

SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 122, NUMBER 9

# INSECT METAMORPHOSIS

BY

R. E. SNODGRASS

Collaborator of the Smithsonian Institution and of the U. S. Department of Agriculture



(PUBLICATION 4144)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
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The Lord Baltimore Press  
BALTIMORE, MD., U. S. A.

## CONTENTS

	Page
Introduction .....	I
I. Metamorphosis and classification.....	10
II. Hormones and metamorphosis.....	13
Secretory cells of the brain.....	14
The corpora cardiaca, or paracardiaca.....	14
The corpora allata.....	16
Pericardial glands .....	19
Ventral glands of the head.....	19
The prothoracic glands .....	20
The ring gland of cyclorrhaphous Diptera.....	21
The nature of hormonal action.....	23
III. Apterygota .....	24
IV. Plecoptera .....	26
V. Ephemeroptera .....	28
VI. Odonata .....	32
VII. Hemiptera .....	38
VIII. Thysanoptera .....	44
IX. Oligoneoptera, or typical Endopterygota: Neuroptera to Hymenoptera .....	48
X. Larval heteromorphosis .....	61
Parasites with a planidial stage.....	62
Coleoptera .....	62
Neuroptera .....	66
Strepsiptera .....	66
Lepidoptera .....	70
Diptera .....	70
Hymenoptera .....	72
Parasites without a planidial stage.....	75
Diptera .....	75
Hymenoptera .....	77
XI. The pupal transformation .....	82
The epidermis .....	83
The appendages .....	86
The alimentary canal .....	87
The Malpighian tubules .....	93
The fat body .....	95
The oenocytes .....	96
The tracheal system .....	97
The dorsal blood vessel.....	98
The nervous system .....	99
The muscular system .....	101
XII. Muscle attachments and the nature of the pupa.....	107
References .....	111



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By R. E. SNODGRASS

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## INTRODUCTION

Ancient mythologies are replete with stories of the transformation of one creature into another, called metamorphosis. So the early students of natural history who first observed a caterpillar turn into a butterfly had a term ready made for the phenomenon they witnessed, and today in entomology we commonly think of metamorphosis as the transformation of a larval insect into the imago. In so doing, however, we overlook the fact, quite as extraordinary, that a caterpillar hatches from the egg of a butterfly. We might truly say, then, that the real metamorphosis in the life history of the species is that which has changed a young butterfly into a caterpillar, the subsequent change of the caterpillar into the butterfly being merely the return of the metamorphosed young to the form of its parents. The transformation of the caterpillar into the butterfly is a visible event re-enacted with each generation; the change of the young butterfly into a caterpillar has been accomplished gradually through the past evolutionary history of the Lepidoptera. Today, there is not even any recapitulation of the butterfly stage in the ontogeny of the caterpillar; the butterfly's egg develops directly into the caterpillar form of its species. The idea that the caterpillar, because of its abdominal "legs," represents a primitive stage in the ancestry of insects is quite out of harmony with the modern structure of the caterpillar's head and with the fact that the caterpillar has wings developing beneath its cuticle. Both the caterpillar and the butterfly are modern end results of evolution, but along different lines of development.

In attaining their present distinctive forms, the butterfly has followed out the evolutionary path adopted by its adult ancestors, and therefore represents the adult line of descent; the caterpillar, on the other hand, in its evolution has departed from the ancestral path and has become a new and distinct juvenile form of its species. Since the caterpillar leads an independent life in a very efficient manner as an

individual, it would seem that it might be capable of developing its reproductive organs to maturity and thus dispensing with the butterfly stage entirely. The caterpillar, however, has limited powers of locomotion; the winged butterfly, therefore, retains the reproductive function because it can widely distribute the eggs for the next generation of caterpillars and thus prevent overpopulation in any one place. The same principle applies to all winged insects, and it is easy to see the advantages insects have attained in acquiring wings, together with specialized types of feeding organs and organs for mating and egg laying. It is to be presumed then that the specialized forms and habits of many young insects also are of some advantage to the species as a whole. In short, we can readily perceive a reason for metamorphosis, but how the differences between young and adult have come about, and how two distinct creatures can develop from one egg are questions difficult to answer.

Since there can be no doubt that the early insects lived on land and developed without metamorphic changes, the metamorphoses that we know among modern insects are of relatively late origin, and have no relation to the more primitive metamorphoses of the annelids and crustaceans. Even among the insects themselves metamorphosis has been independently developed in several groups, though the reason for it may be deduced from pretty much the same premises in all cases.

Wherever a pronounced metamorphosis occurs in the life of an insect it is generally, but not always, true that the young and the adult lead different lives or inhabit different media, and are structurally modified in adaptation to their individual habitats or ways of feeding. Very probably the presence of functional wings only in the adult stage, or conversely, the flightless state of the young, was an important condition that led to structural differentiation between the juvenile and imaginal stages. The winged adult insect has opportunities of extending its activities far beyond the range of the wingless young insect, and, as is amply shown in modern insects, various new ways of life are open to the winged insect if it is free to develop special structures, particularly feeding organs, that enable it to take advantage of them. Likewise, to the wingless young insect there are presented in nature various possible habitats and sources of food, some of which might better its condition if it were free to make the anatomical adjustments that would accommodate it to a new way of living in some special environment. However, as long as the usual mechanism of inheritance makes it necessary that newly acquired adult characters be transmitted through the young, and that charac-

ters acquired in the juvenile stage must be passed on to the adult, neither the adult nor the young could be free to develop structures that would be detrimental to the other. Consider, for example, the plight of the caterpillar if it had to inherit the mouth parts of the butterfly, or that of a young mosquito equipped with blood-feeding organs but lacking wings. The adult flea, it is true, has mouth parts highly specialized for a blood diet, and still is wingless, but it has substituted the power of jumping for that of flight. The Hemiptera are another exception to the rule that specialized adult mouth parts depend on wings, but here the mouth parts are just as practicable to the flightless young as to the adults.

A prerequisite of metamorphic differentiation between the young and the adult, therefore, is the inhibition of some of the ordinary processes of heredity. The young insect can then vary to any extent by the development of adaptive structures for its own use so long as its new characters are suppressed at the change to the adult; and the adult, on its part, can acquire special feeding organs that would be entirely impracticable to the wingless young. The individual, furthermore, thus derives whatever advantages there may be in living a double life, or that may accrue from inhabiting successively two different media. Moreover, the different specializations of the young and the adult may be mutually advantageous and therefore beneficial to the individual as a whole. The larva, for example, usually becomes the chief, and sometimes the only, feeding stage, thus giving the adult a large measure of freedom for the functions of mating and procreation.

When the divergence becomes too great between the young insect and the adult, especially with regard to habitat, a liaison between the two must be established by compensating instincts in order to maintain continuity of the individual life history. The adult female, for example, must know where to lay her eggs so that the emerging larva shall find its proper food, or be in its appropriate environment. The egg-laying instinct must be more and more precise as the habits of the larva become more restricted. The parent of an aquatic larva has only to deposit her eggs in some suitable place in the water, but the parent of a parasitic larva specific to some particular host must be able to insert her eggs into a member of this same host species. It has been shown by Thorpe (1938, 1939) that the egg-laying response of the adult may be a result of conditioning during the feeding of the larva. Likewise the larva, on its part, must be endowed with an instinct that brings it to undergo its transformation at some place

appropriate for the ecdysis of the winged adult. Most aquatic larvae come out of the water to pupate, some crawl up on rocks or plant stems, others travel inland; the parasitic larva emerges from its host; overwintering species find protection from the cold in concealed places or within the ground, and do not transform until the return of warm weather.

Changes of structure adaptive to environmental conditions, however, are not limited to the postembryonic stages of insects. The embryo itself may acquire adaptive characters as well as the larva. The embryo is commonly said to recapitulate ancestral stages in the evolution of its species, but, shut up in an egg shell, it can hardly be expected to follow in all ways the course of evolution that was practical to its free-living progenitors, and it needs special features for its own purposes. The insect embryo, for example, may have amniotic folds for protection, perhaps a trophamnion for its nourishment, a tooth on its head for breaking out of the egg shell. Then there are those embryonic organs on the first abdominal segment of some insects known as pleuropodia, but which take on special embryonic functions quite foreign to the usual purpose of a leg. All such adaptations of the embryo to life in an egg shell are just as truly aberrations from phylogenetic evolution as are the adaptive characters of free-living larvae that fit them to their particular environments, such as gills of aquatic species or the abdominal "legs" of crawling and climbing species.

A most interesting case of adaptive embryonic metamorphosis is seen in scorpions of the family Scorpionidae (Mathew, 1948; Vachon, 1950, 1953), in which the eggs are provided with very little yolk. The embryos undergo their development in follicles of the ovarian tubes, and are nourished on material from the blood of the mother absorbed into slender apical diverticula of the follicles. Each diverticulum is traversed by an inner feeding tube reaching to the mouth of the embryo. As a special adaptation on the part of the embryo, the movable digits of the chelicerae take the form of flat pads or long vesicular arms that clasp the feeding tube and bring it against the mouth, into which the food material is sucked by the muscular pharyngeal pump. At birth the young scorpion retains the embryonic chelicerae until the first moult, when these organs revert to the adult form.

The embryonic modification of phylogenetic evolution forced upon the embryo because of its development in the egg is well illustrated by the manner in which the insect embryo commonly forms its stomach. The food of the embryo, the yolk, is stored in the egg and thus

comes to be inside the body of the embryo; consequently it cannot be ingested in the ancestral manner by way of the mouth. In embryonic development, therefore, the stomach grows around the yolk, a method of "gastrulation" certainly that does not in any sense recapitulate stomach formation in the evolution of a free-living ancestor whose food had to be taken in from the outside. The embryo simply follows a modified process of gastrulation in adaptation to life in an egg shell, but in the end it produces an alimentary canal the same as that which its free-living ancestors produced by quite different evolutionary methods.

The insect embryo may develop into a juvenile form resembling its parents except in matters of immaturity, such as the rudimentary nature of the wings and the organs of reproduction. In such cases the young insect successively approaches the adult structure at each moult and finally assumes the imaginal form. At the other extreme, the embryo throws off all adult ancestral influences and develops into a creature having no likeness to its parents. There is here no phylogenetic recapitulation, the young insect in its growth takes no steps toward the adult structure; development of the adult, except for the growth of invaginated appendage rudiments, is inhibited until the young insect has accomplished its particular function in the life history of its species. Then the juvenile tissues disintegrate and the imago is rapidly built up in the form of its parents.

Inasmuch as the terminology of metamorphosis is not standardized, the same names being used in different ways by different zoologists, it will be necessary before proceeding with a further discussion of insect metamorphosis to explain a few common terms as they will be applied in the following pages.

*Metamorphosis.*—The word "metamorphosis" means merely a "change of form." In general zoology any pronounced change of form during growth, such as the changes of a crustacean larva in its development from the nauplius to the adult, or the changes of a tadpole in becoming a frog, is called metamorphosis. Entomologists, on the contrary, are inclined to restrict the idea of metamorphosis to the final change from a differentiated juvenile form to the imago, whether the change is direct or accomplished in an intervening pupal stage. Such a definition of metamorphosis is clearly too restrictive, since it would eliminate the use of the term as commonly used in other branches of zoology, and even in the insects there may be pronounced metamorphic changes between larval instars. Students of the action of hormones in the postembryonic development of insects commonly refer to the change to the adult as the "metamorphosis" of the insect

regardless of the degree or nature of the change. Bodenstein (1953b, p. 879), for example, says: "We speak of metamorphosis when the animal shows adult characters after a molt." Wigglesworth (1953a) finds that in *Rhodnius*, in addition to the full development of the wings and reproductive organs at the final moult, the epidermal cells now lay down an imaginal cuticle that is totally different in structure and color pattern from that of the nymph, and hence he calls the changes at the last moult the metamorphosis of the insect. Such final changes as those that occur in most of the Heteroptera, however, would appear to involve merely the completion or final acquisition of adult characters, and are therefore not comparable to the metamorphic changes in other insects resulting from the suppression of juvenile aberrations in form or structure.

It will probably be useless to attempt to write a definition of metamorphosis, since none would be generally acceptable. With nearly all insects there is necessarily a change of some kind or degree from one instar to the next, since the insect grows by stages, and the change at the last moult is usually greatest because the insect now takes on the fully developed adult characters. However, regardless of definitions, we must distinguish between changes that are consequent on growth from youth to maturity, and those that result from structural aberrations on the part of the young insect from the direct line of development. True metamorphic characters, as here understood, are adaptive structures, temporarily assumed usually by the young insect for its own purposes, that have no phylogenetic counterpart in the adult evolution, and which are discarded at the transformation to the imago. Metamorphic changes may take place between the immature stages of the insect, but metamorphosis is most pronounced at the change to the adult because it now involves the assumption of imaginal characters as well as the discarding of juvenile characters. However, if the assumption of imaginal characters alone is called "metamorphosis," then all insects undergo metamorphosis in some degree at the last moult, and the term has no specific meaning.

If the metamorphic change between the young and the adult is of small degree it is termed *paurometabolism*. If the young insect differs conspicuously from the adult or has distinctive adaptive characters of its own, but still makes the change to the adult at one moult, the insect is said to be *hemimetabolous*. When two moults are involved in the change and a pupal stage thus intervenes between the young and the adult, the insect is said to be *holometabolous*. These terms, of course, have no literal significance. An insect may be classed as *ametabolous* if it goes through no changes during its development

that are not related to growth from youth to maturity, but such changes may be considerable and are often difficult to distinguish from paurometabolism.

