of dividing the prospective germ band by ultra-violet irradiation at the stage when the cells were beginning to collect around the differentiation centre (Fig. 5 (iii)) (from a photograph by SEIDEL)

Determination is completed at different times in different insects. In the bee, as we have seen, it is complete in 24 hours after laying<sup>34</sup>; in the bean beetle *Bruchus* in 6½ hours<sup>6</sup>; while in Muscidae<sup>29, 30</sup> and in *Drosophila*<sup>18</sup> the egg has already reached the 'mosaic' state by the time it is laid. The process of determination, like the changes which precede it, is likewise independent of the nuclei in the egg. In *Platynemis*, regulation is still possible in the late blastoderm stage.<sup>36</sup> In *Sitona*, the parts are fully determined by the time the blastoderm is formed.<sup>30</sup> In *Bruchus*, the posterior cytoplasmic regions of the egg are determined before the entrance of the cleavage nuclei, the more anterior parts shortly after the cleavage cells arrive.<sup>6</sup> Whereas in Muscid eggs, determination in the cortical plasma is complete before cleavage has begun (Fig. 6, D).<sup>30</sup> In all cases, determination of the main outline of the body takes place before the individual organs. When the process is complete it is possible to map out the prospective embryo by destroying localized spots on the egg surface with ultra-violet rays. In *Platynemis* it has been found that at first the embryonic map delimited in this way covers almost the entire egg; as the cells congregate to form the embryonic rudiment the various zones become concentrated around the differentiation centre towards the posterior half of the egg.<sup>36</sup>

**Determination of imaginal structure in the egg**—In *Drosophila*, as in the Muscidae, the egg at the time of laying is a mosaic egg. Local injuries effected by ultra-violet light during the first 4 hours after laying cause local defects in the resulting larva. But the imaginal characters are unaffected; in respect to imaginal characters the egg is still capable of 'regulation'. But if the egg is irradiated similarly 7 hours after laying or later (between 4 and 7 hours the egg is so sensitive to treatment with ultra-violet light that experiments cannot be made during that period) localized defects are produced in the corresponding region of the adult epidermis without any visible effect during larval development.<sup>18</sup> Similar results can be obtained by puncturing the egg at different levels with a needle.<sup>21</sup> Indeed it can be shown that during this second developmental period a wave of 'determination' in respect of imaginal characters spreads backwards from the thorax until the egg becomes a mosaic egg in respect to adult structure also—just like the determinative change that spreads from the differentiation centre of *Platycnemis* and other 'regulation' eggs.

**Later development**—The later stages of embryonic development, the formation of the germ layers, the sinking of the embryo into the yolk and its subsequent revolution around the egg (blastokinesis), in the course of which the invaginated part of the blastoderm (the amnion) and the superficial part (the serosa) are absorbed into the body of the embryo, the growth of the embryo around the yolk, the formation and histological differentiation of the various organs and tissues, and the variations in these processes which occur in different groups of insects are fully described in the text-books.

**Factors controlling the rate of development**—The physiological control of the separate processes of later development has not been studied; but much information exists about the factors that determine the rate of development as a whole. The most important factor is temperature (p. 366): within the vital limits of each species development is accelerated by high temperatures and retarded by low, so that below a given temperature, peculiar to each species, no development takes place; growth is restored when the temperature is raised.

In many insects development is delayed by low humidity in the surrounding air.<sup>8</sup> At 20° C. the egg of *Sitona* (Col.) has an incubation period of 10½ days at a relative humidity of 100 per cent., 21 days at a humidity of 62 per cent.,<sup>2</sup> and in *Lucilia* there is a linear relation between saturation deficiency and the duration of egg development.<sup>18</sup> Presumably the delay under dry conditions is due to lack of water in the egg. For example, at the time of laying the egg of *Notostira* (Capsidae) does not contain enough water for complete development. If it is not given the opportunity of absorbing water (p. 3) embryonic development ceases, recommencing only when water is supplied.<sup>24</sup> Development is delayed from the same cause in the eggs of Aleurodids (p. 3) if laid on drying or wilting leaves,<sup>46</sup> and in the egg of the grasshopper if the 'hydropyle' (p. 3) is covered with material impermeable to water.<sup>40</sup>

Eggs of some insects can remain dormant for long periods in a desiccated state. Those of *Sminthurus* (Collembola), which hatch in moist conditions in 8 or 10 days, will shrivel and collapse if dried. They have been kept in this state for 271 days. When wetted they quickly become spherical again and hatch in 12 days or so.<sup>20</sup> Eggs of the South African locust, *Locusta pardalina*, which hatch in moist soil in about two weeks, have survived desiccation for

3½ years.<sup>8</sup> In such cases it is only at a restricted and usually an early stage of development that the eggs show this resistance.