*Nymph.*—In its biological application this term is almost exclusively entomological, but entomologists are not consistent in its usage. According to American and most English usage a “nymph” is generally the young of an insect without a pupal stage, while with European entomologists a “nymph” is more commonly the pupa. In the following discussion the term *nymph* will be limited to the young of ametabolous or paurometabolous insects that in all essential respects, except those of immaturity, resemble their parents and have no important characters that obscure their likeness to the adult.

*Larva.*—In general zoology the term “larva” is commonly used to designate the immature stages of any invertebrate animal, or even the tadpole stage of frogs and salamanders. Some entomologists limit its application to the young form of insects that have a pupal stage in their life cycle; others call any juvenile insect a “larva.” Definitions may be arbitrary, but it is better if a scientific term has some relation to the original meaning of the word involved. If we take the word “larva” in one of its Latin meanings, that of a *mask*, it becomes an appropriate term for any young form, particularly of an arthropod, that differs so much from its parents that its identity is not apparent in its structure, being “masked” under a specialized juvenile disguise. A *larva*, in this sense, may be defined specifically as an immature post-embryonic stage that has acquired for its own use adaptive characters that its adult ancestors did not possess, and which are not carried over into its own winged instar. Unfortunately, the insects will not always conform with definitions. There are some young insects that are essentially nymphs, and yet have a few special characters of their own. Such borderline cases, however, only show how easily a nymph might become a larva.

True larval forms among modern arthropods occur principally in the crustaceans and the insects, but in these two groups the larvae are not equivalent ontogenetic stages. The crustacean larva in most cases is hatched at an early stage of embryonic development long before body segmentation is completed. The earliest larval form in the Crustacea is the *nauplius*, a minute creature without body segmentation, but provided with three pairs of appendages, which are the first and second antennae and the mandibles, a simple nervous system, a single median eye, and an alimentary canal with oral and anal apertures. The swimming nauplius serves for the distribution of its species, and,

though it is derived from an early stage of ontogeny, it is specifically modified in adaptation to an aquatic life, and therefore in its form and structure does not recapitulate any primitive ancestral form in the evolution of the Crustacea. In its growth the crustacean larva goes through subsequent stages in which body segmentation appears, and both the segments and the appendages increase in number until the final organization is attained. The young of a terrestrial animal could not survive if hatched at such an early stage of development as that of the nauplius. The insect larva, with a few exceptions among parasitic species, is hatched with the definitive body segmentation, and thus in its youngest stage represents a relatively late period of development. The typical crustacean larva is *anamorphic*, the insect larva is *epimorphic*. Here are two more terms that will need some attention farther on.

In both the crustaceans and the insects the larva may be *heteromorphic* in that it develops through a series of different forms. In the Crustacea the heteromorphic larva progresses toward the adult structure; with the insects successive larval forms are adaptations to different functions or living conditions of the larva itself and have no relation to the adult. Larval metamorphosis among the crustaceans, however, especially in parasitic species, is often retrogressive and ends in the production of a greatly modified or highly degenerate metamorphosed adult form. With the insects, simplified, or "degenerate," forms occur mostly in the early larval stages of heteromorphic parasitic species, which have normal adults.

*Pupa*.—There is no ambiguity in the use of this term; the pupa is the stage of a holometabolous insect in which the final development of the imago takes place. There is, however, a difference of opinion as to the nature of the pupa. A common idea is that the pupa represents the last nymphal instar of an ametabolous insect; another is that it is a condensation of all the former nymphal instars of its species; a third sees in the pupa a preliminary sketch of the adult furnishing a mold for the proper reconstruction and attachment of the adult musculature. The respective merits of these several pupal concepts will be discussed later.

The degree to which reconstructive processes take place in the pupa varies with different insects. In some cases most of the larval tissues are merely made over into corresponding parts of the adult, in others the larval tissues go into a state of dissolution and the adult organs are built up from special groups of undifferentiated embryonic cells, called *imaginal discs* or *histoblasts*, which are carried by the larva but form no essential part of the larval structure. That the larva

is a "double" organism, as it is often said to be, is thus seen to be true only in the more specialized members of some of the holometabolous orders. The embryo, however, is charged with the double potentiality of forming first a larva and then an imago; the larval structure is completed in the egg, the latent adult structure is built up in the pupa. Of all the reconstructive processes that take place in the pupa the most important is that of the muscular system, which is perhaps the primary reason for the pupa. The dissolution of the larval muscles before the imaginal muscles are formed at least accounts for the immobile condition of the pupa, though, since all the larval muscles are not destroyed at the same time and some may go over intact from the larva to the adult, various pupae retain some degree of activity.

*The imago.*—Rarely does the adult insect undergo any metamorphic changes after it emerges from the pupal skin. There is the curious case of the streblid fly *Ascodipteron*, however, which is parasitic on bats. As described by Jobling (1939) the female fly pierces the skin of the host with her enormous proboscis and pulls her body into the wound. The legs and wings are then cast off, while a circular fold of the integument grows forward over the abdomen and thorax until the body acquires a flask-shaped form. On a posterior setose knob of the body, which alone projects from the skin of the host, are situated six spiracles and the slitlike aperture of a chamber containing the openings of the vagina and rectum.

*Anamorphosis.*—The term *anamorphosis*, as usually defined, refers to the completion of body segmentation after hatching. Though anamorphosis thus involves a "change of form," it should not be confused with metamorphosis; it is merely a way of growing. The manner by which body segments are formed in anamorphic development is always essentially the same. Just anterior to the terminal lobe of the body, or telson, is a mass of undifferentiated tissue, the *zone of growth*, which is capable of active cell proliferation, and it is here that the new segments are generated. As each new segment is formed it lies between the segment before it and the zone of growth, so that the animal extends its length posteriorly, but the anterior segments are the oldest. This method of growth from behind forward, which may begin in the embryo or be completed in the embryo, is in general known as *telogenesis*. Anamorphosis, by definition, therefore, is telogenesis continued after hatching. The number of segments added by anamorphosis depends on how many segments the young animal has on hatching and on the number of segments it will have when mature.

Anamorphosis is characteristic of the polychaete annelids; it was the mode of development in the trilobites; it still prevails in most of

the crustaceans, in two groups of chilopods, in all the diplopods, pauropods, and symphylans; and a remnant of it persists among the hexapods in the Protura. It would seem, therefore, that anamorphosis was the primitive method of growth in the arthropods, and that it is an inheritance from their remote common ancestry with primitive annelids.

The addition of new segments in the arthropods takes place at the moults, and is usually accompanied or followed by the formation of new segmental appendages. If the growing animal takes on a different form or distinctive characters at successive anamorphic stages, as is common among the Crustacea, such features are metamorphic aberrations or adaptations superposed on anamorphosis. Anamorphosis, therefore, may be accompanied by larval heteromorphosis.

*Epimorphosis*.—The development of an animal is said to be *epimorphic* when the maximum number of definitive segments is present at hatching, though some segments may be suppressed later. The segments in some cases are formed teloblastically as in anamorphosis by generation from a subterminal zone of growth, but in most epimorphic arthropods, as in insects, the prospective body is first laid out as an unsegmented *germ band*, which later becomes segmented. Segmentation in the germ band commonly begins anteriorly and proceeds posteriorly, and the segmental appendages appear in the same order. In this case, therefore, metamerism might appear to have no relation to a supposedly primitive anamorphic method of growth, and the anteroposterior progress of development has been regarded as indicative of a "metabolic gradient" in the embryo, meaning that the developmental processes are most intense first at the anterior pole and proceed posteriorly. However, since in anamorphic growth the anterior segments are the oldest, the apparent formation of segments and appendages from before backward in an epimorphic animal may be merely the visible results of delayed segment differentiation in the germ band. Epimorphosis is clearly a specialized and more expeditious way of growing than is anamorphosis; it delivers the young animal into the world in a more nearly mature condition, and therefore in a more practical stage of development for meeting the contingencies of a free existence.

## I. METAMORPHOSIS AND CLASSIFICATION

Insects cannot be classified taxonomically according to the type of metamorphosis they undergo. Hemimetabolism occurs among several unrelated orders, and holometabolism is not limited to the group

of orders formerly known as the Holometabola. Even among the orders that are typically ametabolous there may be juvenile changes during growth sufficient to warrant the term paurometabolism.

The ametabolous and paurometabolous insects include the Apterygota, and, among the pterygote orders, the Dermaptera, Orthoptera, Embioptera, Isoptera, Zoraptera, Corrodentia, Mallophaga, Anoplura, Heteroptera, and most of the Homoptera. Growth changes among the ametabolous insects are often fairly conspicuous, since they may include the acquisition of abdominal styli, developmental changes in the mouth parts, antennae, legs, wings, and the external reproductive organs, and furthermore they may involve changes in the shape and proportions of the head, thorax, and abdomen, accompanied by changes in the shape of the sclerites, and possibly in the number and arrangement of setae. Changes of this kind, however, are for the most part merely alterations that a young animal must go through in attaining the adult form, and are not of the adaptive kind here treated as true metamorphosis. Marked changes in the nymphal instars of an insect, furthermore, may be due to some specialized development of the imago, as is well illustrated by the Tingitidae, in which the apparent metamorphoses of the nymph are merely juvenile steps leading up to the unusual form of the adult insect, and have no adaptive significance for the immature stages themselves.

The postembryonic development typical of ametabolous insects is well exemplified in the nymphal growth of a cockroach or a grasshopper. The newly hatched insect may differ considerably in shape from its parents, but its form is the result of its having been developed in an egg, and is not an adaptation to its juvenile life. As the young insect grows it takes on more and more of the adult form at successive moults; the wings grow out as padlike extensions of the back plates of the mesothorax and metathorax, the head becomes relatively smaller, the abdomen larger, and the external genitalia develop. There may perhaps be changes of color, or minor features found only in the immature stages, but such characters are insignificant. The young insect generally mingles with its parents in the same habitat, feeding on the same kind of food with the same kind of mouth parts. The adults on their part have taken no advantage from their wings to lead a different kind of life. In short, it may be said of the orthopteroid insects in general that they lead the normal life of most other animals instead of adopting a dual existence as do those with metamorphosis. They should, therefore, be the direct descendants of more primitive winged insects, the young of which never wandered from the parental habitat, or took on a form or characters that had to be

discarded at the moult to the imago. In a study of metamorphosis the orthopteroid insects are thus of particular interest in that they show us the simple course of postembryonic development in winged insects, one that has not been complicated by the addition of juvenile characters for the specific use of the young.

The insects here classed as hemimetabolous are the Plecoptera, the Ephemeroptera, the Odonata, and some of the Homoptera. The metamorphoses of these insects undoubtedly have been developed independently in each group; they have nothing in common and need no further discussion here since each order will be treated in a separate section following.

The holometabolous insects include the males of Coccidae, the Thysanoptera, the Neuropteroidea, Coleoptera, Strepsiptera, Trichoptera, Lepidoptera, Mecoptera, Siphonaptera, Diptera, and Hymenoptera. The presence of a pupal stage in the life history is diagnostic of holometabolism, but it is probable that the pupa is not in all cases a homologous stage. It is the intensity or degree of the transformation processes, particularly the reconstruction of the muscular system, that characterizes holometabolism and makes a resting stage necessary between the larva and the imago.

The larvae of holometabolous insects are endopterous and some of them are endopodous, that is, they have no external wing rudiments, and may have no functional legs. The "wingless" condition of the larva, as well as the "legless" condition, however, is apparent rather than real, since wing and leg rudiments are usually present but concealed within pouches of the epidermis beneath the outer cuticle. A truly apodous larva, therefore, is rare or perhaps does not exist, and probably the only wingless larvae are those of insects that have no wings in the adult stage. Wing rudiments, however, are sometimes present on the pupae of wingless adults, and in such cases are performed in the larva.

The endopterous condition of the larva is not entirely characteristic of any particular taxonomic group of insects. In the Coccidae the wings of the male do not appear externally until the third or fourth moult, and in Aleyrodidae they do not become external until the last moult. The winged males of Embioptera also, as shown by Melander (1903), develop their wings internally up to the last nymphal stage. In the case of the male coccids and the aleyrodids a variable degree of metamorphosis, aside from the wing and leg development, may accompany the larval growth, but the embiids show no juvenile changes that do not lead up to the adult structure. It is evident that

the endopterous condition of the larva has been acquired independently by different insects, and it is questionable whether it is to be regarded necessarily as a metamorphic feature, or merely as a device for protecting the wings during the early stages of their growth. Clearly it is an advantage to the young insect to have temporarily useless appendages removed from the surface.

Inasmuch as the type of metamorphosis that an insect goes through, or whether the young insect is exopterous or endopterous, does not in all cases conform with the insect's taxonomic relationships, it will be more appropriate to discuss the metabolous insects according to their usual classification rather than according to their kind of metamorphosis. Among the ametabolous insects special attention must be given to the Apterygota, because certain features of hemimetabolous and holometabolous larvae have been thought to be derived from adult ancestral forms resembling the modern thysanurans.

## II. HORMONES AND METAMORPHOSIS

The transformations of insects have long furnished a popular theme for writers on the "marvels of insect life," but in recent years serious investigators have given more and more attention to the vital mechanisms that control the phenomena of metamorphosis. Though their studies have not eliminated the mystery, they have revealed something of its nature, and insect metamorphosis has now become a subject for experimentation rather than one that merely excites our visual curiosity. The young insect contains two opposing forces in the nature of hormonal secretions that regulate its growth and development; one maintains the juvenile status, the other stimulates moulting and normal development that culminates in the production of the imago.

Though insect endocrinology is still a youthful science, it has many devotees. The insects are excellent experimental subjects; they submit to amputations, graftings, and transplantations without complaint and apparently without discomfort. It would go too far beyond the scope of the present discussion to list the great number of papers now available on the endocrine organs of insects, or to review all the experimental evidence of the action of hormones in controlling the metamorphic processes. The student may find ample bibliographies in the more recent papers to be cited in connection with the following summary of what may now be regarded as known concerning the organs of internal secretion and the hormones that regulate metamorphosis.

The endocrine organs of insects that control nymphal and larval

growth, moulting, development, pupation, transformation of the nymph or larva to the imago, and the ripening of the eggs in the ovaries include the following: (1) Secretory cells in the intercerebral part of the brain, (2) the corpora cardiaca, (3) the corpora allata, (4) pericardial glands, (5) perhaps glands in the posterior ventral part of the head, (6) thoracic glands, and (7) the ring gland of cyclorrhaphous Diptera.

*Secretory cells of the brain.*—In insects of most of the principal orders secretory nerve cells that play an important part in moulting and imaginal development are present in the pars intercerebralis of the protocerebrum. According to Scharrer and Scharrer (1944) such cells have been shown to be present in Orthoptera, Hemiptera, Neuroptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, and Diptera. In the blattid *Leucophaea*, these authors observe, some of the cells of the pars intercerebralis contain varying numbers of distinctly staining colloid inclusions, which are continued for some distance into the cell axons. The fibers from the secreting cells go downward in the brain, where most of them cross from one side to the other, and then turn backward through the nerves of the corpora cardiaca to innervate these bodies. It has been shown by Wigglesworth (1940) and others that the brain secretion has to do with the induction of moulting, but from further research it is now known that moulting and imaginal development depend on a hormonal complex derived from the brain and the prothoracic glands. According to Williams (1948) there are two groups of secretory cells in the larval brain of the *Cecropia* moth producing two different hormones, both of which are necessary to induce moulting.

*The corpora cardiaca, or paracardiaca.*—The corpora cardiaca (fig. 1 A,Cc) are usually paired oval or elongate bodies lying behind the brain, with which they have nerve connections, and are closely attached to the sides of the aorta. They arise, however, as cellular outgrowths from the dorsal wall of the stomodaeum at the sides of a similar median outgrowth that becomes the hypocerebral ganglion of the stomodaeal nervous system (*hcGng*). According to Pflugfelder (1937) the corpora cardiaca in an early embryonic stage of the phasmatid *Dixippus* lie against the lower surfaces of the cardioblasts, but when the cardioblasts unite to form the aorta, they push into the aortic wall; the lower cells remain as compact masses which are soon differentiated into ganglion cells, while the others appear to be secretory.

An extensive comparative account of the corpora cardiaca in most of the principal groups of insects is given by Casal (1948), who more

appropriately calls these bodies *paracardiaca*, since their connection with the heart is entirely secondary. Typically each corpus cardiacum is connected with the back of the brain by two nerves (fig. 1 A, *ccNvs*), one lateral, the other median. The lateral nerves have their roots in the lateral parts of the protocerebrum, the median nerves arise in the

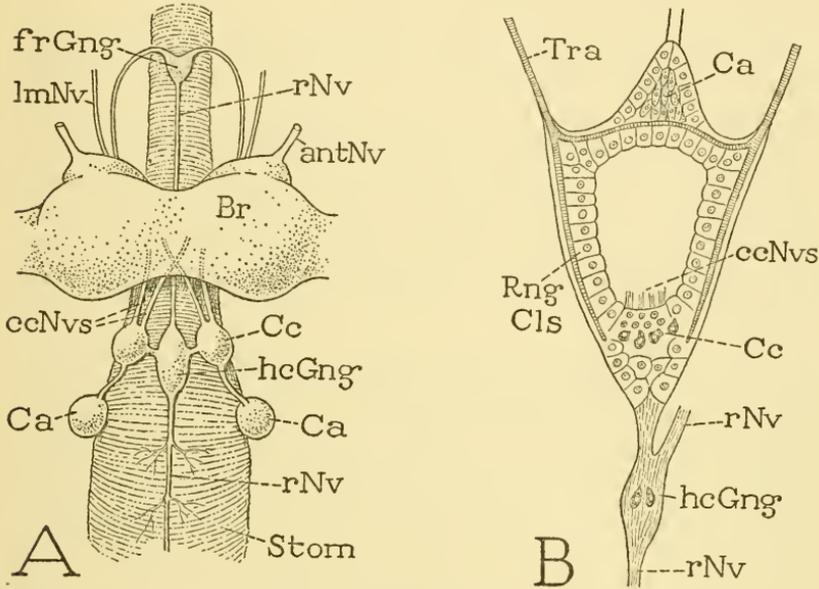


FIG. 1.—The retrocerebral endocrine organs.

A, diagram of a simple, perhaps generalized, arrangement of the corpora cardiaca and corpora allata on dorsal surface of stomodaeum behind the brain in association with the hypocerebral ganglion. B, diagram of ring gland of larva of *Calliphora* (from M. Thomsen, 1951).

*AntNv*, antennal nerve; *Br*, brain; *Ca*, corpus allatum; *Cc*, corpus cardiacum; *ccNvs*, corpus-cardiacum nerves; *frGng*, frontal ganglion; *hcGng*, hypocerebral ganglion; *lmNv*, labral nerve; *RngCls*, ring cells; *rNv*, recurrent nerve; *Stom*, stomodaeum; *Tra*, trachea.

pars intercerebralis and cross each other from one side to the other. Nerve fibers traversing the corpus cardiacum form a nerve connection between the latter and the corpus allatum of the same side.

Because of the intimate nerve relation of the corpora cardiaca to the secretory cells of the brain, and the observation that colloid granules similar to those in the brain can be traced along the nerve fibers into the corpora cardiaca, Scharrer and Scharrer (1944) point out that "the pars intercerebralis and the corpus cardiacum of insects may be viewed as one neuro-endocrine complex rather than as two separate sources of hormones." The presence of a brain hormone

concerned with moulting and development is now well known, but the specific function of the corpora cardiaca has been but little investigated. It is noted by Pfeiffer (1942) that removal of the corpora cardiaca from nymphs of *Melanoplus* is followed by a delay in moulting, but does not prevent moulting. This observation suggests that a corpus-cardiacum hormone is a part of the hormone system that activates moulting and imaginal development. The most definite information we have on the action of the corpus-cardiacum hormone, however, has to do with its effect on crustaceans. It had been known that extracts of the head of insects injected into blinded shrimps would cause a contraction of the chromatophores, just as does the hormone of the crustacean sinus gland in the eyestalk. M. Thomsen (1943) then showed that the activating element of the insect head comes from the corpora cardiaca, since transplantation of these bodies into a shrimp with amputated eyestalks had the same effect as head extract.

*The corpora allata.*—The corpora allata (fig. 1 A,Ca) are typically a pair of small oval bodies lying usually behind or laterad of the corpora cardiaca, with which they are connected by nerves, but in some insects the two bodies on each side are united, and the corpora allata themselves may be fused into a single mass. Variations in the relative position and connections of the corpora allata and cardiaca, and their association with the hypocerebral ganglion are illustrated in various insects by De Lerma (1937), Nesbitt (1941), and Bickley (1942); an exhaustive review of the structure of the retrocerebral organs in most of the insect orders is given by Casal (1948). The first general description of the histology of the organs is due to Nabert (1913).

The corpora allata arise during embryonic development from the head ectoderm between the mandibular and maxillary segments, and are later transposed, as the name "allata" implies, to their definitive position behind the brain. In most insects they come to lie above the stomodaeum; according to Casal (1948) they lie below the stomodaeum in Ephemeroptera and Odonata. Formerly it was thought that corpora allata are absent in the Thysanura, but Chaudonneret (1949) has given reasons for believing that small glandular bodies in these insects lying against the outer surfaces of the adductor muscles of the maxillae are the corpora allata in a relatively primitive position.

The action of the corpus-allatum hormone is better known than that of the other incretory organs. The experiments of Wigglesworth

on the hemipteron *Rhodnius*, of Scharrer (1946a) on the blattid *Leucophaea*, of Pflugfelder (1937, 1938) on the phasmatid *Dixippus*, of Bounhiol (1938) on lepidopterous larvae all go to show that the corpus-allatum secretion in the young insect is the factor that maintains the juvenile status. This hormone, therefore, is known as the *juvenile hormone*. Wigglesworth (1951a) summarizes the results of his experiments on *Rhodnius* demonstrating the inhibitory effect of the corpus-allatum hormone on adult development as follows: "If the corpus allatum is removed from one of the young stages and implanted into the abdomen of a fifth-stage larva, when this moults it turns into a giant or sixth-stage larva instead of undergoing metamorphosis to an adult. Even a seventh-stage larva has been produced this way, and some of the sixth-stage larvae have transformed successfully into giant adults." Scharrer (1946a) obtained the same results from experiments on *Leucophaea*. Removal of the corpora allata from the last (8th) instar of the cockroach had no visible effects on development, but removal at earlier stages resulted in an abbreviation of development and the production of small adultlike forms, the adult characters being more accentuated with the age of the operated insects. Pflugfelder (1938) working with *Dixippus*, found that removal of the corpora allata from first and second instars was followed by a degeneration of certain tissues, including the fat bodies, the mesodermal sheath of the nervous system, muscles, and the Malpighian tubules. These changes are those that normally take place at the end of larval life in holometabolous insects, showing that it is the corpus-allatum hormone that maintains the integrity of the juvenile tissues, and that the dissolution of specialized larval tissues is due to the weakening or cessation of secretory activity by the corpora allata in the last juvenile stage. Similar results have been obtained in Lepidoptera by Bounhiol (1938) and other investigators (see Hinton, 1951). Removal of the corpora allata from a young caterpillar brings on precocious pupation, but removal of the organs from a last-stage larva has no effect on pupation. It is noted by Wigglesworth (1936), furthermore, that "the corpus allatum also determines the characters of each nymphal instar by limiting the degree of differentiation toward the adult form which occurs during the moults."

In the adult insect the corpora allata again become active, but now their secretion is operative on egg production in the female and on secretion by the accessory genital glands in the male. The effect of eliminating the corpora allata from the adult insect has been studied by various investigators, including Wigglesworth (1936, 1948), Pfeiffer (1939, 1942, 1945), and Scharrer (1946b). From experiments

on the grasshopper *Melanoplus*, Pfeiffer (1939) found that complete removal of the corpora allata from adult females prevents the production of ripe eggs in the ovaries and of secretion in the oviducts. The eggs will develop without corpora allata until they reach the stage at which yolk deposition normally begins, but after that time they stop development, degenerate, and are resorbed. In later work on the same insect Pfeiffer (1945) showed that in normal females, during the early period of adult life before yolk formation in the ovaries, the fatty acid content of the body increases, the fat body hypertrophies by rapid storage of fat, nonfatty dry matter increases in correlation with fatty acid increase, and the blood volume moderately increases. These changes, however, do not take place if the corpora allata are removed at the beginning of the adult stage. In the normal female the metabolic processes are reversed after yolk formation begins. From these findings Pfeiffer concludes that "the corpora allata control egg production principally, if not entirely, through the agency of a metabolic hormone, and that a primary function of this hormone is to facilitate the mobilization or production of materials necessary for egg growth." According to Scharrer (1946b) the corpora allata are necessary in the blattid *Leucophaea* for approximately the first third of the total period required for egg development, which time corresponds to the period of growth and yolk deposition. Reimplantation of corpora allata into females from which these organs had been removed caused the eggs to develop and produce normal nymphs.

It is a curious fact that the corpus-allatum hormone of the adult seems to be the same as that which inhibits adult development in the young insect. By implanting from two to six corpora allata from young adult females of *Melanoplus* into a nymph, Pfeiffer (1942) found that the nymphs never transformed into adults, though some of them made one or two further moults. The same hormone apparently is present in both the female and the male, since Wigglesworth (1936) reports that in *Rhodnius* the corpora allata of the male will induce egg development in the adult female, and those of the female will activate the accessory glands of the male. He concludes (1948), therefore, that "it is probable that the yolk-forming hormone and the juvenile hormone are identical." On the other hand, Wigglesworth finds that the moulting hormone of the nymph will not induce egg formation, nor will the egg-forming hormone of the adult induce moulting in the nymph. A dual function of an apparently single hormone, Wigglesworth notes, recalls the multiple action of thyroxin in Amphibia. In the case of the insect, however, it now appears that the principle of "tissue competence" emphasized by Bodenstern (1943)

and by Bounhiol (1938, 1953) plays an important part in the action of a hormone. With respect to the corpus allatum, Bounhiol (1953) says, it is very probable that it has only a general effect on metabolism, and that it is the variable state of sensitivity in the different organs, or in any one organ according to its age, that determines the varying responses. Evidently, what is a stimulus in one case may be an inhibition in another.

Though the corpus-allatum hormone acts as an inhibitor of development in the larval tissues between moults, the rudiments of imaginal organs developing in the larva, such as the antennal, leg, and wing buds, continue to grow during the larval instars. Eassa (1953) gives measurements of the antennal growth in the larva of *Pieris brassicae* between moults, and notes that mitosis may be observed in the antennal cells. It would appear, then, either that the larval corpus-allatum hormone is selective for larval tissues, or that imaginal tissues are not affected by it.