**Arrested development**—This type of arrested development, controlled directly by external conditions and brought to an end when the temperature or water relations are favourable again, is sometimes termed 'quiescence'. But many insects, particularly those which pass the winter in the egg, undergo a spontaneous arrest of development which supervenes irrespective of the environmental conditions. For this state of dormancy Henneguy proposed the term 'diapause'. We shall discuss later the occurrence of this state in larval, pupal and adult life (pp. 67, 394); here we shall consider diapause only in relation to embryonic development. The arrest takes place at a different stage in different groups. Among Lepidoptera, almost no development occurs until the spring in *Zephyrus betulae*, &c., whereas the larva of *Argynnis paphia*, &c., is fully developed in the autumn<sup>44</sup>; *Orgyia* eggs cease developing when the germ band has formed and is beginning to give rise to mesoderm.<sup>11</sup>

**Diapause in *Bombyx mori***—The classic example of diapause in the egg is afforded by the silkworm. Silkworm eggs laid in the autumn will not develop immediately even if kept warm; growth is completely arrested at an early stage. As was shown originally by Duclaux,<sup>18</sup> they will not hatch even in the spring if they have been kept warm (15–20° C.) throughout the winter; they will complete their development only if they have been exposed to a temperature around 0° C. for several months. Some races of *Bombyx mori* are single brooded or 'univoltine', so that every generation shows a prolonged period of arrest during embryonic development; other races are 'bivoltine' or even 'tetravoltine'; in these there are one or more uninterrupted generations during the summer before the winter generation of diapause eggs is produced.

The mechanism of diapause and the mode of action of low temperature in bringing it to an end (this 'reactivation' by cold is a characteristic of diapause at all stages of growth) will be discussed in conjunction with post-embryonic development (p. 67). But some indication of the kind of physiological factors that are at work is given by the study of voltinism in the silkworm. Voltinism is to some extent hereditary; but when the races are crossed, clear cut segregation does not occur. For the voltinism of the offspring is influenced by the temperature at which eggs of the preceding generation were incubated (eggs incubated at 25° C. tend to produce moths laying hibernating eggs; those incubated below 15° C. tend to produce non-hibernating eggs) and by the effect of temperature on the larva. The voltinism of the eggs seems in fact to be determined by some influence from the somatic cells of the mother. For a batch of eggs from a single female is generally uniform as regards voltinism; and if the ovaries of one race are transplanted into another race during the larval stage, the eggs from these ovaries always show the voltinism of their new host.<sup>45</sup>

**Diapause in *Melanoplus***—There are all degrees of dormancy between a simple quiescence and a true diapause. The silkworm is an extreme example of the latter type; the grasshopper *Melanoplus differentialis* may be taken as an example of arrested development which is much more readily influenced by environmental factors.

In the winter generation of *Melanoplus* growth ceases when the embryo



is fully differentiated but quite small.<sup>7, 39</sup> It remains in this state without further cell divisions until the spring. Then growth is vigorously resumed; the embryo undergoes blastokinesis, moving around the lower end of the egg,

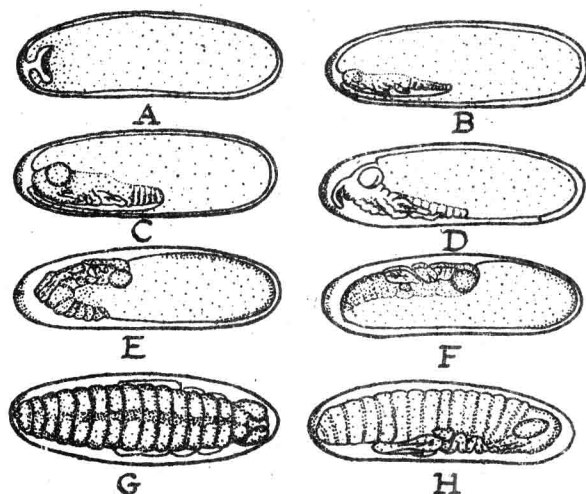


FIG. 8.—Embryonic development in *Melanoplus differentialis* (after BURKHOLDER)

A, appearance of germ band (5th day); B, embryo sunk into the yolk (10th day); the peak of oxygen consumption occurs at this stage; C, embryo in diapause; D, embryo beginning to revolve; amnioserosal membranes have ruptured; E, embryo half revolved; F, early revolution completed; G, dorsal view, and H, lateral view after the dorsal line has fused and lateral rotation has taken place.

rotating on its long axis, and finally growing dorsally to enclose the remaining mass of yolk (Fig. 8).<sup>39</sup> These changes in growth activity are marked by changes in respiration (p. 344): there is a peak of oxygen uptake during the initial stage of growth (which occupies about three weeks at 25° C.), a long period of very low oxygen uptake during the diapause, and a rapid rise when growth is resumed (Fig. 9, B).