*Pericardial glands.*—These glands were first described by Pflugfelder (1938) in the phasmatids *Dixippus* and *Phyllium*, but later (1947) he reported them present also in Ephemeroptera and Plecoptera. The glands of *Dixippus* and *Phyllium* lie in the posterior part of the head close above the dorsal blood vessel, mesad of the pericardial cells, from which they are distinctly different. The pericardial glands, according to Pflugfelder, arise from the lateral walls of the head coelom, and are therefore mesodermal organs. They attain their greatest development in the last nymphal stage, and in the adult they soon degenerate and disappear, from which facts it is deduced that the pericardial glands are endocrine organs, though there is no direct evidence of their function. It is probable, as will be explained later, that the pericardial glands compose the major part of the ring gland of cyclorrhaphous fly larvae, and that functionally they are equivalent to the thoracic glands of other insects.

*Ventral glands of the head.*—These organs are small glandular bodies lying ventrally in the posterior part of the head, described by Pflugfelder (1938) first in Phasmatidae, but later (1947) reported as present also in Ephemeroptera, Odonata, Plecoptera, Dermaptera, Acrididae, Blattidae, and Isoptera. They are of ectodermal origin and degenerate after the last moult except in the workers and soldiers of termites. Williams (1948) suggests that the glands may be homologous with the prothoracic glands, but it is said by Hinton (1951) that prothoracic glands also are now known to be present in Odonata and Orthoptera.

*The prothoracic glands.*—Glands of the prothorax were described in a caterpillar by Lyonet as "granulated vessels," and little further attention was given to them until recent times. It is now well demonstrated that these glands are important endocrine organs, probably present in most insects; according to Hinton (1951) they are known to occur in Odonata, Orthoptera, Hemiptera, Lepidoptera, Hymenoptera, and Diptera. They are said by Toyama (1902) to arise in the early embryonic development of the silkworm as epithelial invaginations of the lateral part of the second maxillary segment and to extend into the thorax. In lepidopterous larvae the glands are loose, branching masses of cells associated with the tracheae in the sides of the prothorax. Their structure has been described by Williams (1948) in the larva of *Platysamia cecropia*, and a well-illustrated comparative account of them in various lepidopterous species is given by Lee (1948). Prothoracic glands in the hemipteron *Rhodnius* are described by Wigglesworth (1951b, 1952a).

The probable function of the prothoracic glands is best known from experiments by Williams (1947) in connection with the pupal diapause of *Platysamia cecropia*. It appears that there is an intimate functional relation in the caterpillar between the prothoracic glands and the brain. The pupa of the Cecropia silkworm as soon as it is formed goes into a prolonged state of diapause, which normally is broken only when the pupa is exposed to low temperatures. It is shown by Williams, however, that if the brain is removed from a diapausing pupa, chilling has no effect and further development permanently ceases. On the other hand, if the brain from a chilled pupa is implanted into a brainless pupa, normal development takes place. It is evident, therefore, that the chilling of the brain renders it competent to release its developmental hormone. However, further experiments by Williams showed that a pupal abdomen severed from the thorax will not develop even if a chilled brain is implanted into it, but when reattached to the thorax such an abdomen proceeds with development. The head and the thorax, on the contrary, develop when a chilled brain is inserted. Normal development, in short, requires besides a chilled brain the presence of the thoracic glands, which do not need exposure to cold for activation. Thus the brain, Williams points out, evidently exerts a controlling action on the prothoracic glands. In other words, the resumption of normal development in the diapausing Cecropia pupa is brought about by the interaction of a hormone from the brain and another from the prothoracic glands, but the gland hormone, Williams says, "most probably, has the ultimate action on the tissues in terminating diapause." The same rela-

tion between the brain hormone and a prothoracic hormone has been demonstrated in the hemipteron *Rhodnius* by Wigglesworth (1952b). The brain hormone activates the thoracic gland, which latter "then produces the factor initiating growth and moulting."

Considering, then, the intimate relation of the secretory cells of the brain both to the corpora cardiaca and to the prothoracic glands, it is evident that the brain is of primary importance in the activation of imaginal development. It is to be noted, however, that in this case the brain does not function in the usual manner by nervous control, but through having taken on a secondary function of hormone secretion. The secretory action of the brain, however, is induced by nerve activity.

*The ring gland of cyclorrhaphous Diptera.*—In the larvae of cyclorrhaphous Diptera a glandular structure surrounding the aorta behind the brain is known as the *ring gland*. Though formerly regarded as the corpus allatum, it is now known to be a complex endocrine organ that includes the corpora allata and corpora cardiaca of other insects embedded in a ring of cells of different origin. In the lower Diptera there is no ring gland. As shown by Casal (1948) corpora allata and corpora cardiaca are present in the usual manner in Nematocera, either separate or united. In *Tabanus* and other Brachycera the corpora allata are united above the aorta and are connected by nerves going around the aorta to the ventrally placed corpora cardiaca, which are separate. In *Melophagus ovinus*, according to Day (1943), the corpora allata are paired bodies in the larva and the corpus cardiacum is a single median organ.

Investigators are mostly in accord as to the structure of the ring gland in the Cyclorrhapha, and we may follow the account of the organ given by M. Thomsen (1951). The larval ring gland of *Calliphora erythrocephala* as illustrated by Thomsen (fig. 1 B) is triangular rather than circular; its wide anterior part is prolonged forward as a median tongue above the aorta, its narrow posterior part lies below the aorta. A trachea (*Tra*) enters on each side and the two lateral trunks are connected by a commissure through the anterior part of the gland. The major part of the organ is formed of large cells termed the *ring cells* (*RngCls*). Within the anterior tongue in front of the tracheal commissure is a group of small cells (*Ca*) representing the corpora allata of other insects. In the posterior angle of the ventral part of the ring is a second group of small cells (*Cc*) apparently representing the corpora cardiaca. The ring cells themselves were formerly regarded as the corpora cardiaca, but it was sug-

gested by Ellen Thomsen (1942) that they correspond with the pericardial glands described by Pflugfelder in the phasmatids, and M. Thomsen concurs in this view, which is now generally accepted. Furthermore, there is reason to believe that both the pericardial glands and the lateral cells of the ring gland represent the thoracic glands of other insects. Though Poulson (1950) says the lateral ring gland cells of *Drosophila* arise from the roof of the stomodaeum, and would therefore appear to be the corpora cardiaca, M. Thomsen shows that the usual four corpora-cardiaca nerves (*ccNvs*) from the brain go to the group of small cells in the posterior angle of the ring gland, which fact would suggest that these cells alone are of corpus-cardiacum origin. Lying behind the ring gland of *Calliphora*, and connected with its posterior end by a short nerve is the hypocerebral ganglion (*hcGng*) of the recurrent nerve (*rNv*). In *Drosophila* Bodenstein (1950) shows that the corpus cardiacum and the hypocerebral ganglion are apparently united in the posterior end of the ring gland.

From experimental work it is known that the ring gland of cyclorhaphous larvae is necessary for the inducement of moulting and pupation. Burt (1938) observed that removal of the gland from larvae of *Calliphora* prevents pupation and that growth of the imaginal buds is arrested. Day (1943) reports that experiments on *Lucilia* and *Sarcophaga* suggest that the ring gland produces a hormone concerned with normal development; in the larva it induces puparium formation. Bodenstein (1944) showed that larval moulting is dependent on the presence of a ring-gland hormone. Possompès (1950), however, demonstrated that the action of the ring gland as an effector of metamorphosis depends on its stimulation by a hormone from the brain. He suggests that the ring-gland elements thus activated from the brain are the lateral cells ("peritracheal glands"), which thus correspond at least in function with the thoracic glands of other larvae. There appears to be no experimental demonstration of the specific function of the corpus-allatum element of the ring gland on the larva, but presumably it is the same as in other insects.

The ring gland of the larva moves backward in the pupa and comes to lie in front of the proventriculus. In the newly emerged adult of *Calliphora*, according to Ellen Thomsen (1942), the ring gland is present, but in the mature fly all of it except the corpus-allatum component disappears. In the adult of *Drosophila*, Bodenstein (1950) says the lateral ring cells degenerate, but the anterior group of cells remains as the corpus allatum, and the cells of the posterior part form

an elongate body representing the corpus cardiacum and the hypocerebral ganglion. The metabolic changes that the ring gland produces in the adult fly are those that are ordinarily attributed to the corpora allata. The action of the ring gland in the adult fly according to Day (1943) is seen "first in changes which occur during the breakdown of the larval fat body cells and subsequently in the changes undergone by the adult fat body cells, the oenocytes, and the development of the ovaries." Bodenstein (1950) attributes to the corpus-allatum remnant of the ring gland in the adult female of *Drosophila* the formation of a hormone that regulates egg maturation. The necessity for the presence of the ring gland in the adult fly for the ripening of the eggs is well attested by the works of Ellen Thomsen (1940, 1942) and others.

*The nature of hormonal action.*—The hormones concerned with growth and metamorphosis are not in themselves the determiners of development; the course of development is determined by hereditary factors inherent in the tissues of the animal. The hormones are mere regulators, and in most cases they are found to be nonspecific as to species, a hormone from one insect having the same effect when introduced into another, regardless of different species structure. Furthermore, the effect of a hormone depends not entirely on the nature of the hormone, but also on the receptive state of the affected tissue.

Most of the experimental work that has been done on the hormones of insects has had as its object the ascertaining of the effect of specific hormones. It is now coming to be recognized, however, that the various endocrine glands and their secretions interact upon one another, and that the hormonal effect at any one time may depend on the relative amount of a particular hormone or hormone complex present in the blood. As stated by Bodenstein (1953a) the insect is able to keep a hormonal balance by "a mechanism of compensating hypertrophy or atrophy of its glands." The glands are in constant interaction with one another so that the amount of any hormone in relation to the others can be changed. "It is the hormone balance at a given time that determines the specific activity of the humoral system." In further work on the endocrine glands of insects Bounhiol (1953) says "it will be necessary to study more and more the action of the glands on one another," or, in the words of Bodenstein (1953a), "to disentangle the complicated relationships existing between the various hormones and to understand their action in physiological terms, not forgetting the vital role played in all these responses by the reacting systems."

## III. APTERYGOTA

The insects of this group, which are wingless at all stages, as presumably were their ancestors, go through no truly metamorphic changes in their postembryonic growth. They might, therefore, be omitted from a discussion of metamorphosis were it not for the fact that they have certain structures that have been thought to recur in the larval stages of some winged insects, and which thus give them a theoretical value in the interpretation of juvenile characters among the metabolous insects. Of the several groups of apterygote insects, the Thysanura are the most closely related to the Pterygota. Though thysanurans are known in paleontology only as far back as the Tertiary, while winged insects were fully developed in the Carboniferous, a thysanuran (fig. 2 A) undoubtedly gives us a concrete example of what the wingless ancestors of the winged insects were like.

The organs of the Thysanura that are of particular interest in connection with a study of the larvae of the higher insects are the abdominal *styli* and the associated *eversible vesicles*. As typically developed in the Machilidae, there may be a pair of styli on the venter of each abdominal segment from the second to the ninth inclusive (fig. 2 A), and a pair of vesicles (E,*Vs*) on each of the first seven segments, or two pairs on some of the intermediate segments. In each segment the styli and vesicles are borne on lateral plates of the venter (C,D,E,*Cx*) commonly regarded as the bases of otherwise suppressed abdominal limbs. In the embryonic development of *Lepisma*, Heymons (1897) has shown that rudiments of appendages are formed on the first ten abdominal segments, but with the dorsal growth of the body wall they are stretched transversely and become flattened until finally they form merely the lateral parts of the definitive abdominal sterna. Eversible vesicles are absent in the lepismatids, and styli are present only on the eighth and ninth segments, or also on the seventh segment. In the machilids the so-called coxal plates (C,D,E,*Cx*) bearing the styli and vesicles remain separated from a median sternal plate (*S*). That the styli are coxal appendages and not limb vestiges is shown by their occurrence on the coxae of the middle and hind legs (B,*Sty*). The abdominal styli, therefore, are appurtenances of former limbs, but do not themselves represent abdominal legs. The same evidently is true of the eversible vesicles. Both styli and vesicles occur also among the other groups of apterygote insects, and among the pterygotes styli are present on the ninth abdominal segment of the adult male in the cockroaches, mantids, and termites. We may reasonably conclude, therefore, that the

immediate ancestors of both the wingless and winged insects had abdominal styli.

In Thysanura and Diplura the abdominal styli and vesicles are provided individually with muscles that arise on the supporting plates (fig. 2 D,E). The styli are flexibly movable on their bases; the vesicles are retracted by their muscles, and protracted probably by blood pressure. The styli are developed during postembryonic growth; ac-

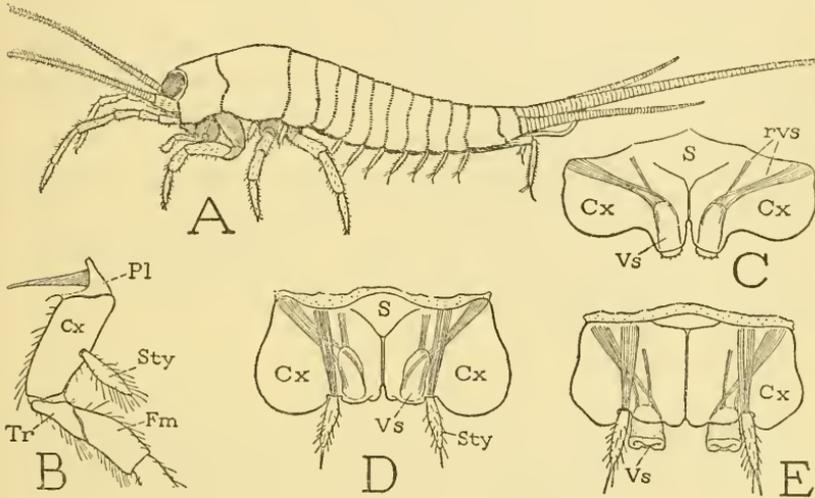


FIG. 2.—Structural details of Machilidae.

A, *Machilis* sp., whole insect, showing thoracic and abdominal styli. B, *Neso-machilis maoricus* Tillyard, middle leg, showing stylus on coxa. C, same, ventral surface of first abdominal segment, vesicles retracted. D, same, ventral surface of second abdominal segment, with vesicles and styli. E, same, ventral surface of sixth abdominal segment, vesicles everted.

Cx, coxa; Fm, femur; Pl, pleuron; rvs, retractor muscles of vesicle; S, sternum; Sty, stylus; Tr, trochanter; Vs, eversible vesicle.

ording to Heymons (1897, 1906), Adams (1933), Sweetman and Whittemore (1937), and Lindsay (1939) they first appear on the fourth or fifth instar of lepidmatids, or even on much later instars.

Thysanurans moult many times throughout life, the number of moults depending on how long the insect lives. Sweetman and Whittemore (1937) record as many as 42 observed moults for one individual of *Thermobia domestica*, and they state that both moulting and growth continue long after the first eggs are laid. The lifelong periodic moulting of the Thysanura suggests that in this respect the primitive insects resembled the other wingless arthropods. With the acquisition of wings, moulting became too arduous, and among modern winged

insects a moult in the active imaginal stage occurs only in the Ephemeroptera.

The few structural changes that the thysanurans go through during their postembryonic life are merely those of development from youth to maturity. Body scales do not appear until after the first moult, the rings of the antennae and of the caudal filaments increase in number, the abdominal styli are formed at various moults, the leg styli of *Machilis* are said by Heymons (1906) to be absent on the first instar, there are some changes in the shape and proportions of the parts of the body, and the external genitalia develop during late stages. Such changes, however, do not constitute a true metamorphosis; they are progressive toward the adult structure, and do not give rise to adaptive juvenile characters.

The fossil records of early insects give no evidence as to how insects acquired their wings. There is no doubt that insects were hexapods before wings were developed, and it seems highly probable that wings were evolved from paranotal lobes on the thoracic segments that first served as gliders.

#### IV. PLECOPTERA

Among all the "orthopteroid" insects the stoneflies are the only ones of which the young have adopted a medium different from that of the adults, and, though the young stoneflies live in the water, their structural adaptation to aquatic life is relatively little. Aside from features of immaturity, such as the unfinished development of the wings, there is little to distinguish a young stonefly from an adult other than the presence of gills for aquatic respiration, and differences in the shape and proportions of the parts of the body. The stonefly larvae have no outstanding features common to all species by which they differ from the adults, and they could hardly be mistaken for anything other than immature Plecoptera.

A typical stonefly larva has well-developed compound eyes and frontal ocelli; the antennae are long, slender, and multiarticulate; at the end of the body are two caudal filaments representing the orthopteroid cerci, but no median filament; there are three subsegments in the tarsi, and two pretarsal claws; the fully exposed wing pads undergo a gradual development. In all these characters except those of immaturity the stonefly larva is essentially like the adult, and is entirely comparable to an orthopteran nymph; in short, it is simply a nymph that has taken to the water, where most species have acquired gills of a simple kind. If there is a difference in the mouth parts or

in the length of the caudal filaments between the larva and the imago, the difference is usually due to a reduction of these structures in the latter. The life cycle of the larva varies, according to the species, from one to three or four years, and there are correspondingly many instars, as many as 33 being recorded by Schoenemund (1912) for *Perla cephalotes*.

The gills of the stonefly larva are mostly tufts of delicate filaments penetrated by tracheae; they are generally present on the sides or sternal region of the thorax, but sometimes on the abdomen, particularly at the posterior end around the anus. Gills of a different type, however, may occur on the bases of the legs. As described by Lauterborn (1903), these leg gills in *Taeniopteryx nebulosa* L. are soft, "3-segmented," tapering processes arising singly from the mesal ends of the coxae, and are retractile by muscles. When retracted the three "segments" are telescoped into each other until only a soft papilla remains visible externally. Lauterborn compares these gills with the coxal sacs of Diplopoda; they might be likened to the eversible vesicles of Thysanura, but their position on the mesal ends of the coxae precludes a comparison with styli. Similar tapering gill processes are present on the sides of the first six segments of the abdomen in the genus *Eusthenia*, as illustrated by Tillyard (1926) in *E. spectabilis* Wwd. Though these abdominal gills are suggestive of styli, it seems probable that all the gills of stonefly larvae are special developments and have no relation to any other structures, including the gills of mayfly larvae. Besides the gills there may be a subepidermal system of tracheoles serving for respiration direct through the body wall. Wu (1923) has described in the larva of *Nemoura* the presence of numerous tufts of tracheoles on the epidermis of the submentum, the coxae, the ventral sides of the femora, and on the first eight sterna of the abdomen. A group of long tubular processes arising in the anterior end of the rectum he regards as "blood gills" because they do not contain tracheae.

The stonefly larva generally retains the feeding habits of the adults; most species feed on vegetable matter (see Claassen, 1931), only members of the family Perlidae being carnivorous. The mouth parts are modified according to the nature of the food, and there may be differences also in the general form of the body between vegetarian and carnivorous species. When the larva is ready to transform into the adult it crawls out of the water onto a stone or log, and may go some distance from the shore, showing that it has not entirely lost the ability to comport itself on land. The adult stonefly does not depend on the larva for stored nourishment to the extent that do insects

with more specialized larvae. Though the adult mouth parts are more or less reduced in some species (Lucy W. Smith, 1913), in others they are well developed, and such species feed extensively in the adult stage on vegetation. The female stonefly goes back to the water to discharge her eggs.

In the Plecoptera we have an example of metamorphosis in its simplest form, and one that shows very clearly that insect metamorphosis can have its inception in the adaptation of the juvenile stage to a medium different from that inhabited by the adults. The higher degrees of metamorphosis, therefore, arose from more extensive structural modifications of the young in adaptation to a secondarily adopted medium or way of living. Probably the nymph of the primitive stonefly simply found that it could obtain a better living in the water than on land, and natural selection then eventually furnished it with gills for a permanent aquatic existence.

#### V. EPHEMEROPTERA

The young mayfly (fig. 3 A) is distinctly more specialized in its adaptation to life in the water than is the young stonefly. Still, the young mayfly is simply a juvenile insect of generalized structure; it has compound eyes and frontal ocelli, well-developed legs, mouth parts of the biting type, and during its growth it develops wing pads that increase in size up to the last moult. In these characters the young mayfly has the developmental status of an orthopteroid nymph, and that it was primarily a land-inhabiting nymph may be deduced from the presence of an elaborate tracheal system in both the adult and the larva. Since the young of the earliest known fossil mayflies, found in the Permian, already had gills, the mayfly larva has come down to us with surprisingly few changes.

The larval gills of the mayflies are organs of particular interest because of their apparent likeness to the abdominal styli of Thysanura. In modern species the gills are present on the sides of, at most, the first seven segments of the abdomen; larvae from the lower Permian, however, had nine pairs of gills, and some Jurassic species had eight. The gills are highly variable in form in different species, but they are borne singly on lateral lobes of the abdominal segments (fig. 3 B,C) interpolated between the tergal and sternal regions. The gill-bearing lobes fall directly in line with the bases of the thoracic legs (*Cx*), and thus may be likened to the stylus-bearing plates of *Machilis*. Moreover each gill is movable by muscles arising in the supporting lobe (C,D). The movements of the mayfly gills has been made the

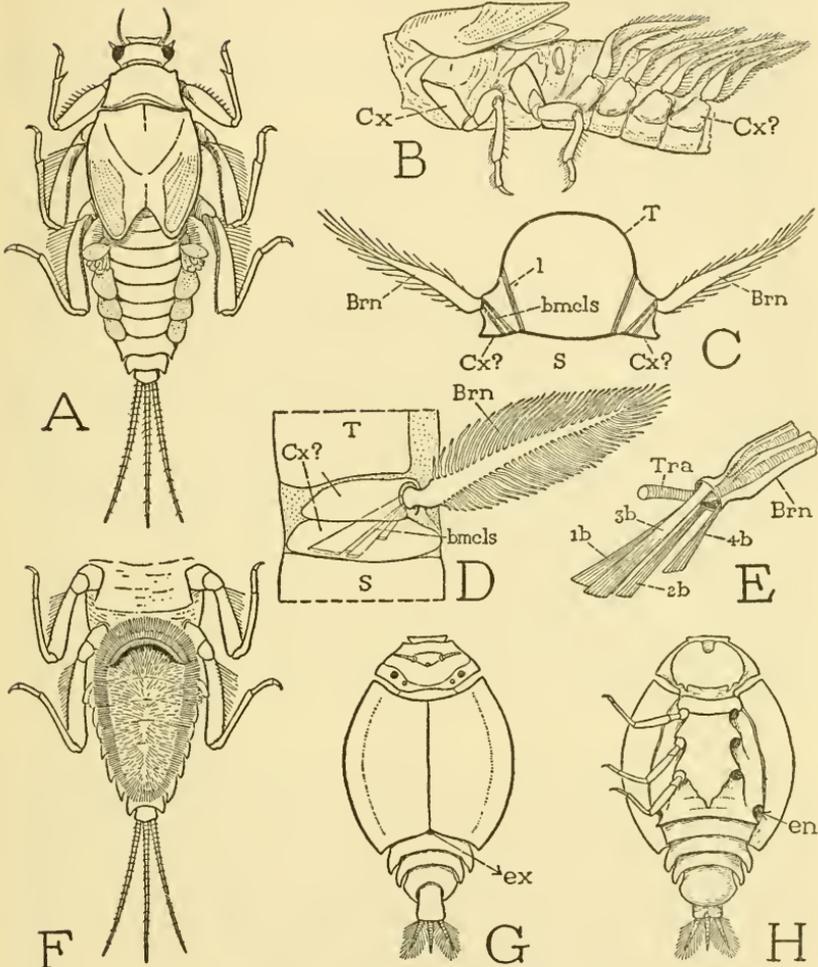


FIG. 3.—Characters of larvae of Ephemeroptera.

A, *Ephemerella* sp. B, *Ephoron* sp., part of thorax and abdomen, showing gill-bearing lobes in line with coxae of legs. C, diagrammatic cross section of abdomen. D, a single gill, showing muscles arising in supporting body lobe. E, base of gill, with tracheal trunk and muscles. F, *Ephemerella* sp., showing adhesive disc on venter of abdomen. G, *Prosopistoma foliaceus* Fourcroy, dorsal (from Vayssière, 1890). H, same, ventral (from Vayssière, 1890).

1b-4b, *bmcls*, branchial muscles; *Brn*, branchia, gill; *Cx*, coxa of leg; *Cx?*, gill-bearing lobe of abdomen; *en*, respiratory entrance; *ex*, respiratory exit; *l*, lateral body muscle; *S*, sternum; *T*, tergum; *Tra*, trachea.

subject of a special study by Eastham (1938, 1939). Just as the thysanuran styli do not appear until after the first moult, so the gills of the mayfly larva are absent in the first instar. It is said by Ide (1935) that all the gills appear with the first moult in some species, but that in other species most of them may be delayed until several moults later.

Gills of the simplest form are slender processes penetrated by tracheae, others are fringed with long filaments, some are lamelliform, and most of them are branched. According to Ide (1935) all the gills are at first uniramous, and some that eventually become lamelliform grow out first in the form of filaments. It would appear to be true, therefore, as Spieth (1933) says, that the primitive gills of the ancestral mayflies were simple slender tubular structures, into which the tracheae enter, and that the compound gills of the present-day forms have arisen as modifications of the primitive type. If the modern gills do represent styli, we may suppose that the young mayfly in its primary terrestrial life may have had abdominal styli similar to those of the Thysanura and Diplura, which, when it took to the water, were readily converted into gills. That the mayfly gills have been derived from styli, however, is merely a theoretical concept, but considering that the Ephemeroptera are relatively primitive insects the concept is sufficiently reasonable to be accepted as not too improbable. Unlike styli, however, the mayfly gills are discarded at the moult to the subimago.

Some remarkable larval modifications occur in connection with the gills. In the genus *Baetisca*, described by Vayssièrè (1934), the mesonotum is extended posteriorly to the middle of the sixth abdominal segment to form a carapace covering the gills and the meta-thoracic wing pads, the pads of the first wings being fused with its under surface. In *Prosopistoma* (Vayssièrè, 1882, 1890) a carapace is even more extensively developed (fig. 3 G) and covers a respiratory chamber enclosing the gills, which is shut in ventrally (H) by the pleural regions of the thorax and lateral extensions of the first five abdominal sterna. The *Prosopistoma* larva thus resembles a small crustacean in appearance. Water has entrance to the respiratory chamber by way of lateral openings (H,*en*) between the carapace and the sternum, and is discharged through a median dorsal aperture (G,*ex*) in the notch of the posterior end of the carapace. A preliminary stage in the development of a carapace is suggested in the larva of *Ephemerebella* (A) in which the mesonotum including the fore wing pads is extended posteriorly over the base of the abdomen and completely covers the hind wing pads.