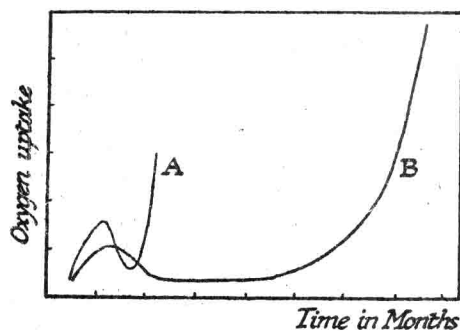


FIG. 9.—Oxygen uptake in eggs of *Melanoplus differentialis*

A, eggs at constant temperature of 27° C.; B, eggs kept at outdoor temperature and oxygen uptake estimated at that temperature (after BODINE).

and once development has been resumed it cannot be arrested again by cold.<sup>5</sup> Moreover, *Melanoplus* eggs kept throughout at 25° C., which appear to have no diapause, still show an initial peak of oxygen uptake succeeded by a fall (Fig. 9, A); whereas in the eggs of *Chortophaga* (a grasshopper which

This rhythm of development and arrest in the *Melanoplus* egg is not so fixed as that in *Bombyx mori*; for at any time during the winter a constant high temperature will initiate development, and the diapause can be prevented altogether if the eggs are kept at 25° C. from the time of laying. But an inborn rhythm probably exists in this insect also; for the longer is the egg exposed to cold in the winter, the greater is the rate of development upon returning to 25° C.;

spends the winter as a nymph) the oxygen uptake rises steadily as development proceeds.<sup>5</sup>

**Dormancy in mature embryo**—Some insects complete their development in the egg before becoming dormant. That is so in the beetle *Timarcha tenebricosa*. The egg containing the fully developed larva may be kept at 15° C. for 6 months without hatching, and if the larva is extracted it soon dies. Whereas if kept at 5° C. for some time the larvae will survive extraction; and if exposed to severe frost for several months they all hatch simultaneously a few days after return to room temperature.<sup>1</sup> Mosquitos belonging to the genus *Aedes* are another example of this type. The eggs containing fully formed larvae will survive in a dry state for several months (eggs of *Aedes aegypti* have hatched after keeping for 40 days at 28° C. in air dried with sulphuric acid<sup>8</sup>); upon immersion in water many of them hatch within a few minutes.

**Pleuropodia**—In the mature embryo a pair of glandular organs is often present on the first abdominal segment. These were named 'pleuropodia' by Wheeler, who showed that they are homologous with the appendages of the first abdominal segment. They appear to be best developed in the less specialized groups (Blattidae, Mantidae and other Orthoptera, some Coleoptera); less so in other Coleoptera and Hemiptera; while in Hymenoptera and Lepidoptera they are vestigial or wanting.<sup>22</sup> Sometimes, as in *Belostoma* and *Ranatra* (Hem.),<sup>22</sup> they sink into the body wall, their distal ends prolonged into long thread-like structures forming a tuft projecting from the orifice (Fig. 10); sometimes, as in Orthoptera, they are stalked bodies projecting from the surface, made up of a single layer of very large cells.<sup>23</sup> They attain their greatest size just before the insect hatches, and then degenerate.

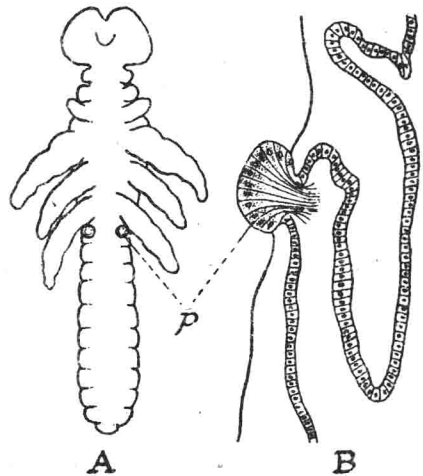


FIG. 10

A, isolated early embryo of *Ranatra fusca* to show position of pleuropodia; B, detail of pleuropodia as seen in sagittal section. p, pleuropodia (after Hussey).

The function of these organs may vary from one insect to another. In the viviparous Polyctenid *Hesperoctenes* their processes form a nutritive sheath which later secretes a protective cuticle (p. 398); in *Rhodnius* they are perhaps responsible for producing the iridescent cuticle which appears over embryo and serosa during blastokinesis<sup>26</sup>; and other secretory and excretory functions have been ascribed to them.<sup>22, 33</sup> In *Melanoplus* the inner white layer of the serosal cuticle (p. 2) is digested and dissolved shortly before hatching, the outer yellow cuticle being unchanged (Fig. 1, D, E). The enzymes responsible for this digestion are secreted by the pleuropodia; for if these are excised before digestion has occurred, the embryo develops normally but is unable to break through the cuticle, which remains thick and tough (Fig. 11).<sup>40</sup> This process is analogous to what happens in the insect cuticle during moulting (p. 26).

**Hatching**—When its development is complete the embryo is faced with the



problem of breaking the membranes and escaping from the egg. The main obstacles are the chorion, the vitelline membrane sometimes (in *Muscids*), and the serosal cuticle (in *Dytiscus*, *Acridiids*, and perhaps in other insects). In addition to these, many insects lay down a provisional cuticle which is later shed and replaced by a more substantial cuticle before hatching takes place. If this provisional or embryonic cuticle is laid down at a very early stage, as in the *Aphidae*,<sup>19</sup> it is a simple sac without appendages (perhaps this is not distinguishable from the serosal cuticle). If it is formed later, when the limbs are differentiated, each of these is invested in an unsegmented sheath, as in most hemimetabolic insects (*Orthoptera*, *Hemiptera*, *Neuroptera*, &c.) and in some holometabolic forms such as *Tenebrio* (*Col.*). Thus the embryo at the time of hatching is frequently enclosed by three sheaths.

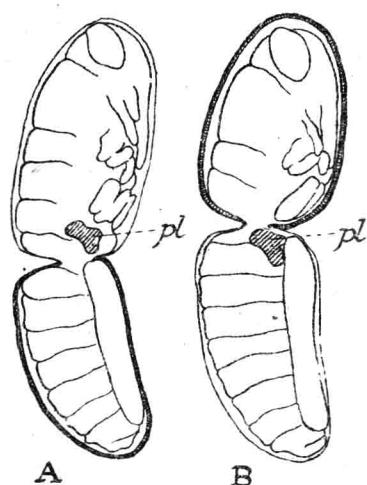


FIG. 11.—Diagram of an experiment to demonstrate the origin of the hatching enzyme in *Melanoplus* from the pleuropodia (after SLIFER)

Eggs with chorion removed are ligatured: A, behind pleuropodia; B, in front of pleuropodia. The white inner layer of the serosal cuticle is dissolved in the half containing the pleuropodia; the thin yellow outer layer is not attacked. *pl*, pleuropodia.

Many insects are provided with cuticular structures, spines or blades, hard plates or eversible bladders, which are used to cut through the membranes of the egg or to force off a preformed egg-cap. These 'hatching spines' are developed on the embryonic cuticle when this is present (in *Hemiptera*, *Neuroptera*, *Anoplura*, &c.); when such a cuticle is absent, they occur upon the true skin of the larva and are thus retained throughout the first instar (in *Nemtocera*, *Aphaniptera*, *Carabids*, *Dytiscids*, *Chrysomelids*, &c.).<sup>15, 37</sup>

The mechanism of hatching is pretty constant. The first sign that it is imminent is the appearance of pumping movements in the pharynx indicating that the insect is swallowing the amniotic fluid. This has been observed in *Agrion* (*Odonata*) and *Hydrobius* (*Col.*)<sup>3</sup> and in many other insects.<sup>37</sup> Swallowing continues until all the fluid is absorbed and the insect fills the shell completely.

It may then rupture the chorion and the other membranes by simple muscular force (we have seen that the serosal cuticle may first be weakened by digestion of the inner parts (p. 11), or it may contract the posterior parts of its body and, by driving the blood forwards to the head, cause this to burst the shell. The hatching spines may serve to concentrate this pressure at one point of the egg (often the egg-cap, as in *Pentatomidae*) or they may be used deliberately to cut an opening in the chorion (as in *Aphaniptera*). The *Lepidoptera* simply gnaw their way out with the mandibles; the *Muscidae* tear a hole in the vitelline membrane with their mouth hooks.<sup>37</sup>

Often, when the amniotic fluid has been swallowed, air diffuses through the chorion and the insect may increase its bulk by swallowing this. Where the insect has to pass the narrow orifice that was closed by the egg-cap, it does so by peristaltic waves of muscular contraction passing forwards over the