In various lesser ways the mayfly larva may be characterized by special juvenile structures. In some forms the incisor processes of the mandibles are produced into a pair of long tusks. The larvae of *Ephemerella* that live in swift currents have an adhesive disc on the under side of the abdomen (F) formed of a dense fringe of soft marginal hairs. In the anterior part of the disc is a deep transverse cavity behind a strong semicircular lip, which possibly has something to do with creating a suction when the disc is applied against the surface of a rock.

It is noted by Ide (1935) that at each moult of the mayfly larva there is some structural change adapting the larva to environmental changes resulting from the growth of the larva. Such changes involve the mouth parts, the wing pads, external genitalia, the claws of the legs, and the caudal filaments. The larva moults many times before changing to the winged imago; observations by Ide show that *Ephemerella simulans* goes through about 30 larval moults, and *Stenonema canadense* as many as 40 to 45 moults. The large number of moults Ide attributes to the necessity for making adjustive physical changes to the environment, rather than to growth, since the larva increases but slowly in size. Some of these adaptive changes of the larva might be regarded as a feeble hypermetamorphosis, but the lack of gills and a tracheal system in the first instar and the expansion of newly formed gills into lamellar gills, cited by Joly (1872) as examples of hypermetamorphosis, are simply developmental changes.

The structural adaptation of an animal to a special environment is much easier to see as a fact, than it is to explain how it came about. The young mayfly larva can breathe through its skin, but as it gets larger it needs gills; the first one that entered the water, therefore, must have suffocated if it persisted in keeping submerged. However, if it possessed tracheated styli, it was but a simple evolutionary process to convert these organs into gills. Adaptation can seldom be one-sided; in the case of an aquatic larva of a terrestrial or aerial adult, the adult must be adapted to the way the larva lives. The female mayfly, therefore, has an instinct for returning to the water to discharge her eggs.

The changes that the mayfly larva undergoes in its metamorphosis to the adult are not due entirely to the special characters of the larva. The adult mayfly lives so short a time that it needs no food, and as a matter of economy its mouth parts are reduced to a functionless condition. Murphy (1922) says the "atrophy of the mouth parts is progressive during the aerial life of an individual," but "varies in extent among members of species." The ingestion apparatus and the

alimentary tract, however, are fully preserved, but for the purpose of swallowing and retaining air. The stomach is shown by Pickles (1931) and by Grandi (1950) to be transformed in the adult into a thin-walled air sack. The air probably serves to make the body more buoyant and by compression to expel the eggs.

Most mayflies undergo a moult after they have attained the state of a winged imago, the adult stage being thus subdivided into two winged stages, distinguished as the *subimago* and the *imago*. Concerning the subimago of *Cloeon dipterum*, La Baume (1909) says that it usually issues from the larval skin toward evening either on the surface of the water or on the shore. The quickness of the change is most noticeable, particularly the almost instantaneous spreading of the wings. The insect now flies to vegetation along the shore, where it remains quiet until the next moult, which, according to the species, may occur in a few minutes, a few hours, or several days. There is probably no specific reason why the adult mayfly should moult again; it is the only winged insect known to moult in the active adult stage, and even some mayfly species omit a second moult. Evidently the imaginal moult is simply a holdover by a primitive insect from wingless ancestors that shed the cuticle periodically throughout life as do the Thysanura and most other wingless arthropods. Extraction of the wings from the old cuticle is a difficult matter and other insects have simply discarded a useless and dangerous habit.

It is clear that the mayfly undergoes a greater degree of metamorphosis than does the stonefly because the young mayfly is more extensively modified in adaptation to life in the water. Inasmuch as the larva in the two cases is differently modified for the same purpose, metamorphosis has arisen independently in the two groups.

## VI. ODONATA

The Odonata present an example of metamorphosis much more accentuated than that of either the Plecoptera or the Ephemeroptera, and there is no relation between the special characters of the odonate larva and those of the other two groups, again showing that larval structures in adaptation to aquatic life have been independently developed in these three orders. In common with other aquatic larvae, the odonate larva has been adapted in its body form and its means of respiration to life in the water, but in addition it has evolved a very special modification of the labium by which this organ is greatly enlarged and converted into an efficient device for the capture of active prey.

The Odonata are predaceous both as larvae and as adults; their mouth parts are of the biting type of structure. The adults entrap their insect prey on the wing by means of their hairy legs, and their mouth parts are not unusually modified. The short body of the adult

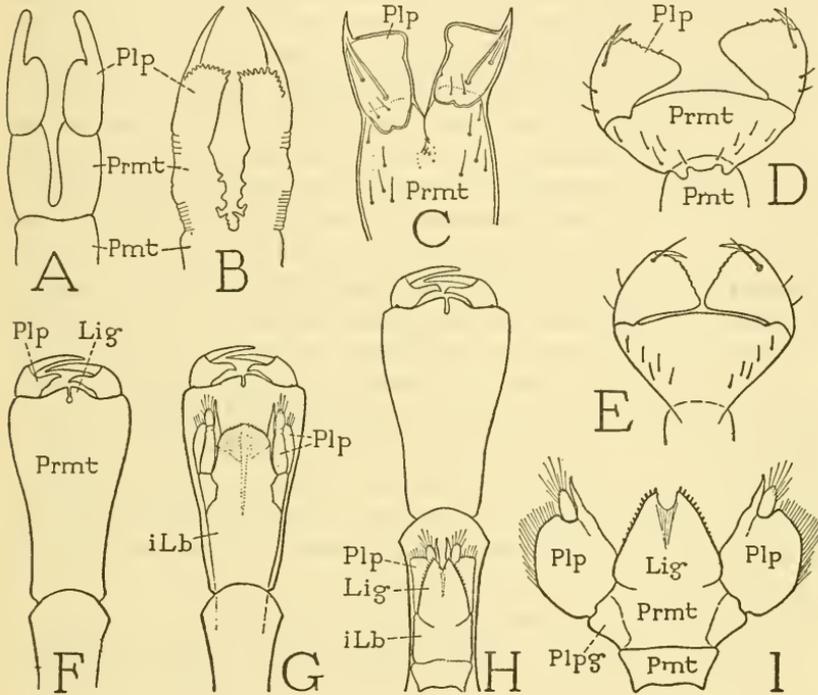


FIG. 4.—Odonata; development and metamorphosis of the labium.

A, *Anax junius* Drury, labium of 17-day embryo (from Butler, 1904). B, same, 20-day embryo (from Butler, 1904). C, *Sympetrum striolatum* (Charp.), labium of pronymph containing labium of second instar (from Corbet, 1951). D, same, free labium of second instar, expanding (from Corbet, 1951). E, same, fully expanded labium of second instar (from Corbet, 1951). F, *Anax* sp., labium of mature larva, posterior. G, same, larval labium and early stage of formation of imaginal labium in the prementum. H, same, later stage, the imaginal labium retracted into postmentum of larva and taking on the adult structure, posterior. I, same, imaginal labium from H unrolled and spread out.

*iLb*, imaginal labium; *Lig*, ligula; *Plp*, labial palpus; *Plpg*, palpiger; *Pmt*, postmentum; *Prmt*, prementum.

labium (fig. 4 I) consists of a distinct postmentum and a prementum; the prementum bears a large median ligular lobe, and two small lateral lobes (*Plpg*) that support the short, thick palpi (*Plp*). The larval labium is more simple in form than that of the adult, but both the postmentum and the prementum are greatly elongated, and are articulated on each other by a freely movable elbow. The larval postmen-

tum is unusual in that, instead of being as in most insects a plate on the under side of the head, it is produced into a long, free stalk supporting the prementum on its distal end. The prementum is highly variable in form in different genera; in the common *Anax junius* (F) it is a long flat lobe somewhat expanded distally where it bears the relatively small palpi, each of which is armed with a long sharp claw. In the passive position of the labium the postmentum is turned posteriorly against the mesosternum of the thorax (fig. 5 A); the prementum in some species is pressed against the under surface of the head (A), in others it is applied like a mask over the lower part of the face (C). In action the postmentum swings downward and forward on the head, the prementum is lowered (B), and the entire labium is then projected far beyond the mandibles to seize a prospective victim. Associated with the larval labium is a long T-shaped apodeme developed from the base of the hypopharynx that extends posteriorly through the head, and the crossbar is embedded in the posterior edge of the base of the postmentum. The labial musculature is surprisingly simple, but it is probable that blood pressure from the abdomen plays an important part in the projection of the labium. While undoubtedly the larval labium is specialized by comparison with the adult labium, the labium of the embryo develops directly into that of the larva, and at metamorphosis the adult labium develops within the larval organ. The hypopharyngeal apodeme is either greatly shortened in the adult or reduced to a ligamentous band.

The embryonic labium of *Anax junius* (fig. 4 A,B), as illustrated by Butler (1904), has a primitive feature in the almost complete separation of the stipital lobes of the prementum (*Prmt*); the unsegmented palpi (*Plp*) bear fingerlike processes (A) that will become the apical hooks (B). In the pronymph of *Sympetrum* (C), according to Corbet (1951), the prementum is undivided and the palpi arise close together from its distal end, but during ecdysis of the second instar (D) the prementum stretches transversely, and later (E) becomes more elongate. The embryonic labium thus goes from a primitive labial structure directly into the specialized structure of the larval labium. The labium of the adult as described by Munscheid (1933) is first formed in the distal part of the larval labium about five days after the larva ceases to feed. At first it takes on approximately the form of the larval labium, but later it becomes shorter until four days after its formation it occupies only the basal two-thirds of the larval postmentum. A further three days now elapses before ecdysis of the imago.

At an early stage of the labial transformation in *Anax junius* the imaginal labium may be seen retracted into the anterior part of the larval prementum (fig. 4 G, *iLb*). The principal changes that have taken place affect the palpi and the ligula, which have become elongated. On the palpus, the movable claw of the larval organ is replaced by a short setigerous lobe, as in the adult (I), and the fixed finger has become a slender tapering median process. At the base of each palpus a palpigerous plate is differentiated. In a later stage (H) the imaginal labium has withdrawn into the postmentum of the larval labium, where it is much compressed and its lateral parts are rolled anteriorly. When the imaginal labium at this stage is removed from the larval labium, unrolled and spread out (I), it is seen to have approximately the form of the adult labium except for the triangular shape of the ligula and its deeper apical notch. The palpi have taken on the form and size of the adult palpi, the prementum and postmentum are distinct in the body of the labium, and the palpigers are well defined. The triangular ligula finally becomes transversely oval.

It is of interest to note that the odonate labium begins its development in the embryo as a labium of primitive structure (fig. 4 A,B). In its later growth it develops directly into the specialized labium of the larva; then finally the more generalized labium of the adult is derived from the larval labium. It is not clear what phylogenetic deductions may be made from these facts, but it seems reasonable to suppose that the larval labium in the first place must have been evolved from a generalized labium approximately of the adult type of structure; if so, it carries the potentiality of reversal.

The transformation period from larva to imago is said by Munscheid (1933) in *Aeschna cyanea* to occupy about 12 days. During this time the structural changes of the labium are accompanied by a total histolysis of the larval labial muscles, followed by regeneration of the imaginal muscles and the formation of new tonofibrillar muscle attachments on the imaginal cuticle. Two pairs of larval muscles are destroyed and not replaced. The processes of muscle histolysis and histogenesis are described in detail by Munscheid, who points out that the transformation of the odonate labium and the regeneration of its muscles is comparable to the pupal metamorphosis in holometabolous insects, except that in the Odonata the process is limited to a single organ instead of affecting the entire insect, which otherwise is hemimetabolous. The long quiescent transformation period apparently allows the regenerated muscles to become attached directly on the new imaginal cuticle without the interpolation of a second moult.

Aside from the specialization of the labium, the principal adaptive characters of the odonate larva are the organs that serve for respiration. In the Anisoptera a spacious rectal sac contains six longitudinal tracheated folds of the walls which are the larval gills. The muscular apparatus of the rectum for the inhalation and exhalation of water becomes also a means of locomotion by the forcible ejection of spurts

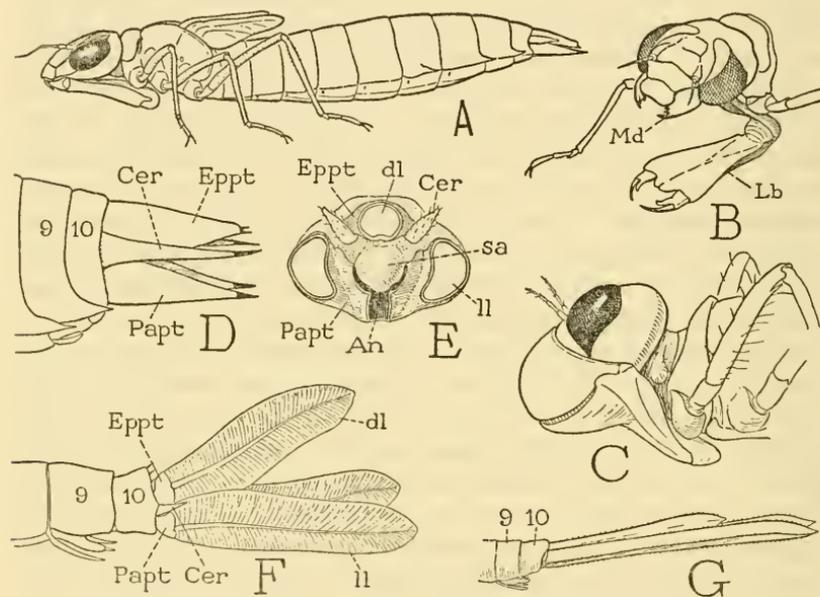


FIG. 5.—Odonata; general features of larvae.

A, Larva of *Anax* sp., labium in passive position. B, same, labium lowered and partly protracted. C, *Crocothemis servilis* Drury, labium applied against the face. D, anisopteran larva, posterior segments and lobes enclosing the anus. E, *Agrion virgo* L., posterior end of body with gill lobes removed. F, *Archilestes grandis* (Rambur), end segments of body and gill lobes. G, *Agrion virgo* L., end segments and apical lobes.

An, anus; Cer, cercus (cercoid); dl, dorsal gill lobe; Eppt, epiproct; Lb, labium; ll, lateral gill lobe; Md, mandible; Papt, paraproct; sa, supra-anal lobe.

of water. Zygopterous larvae are provided with three external gill lobes of various forms at the end of the body, one median and dorsal, the other two lateral, borne on basal plates surrounding the anus. Typically these caudal gills are thin lamellae (fig. 5 F), but they may be sacciform, and in some species they are slender horny blades (G) that do not appear to be suitable for respiratory purposes. The gills are weakly attached to the supporting plates so that they are easily broken off, but they regenerate at the next moult.

The current interpretation of the zygopterous larval gills, taken

from Heymons (1904), is that the dorsal gill represents a median dorsal filament and that the lateral gills are the cerci. Arising on each side between the bases of the gill-supporting plates is a small cercus-like process (fig. 5 F, *Cer*), the "cercoïd" of Heymons, who says it is developed during larval life. The gill-bearing plates (*Eppt*, *Papt*) surround the anus (*E*, *An*) in a manner so exactly comparable to the epiproct and paraprocts of an orthopteroid insect that their identity as such is hardly to be questioned, and the "cercoïds" (*Cer*) have the usual relation of cerci to these plates. The lateral gill lobes (*E*, *ll*, removed at their bases) therefore appear to be mere outgrowths from the paraproctial plates, and as such they could hardly be cerci. In the anisopterous larva (*D*) the gill-bearing plates of the zygopterous larva are produced into long valvelike lobes enclosing the anus, and there is no apparent reason for not identifying these lobes (*Eppt*, *Papt*) with the usual epiproct and paraprocts in the same position. The gills are cast off at the transformation to the adult, except as said by Tillyard (1917) that the lateral gills ("cerci") of the male leave a pair of small processes developed within their bases. If the lateral gills are cerci, it is an unusual thing for an insect to lose these organs.

In some zygopterous larvae, in addition to the caudal gills, there are paired lateral gills in the form of tracheated filaments along the sides of the abdomen (see Calvert, 1911; Needham, 1911; Tillyard, 1917). The tracheal system of the Odonata is present in the newly hatched larva, but according to Calvert (1898) the tracheae do not fill with air until the first moult. Spiracles are present in the larva but ordinarily are not functional except for the withdrawal of the tracheal linings at ecdysis. The early development of the tracheal system and the presence of spiracles in the larva, Calvert points out, attest that the immediate ancestors of the Odonata were air-breathing insects.

The structural changes that take place during larval life of the Odonata have been summarized by Tillyard (1917) under nine headings. Such changes, however, as the growth of the compound eyes, development of the ocelli, increase in the number of antennal joints and of subsegments in the tarsi, changes in the shape of the thorax correlated with development of the wings, progressive changes in the nervous system, and increase in the number of Malpighian tubules are merely stages in the postembryonic development of the adult organs. These are not true metamorphic changes such as those producing the general form of the larval body, the modification of the labium, and the development and differentiation of the rectal and

caudal gills. In addition to these changes, however, there takes place during the transformation period a radical change in the sclerotization pattern of the abdominal segments, accompanied by an almost total destruction of the larval abdominal musculature and the formation of a much more simple musculature for the adult. The Odonata might almost be said to be holometabolous insects without a pupal stage.

As in the case of other insects having aquatic larvae, the adult female of the Odonata has one instinct of responsibility to her offspring, namely, that which impels her to go back to the water to deposit her eggs. Some are so conscientious in this respect that they even enter the water and insert their eggs in the stems of submerged water plants.

## VII. HEMIPTERA

The Hemiptera differ from most other insects having specialized mouth parts in the mature stage in that the adult type of mouth parts is just as practical for the young as for the imago. The adult hemipteron has not evolved feeding organs useful only to an insect with functional wings. The piercing and sucking mouth parts in Hemiptera, therefore, are developed in the embryo and are functional as such in the newly hatched insect. The same is true of the Thysanoptera and Anoplura. If there are metamorphic changes between the young and the adults of these insects, they do not affect the essential nature of the feeding organs, and all instars of a species can live and feed together in the same habitat.

Among the Heteroptera postembryonic development is principally a succession of growth stages from the young to the adult; the Heteroptera, as the Orthoptera, are essentially ametabolous. Though the change between instars may be accentuated at the last moult, there is in general little, if any, structural deviation on the part of the young insect that must be suppressed in the imago. However, a definite case of juvenile aberration in the Heteroptera is to be seen in a species of mirid described by China (1931) in which the nymph (fig. 6 F) is armed on the head, thorax, and abdomen with large dorsal prongs. Though the adult of the species has not been certainly identified, no adult mirid is known to possess any such armature.

Among the Homoptera there is a distinct though sporadic tendency for the young insect to develop special characters of its own that are not carried over into the adult stage, or to take on a form quite different from that of its parents. The aberration of the young insect may even become so pronounced that the final transformation to the imago approaches or actually attains a condition of holometabolism.

A good example of simple metamorphosis in the Homoptera is seen in the structural adaptation of the young cicada to a subterranean life by the modification of its front legs for digging (fig. 6 D). The nymphal structure of the leg is not present in the embryo (A); it appears first on the nymph with the shedding of the embryonic cuticle just after hatching (B) and becomes more fully developed in succes-

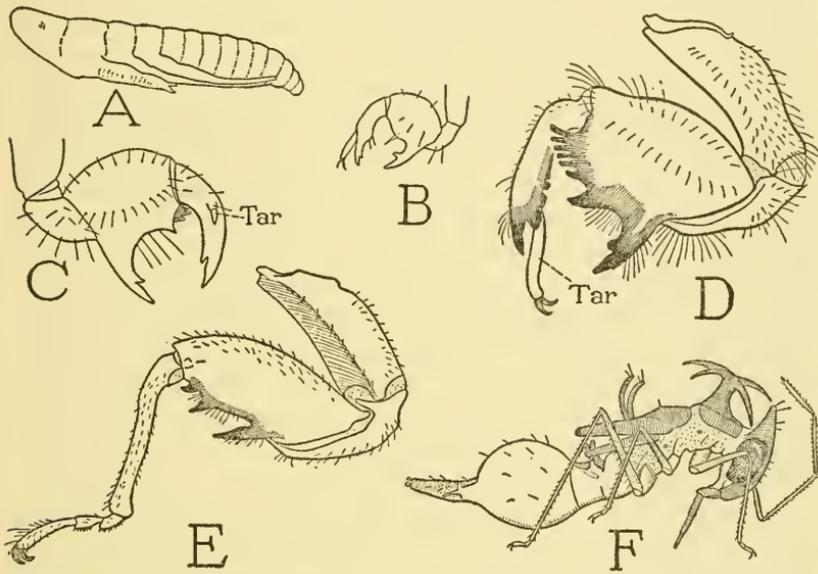


FIG. 6.—Examples of simple juvenile metamorphic characters in Hemiptera.

A, *Magicada septemdecim* (L.), newly hatched nymph still in embryonic cuticle. B, same, left front leg of first instar (from Marlatt, 1923). C, same, front leg of third instar, mesal view showing reduced tarsus (*Tar*). D, same, front leg of mature nymph, lateral. E, same, front leg of adult. F, *Paracarnus myersi* China, nymph, Heteroptera-Miridae (from China, 1931).

sive instars (C,D). The tarsus of the first instar (B) is reduced in later stages to a small spur on the inner surface of the tibia (C,*Tar*), but it is fully restored in the mature nymph (D). At the transformation to the adult, the special features of the nymphal leg are much reduced or obliterated (E). The newly hatched cicada has a pair of small eye spots, but in subsequent instars the eyes are lost, and functional compound eyes are redeveloped only in the imago. Within a chamber just below the surface of the ground, or built up above the surface, the 17-year cicada at last goes through a period of reconstruction inside the nymphal cuticle, during which the adult structure of the insect is developed, including the compound eyes, the external genital organs, and the sound-producing organ of the male. When

the insect emerges from its transformation chamber it is an active adult, but it still wears the nymphal skin until it arrives at a suitable place for ecdysis.

As another example of simple specialization in a young homopteron we may cite the respiratory canal of the spittle bugs, Cercopidae. On the ventral surface of the tapering posterior segments of the nymph is a deep groove that expands anteriorly into a wide space covered on the sides by the extended abdominal terga, which protect the spiracles. This modification is a respiratory device necessary only to the nymph and is discarded at the moult to the imago. As further examples of juvenile aberration we might note the presence of large branched spines on the back of certain membracid nymphs, and of various minor nymphal characters in other homopterous families that are not retained by the adult. Juvenile specialization among the Homoptera, however, is carried progressively further in the Psyllidae, Aleyrodidae, and Coccidae, until in the last family the transformation to the imago attains the status of true holometabolism. In the Aleyrodidae and the Coccidae the young insects are so different from their parents that, following the definitions given in the introduction, we must call them larvae, but admittedly they are nymphs that have acquired the status of larvae by definition.

The Psyllidae go through five juvenile instars, which, except for the flattened form of the body, in general resemble the nymphal stages of ametabolous Hemiptera. The wings appear first in the third instar and increase in size during the fourth and fifth instars; the legs, however, undergo a metamorphosis, which has been fully described by Weber (1930, 1931) in *Psylla mali*. The first instar is active because the young psyllid newly hatched on the twig of an apple tree must find an opening bud on which to feed; the legs are relatively far apart on the under side of the body, and in their movements are fitted for walking. After the first moult the insect becomes sessile, the legs come closer together at their bases and are flexed transversely beneath the thorax in order now to function as clasping organs. From the beginning, however, the segmentation of the legs has been reduced by a suppression of the femoro-trochanteral and the tibio-tarsal joints. At the moult to the fifth instar the young insect takes on something of the form of the adult, the body becomes deeper, the antennae longer, and in the legs there appears a slightly marked division between the tibia and the tarsus and an indication of two tarsal subsegments. Finally, within the cuticle of the legs of the last juvenile instar the imaginal legs are developed, the trochanter being now separated from the base of the femur, the tarsus distinct from the tibia, and two

well-defined tarsomeres present. The first two pairs of clasping legs of the young become normal walking legs in the adult, but the hind legs are elongated and transformed into jumping organs by an enlargement of the coxae and a lengthening of the body muscles of the trochanters associated with a dorsal extension of the sternal apodeme on which they are attached. The general alteration of the body form at the last moult, Weber shows, involves changes and enlargements of muscles in the thorax that are destined to be motors of the wings. The mouth bristles are retracted into a cruminal pocket instead of being looped outside the head as in the immature stages.

While the degree of metamorphosis in the psyllids is thus not large, it is enough to show how a young nymphlike insect can be specifically modified in adaptation to its needs, even in a different way in successive instars. The transformation of the young psyllid into the adult, however, is complicated by the development of special imaginal characters along with the suppression of juvenile characters.

In the Aleyrodidae there is a juvenile metamorphosis somewhat similar to that of the psyllids because here also the first instar is active and the others are sessile. The young aleyroidid, however, is much flattened, the body being of a simple, oval, scalelike form and wingless in all immature instars; the spiracles are on the under surface, and a wide fringe of wax filaments forms a marginal palisade that encloses an air space beneath the body. There are four immature stages, the characteristics of which are described by Weber (1931, 1934) as follows. In the active first stage the antennae and the slender, tapering legs are relatively long; each leg has only three segments and bears a stalked apical adhesive disc, representing the unguitactor plate of the adult insect. In the second instar the antennae are much shortened, and the legs are reduced to small, unsegmented stumps useless for locomotion but retaining the adhesive discs. The same leg structure is carried over into the third instar, but in the fourth instar both the legs and the antennae become again larger, and the legs are now 2-segmented.

From the fourth instar the adult aleyroidid is produced directly, but by an unusual transformation process. As described by Weber (1931, 1934) in *Trialeyrodes vaporariorum*, the body of the young insect in the fourth instar becomes deeper than that of the preceding instars, and the marginal wax palisade stands vertically below the edges. In the early transformation stage the long, slender legs of the imago grow beneath the larval cuticle, but for want of space they become much folded and looped. Above the bases of the legs deep infoldings of the body wall of the imago form large cavities, which separate the

median part of the body of the imago from the wide lateral extensions of the larval body. From the median walls of these cavities the wings are formed as outgrowths that finally extend back into the abdominal region. The lumina of the lateral body lobes of the larva are filled with fat cells, and at first are narrowly continuous above the wing cavities with the haemocoel of the central part of the body, but, as the wings push out, the lateral lobes become disconnected from the central body, and at ecdysis are shed with the larval cuticle. A cavity is similarly formed anteriorly that cuts off the precephalic margin of the nymph, while a third cavity at the posterior end of the body provides for the growth of the external genitalia. At ecdysis, therefore, all the superfluous marginal parts of the larval body are cast off, and the imago is formed from the central part only.

The metamorphic characters of the young aleyrodid are thus seen to include a flattening and simplification of the body and a suppression of the wings, together with modifications of the legs adaptive first to active and then to sessile habits. The characteristic feature of the final metamorphosis, however, is in the manner of transformation to the adult involving the discarding of parts of the larval body. The aleyrodid metamorphosis has been termed *allometabolism* (from *allo*, different), but the development of the wings beneath the cuticle of the last larval instar is entirely comparable to the simplest form of wing development in typical endopterygote insects; the term *Endopterygota* taken literally, therefore, would include the Aleyrodidae.

It is in the Coccidae that metamorphosis among the Homoptera reaches its highest degree of complexity. The young scale insect is a larva adapted to a parasitic life on plants, and in its external aspect it is quite different from the adult. The true form of an adult coccid, however, is known only from the winged male, since the female becomes sexually mature in a late larval-like stage and undergoes no further transformation.

On hatching from the eggs the simple, flattened first-instar coccid larvae are provided with eyes, antennae, mouth parts, and legs. They are active crawlers whose function it is to disperse themselves over the food plant. When the young larvae have settled down at a suitable feeding place, they moult and enter a second larval stage in which the legs in many species are reduced, or lost altogether, though in some forms the legs are fully retained. With typical species (diaspine scales) there are only two larval instars, but in some there are three or more, and generally during the larval period there is only a slight difference between the males and the females. At the last larval moult, however, the sexes are differentiated. The female looks like only

another and larger larval instar, since she has no vestiges of wings; in some species the legs and antennae are retained, but in many the legs are much reduced or suppressed. The female usually preserves her mouth parts and alimentary canal, though the external feeding organs may disappear. The ovaries, however, become functional and soon the body of the female is converted into a bag of eggs. In the reproductive stage the female scale insect thus appears to be a sexually precocious larva, but some coccidologists contend that she has attained a larval form secondarily by a process of reduction or degeneration from a winged adult. Perhaps the only way to settle the question would be to give the female a dose of the proper hormone and see what happens to her.

The male coccid, after the last larval moult, goes through usually two immobile transformation stages, and then becomes in most cases a winged insect. In the first transformation stage, known as a *propupa*, the male of winged species begins to take on the form of the adult; the antennae, legs, and wings appear, and the eyes are fully developed, but the mouth parts are reduced or suppressed. In the next stage, termed the *pupa*, the insect assumes more closely the form of the winged imago, the antennae and the legs increase in length, taking on the character of the adult appendages, and the wings lengthen. In the male of *Lepidosaphes ulmi*, according to Suter (1932), there is only one pupal stage, during which the wings and legs appear and increase in size until the moult to the adult. The adult male usually has a pair of well-developed wings, but is devoid of feeding organs. In some species, however, the male does not attain the typical winged structure; the wings may be absent, the antennae and the legs much reduced in length, while the body retains the larval form with no constriction between head, thorax, and abdomen. The redevelopment of the antennae and legs of the male scale has been shown by Berlese (1896) in the Diaspinae (*Mytilaspis*) to take place in the early pupa by evagination of the appendage rudiments from pouches of the integument beneath the cuticle of the propupa.

In addition to its external transformations the male coccid undergoes a very considerable degree of internal metamorphosis, which has been described particularly in *Pseudococcus* by Mäkel (1942). Along with the casting off of the mouth parts there is a great reduction of the alimentary canal, which retains its form in the pupa, but in the imago the mesenteron is reduced to a mass of cells without a lumen. The oesophagus remains as a slender tube, the proctodaeum is narrowed, though the rectum keeps its original dimensions, and the

Malpighian tubules increase in size. These changes are mostly retrogressive from the larval condition. On the other hand, the reproductive organs develop gradually to the definitive functional state, and there is a thoroughgoing reconstruction of the larval musculature into that of the adult.

In her account of the muscle transformation in the male of *Pseudococcus* Mäkel distinguishes five different groups of muscles, as follows: (1) Larval muscles that go over with little or no change into the imago; (2) larval muscles that undergo such changes as splitting, uniting, or a change of position; (3) larval muscles destroyed by histolysis and not regenerated; (4) transformation muscles formed by addition of imaginal elements to larval muscles; (5) muscles of the imago that arise as new muscles in the propupa. To this last group belong four muscles of the thorax, and seven oblique intersegmental muscles of the abdomen, together with two muscles connected with the external genital organs. The metamorphosis of the muscular system as given by Mäkel is based on a detailed comparative study of the musculature in the larva, pupa, and adult.

It is clear that the transformation of the male coccid is a true holometabolous metamorphosis, and that the larva is a specialized juvenile stage. It may be questioned, however, that the coccid pupa is comparable to the pupa of the higher holometabolous insects. The presence of two pupal stages having a general resemblance to the winged nymphal stages of other Hemiptera suggests that the so-called pupal instars of the male coccid pertain to the juvenile period of the life history and not to that of the imago. The work of Wigglesworth (1948, 1951a) on the hormonal control of transformation in the reduviid *Rhodnius* shows that the juvenile hormone controls the nymphal status up to the imago, and if this is true in other Hemiptera the coccid pupa is not a part of the imaginal stage. Holometabolism can be defined only as a type of metamorphosis; the fact that it occurs among the Hemiptera in the male coccid, and also in the Thysanoptera does not taxonomically relate these insects to each other or to such holometabolous insects as Coleoptera, Lepidoptera, Diptera, and Hymenoptera.

#### VIII. THYSANOPTERA

The Thysanoptera seem to contradict the principle that postembryonic metamorphosis is due to some structural aberration on the part of the young insect that fits it to a special environment or way of living. The active young thrips in appearance differs from the imago little more than a young aphid differs from a winged adult aphid, and

it would seem that in like manner it could grow into an adult thrips without any radical process of transformation. However, after two active, feeding nymphlike stages (fig. 7 A,B) the young thrips becomes

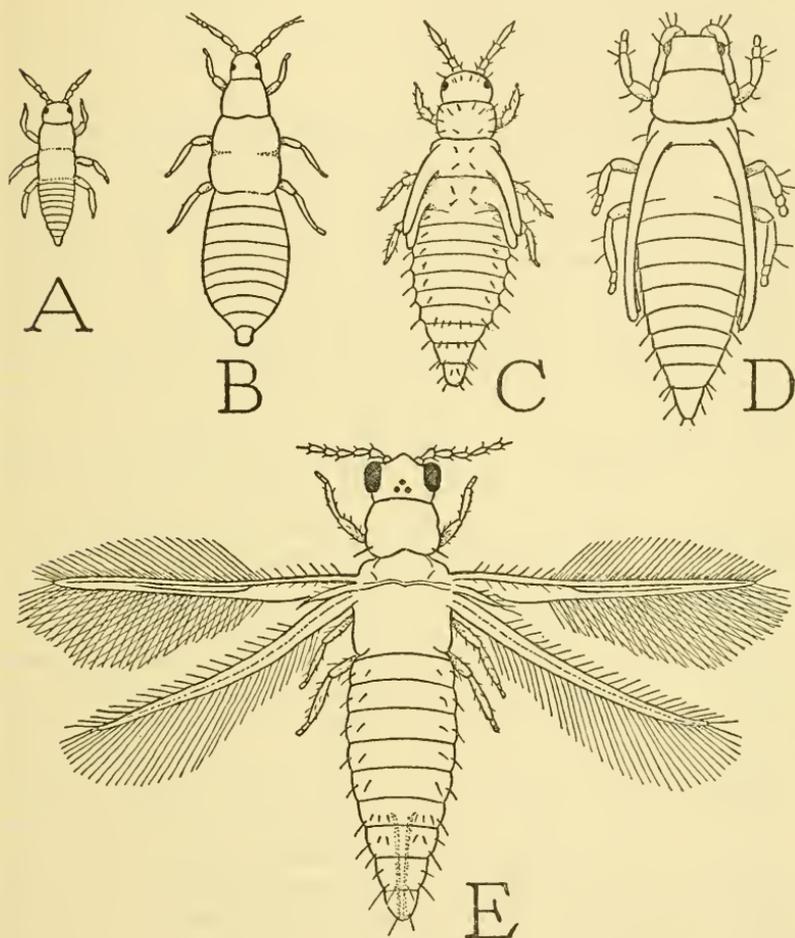


FIG. 7.—Life-history stages of a thysanopteron, *Scirtothrips citri* Moulton (outlines from Horton, 1918).

A, first instar. B, second instar. C, propupa. D, pupa. E, adult female.

inactive, ceases to feed, moults, and enters a quiescent stage known as a *propupa* (C). The propupa in turn is followed by a second resting stage termed the *pupa* (D), from which after a final moult the adult emerges (E). In the Terebrantia the wings appear in the propupal stage as straplike outgrowths, which become still more extended in the pupa. In the Tubulifera the propupa differs little in

external appearance from the second nymph, since in this suborder the wings do not appear until the pupal stage. In most of the Tubulifera, however, there is a second pupal stage separated from the first by a moult, making five immature instars in all, but according to Priesner (1926) a propupal stage is absent in some species and in others there is only one pupal stage.

The few external changes other than the growth of the wings that take place during the postembryonic development of the Thysanoptera are of little consequence. In some forms the antennae are reduced in the propupa and their segmentation becomes indistinct. In the pupal stage the antennae elongate, their segmentation becomes distinct, the form of the head approaches that of the imago, the compound eyes increase in size, the ocelli appear, and the sexes are now distinguishable. Most of these changes are merely those that any ametabolous nymph might go through in its development to maturity. The resting stages in the life history of a thrips, however, suggest that internal changes are going on, and, in fact, a reconstruction of some of the internal organs takes place during the propupal and pupal stages that is entirely comparable to the transformation processes of holometabolous insects. These changes in the thrips affect the alimentary canal, the salivary glands, the fat tissue, the muscular system, and in a lesser degree the nervous system.

The alimentary canal of *Liothrips oleae*, according to Melis (1935), does not differ essentially in external form during preimaginal stages from that of the adult, but the cellular structure of the mesenteron becomes highly unstable and is in a continuous state of reorganization. On the other hand, in *Parthenothrips dracaenae*, as described by Müller (1927), the alimentary canal undergoes changes in shape and size as well as cellular reconstruction during the propupal and pupal stages. In the two nymphal instars the long tubular ventriculus is looped forward upon itself and then turns back to join the intestine; in the propupa the whole canal becomes a simple straight tube with no ventricular loop; in the pupa the ventricular loop reappears but only as a short lateral fold from the middle of the tube; in the imago the ventriculus is again bent forward on itself as in the nymph, and there is a secondary small loop in the descending arm. Since the alimentary canal of the adult becomes practically the same as that of the young thrips the intervening changes might seem useless, except that, as the insect takes no food during the propupal and pupal instars, the ventricular changes may be simply economy adaptations to a lack of need for a digestive organ. In *Parthenothrips*, Müller says, there is one renewal of the midgut epithelium. At the beginning of metamor-

phosis in the last part of the second larval stage the regenerative cells of the ventriculus actively multiply and later spread out to form a new epithelial layer while the old degenerating layer is cast off into the lumen. Elongation of the stomodaeum and the proctodaeum proceeds from cell proliferation by mitotic division in "imaginal rings" of cells at the inner ends of these two ectodermal parts of the canal.

The Malpighian tubules of *Liothrips oleae*, according to Melis (1935), undergo no appreciable transformation, being the same in all stages. The salivary glands degenerate in the propupa and pupa, and are reduced to long bodies crowded with large nuclei in a scant protoplasm, but they are restored in the adult to essentially the nymphal form. The cells of the fat body play the usual role in metamorphosis; they increase in size during nymphal life and store up nutritive products in their cytoplasm, which in the propupa and pupa are given out and consumed in the reconstruction of the muscles. The change in the nervous system involves principally a transposition of the brain from its nymphal position in the thorax into the head of the adult, accompanied by development of the cerebral nerves and their adaptation to the imaginal organs they innervate.

The reorganization of the muscular system is the most important feature of metamorphosis in the Thysanoptera. As described by Melis (1935) in *Liothrips oleae*, during the propupal stage the larval muscles of the head go into complete histolysis, in the thorax and in the last abdominal segment there is a partial myolysis, but most of the abdominal muscles do not undergo any appreciable change. During the pupal stage there follows a total regeneration of the intrinsic head muscles, and a reconstruction of the thoracic and abdominal muscles to fit the needs of the adult. The processes of histolysis and histogenesis as described in detail by Melis are the same as those in typical holometabolous insects; muscles that are to be reconstructed with new attachments undergo a partial dissolution, but the nuclei persist in small fragments of cytoplasm that reassemble to form new muscles, or attach themselves to remnants of old muscles to form reconstructed muscles.

The internal metamorphosis of the Thysanoptera is thus seen to be truly holometabolous, but the nymphlike form of the insects in all the immature stages, and the small degree of external change from nymph to pupa and from pupa to imago suggest that the so-called pupal stages are merely the usual third and fourth instars, which have become inactive because of the reconstructive process that takes place within them. The immature stages of the Thysanoptera thus appear to be comparable to the nymphal stages of ametabolous insects, with

the wings developed in the third or fourth instar. It is, therefore, difficult to account for an internal metamorphosis for which there is no apparent external reason.

IX. OLIGONEOPTERA, OR TYPICAL ENDOPTERYGOTA:  
NEUROPTERA TO HYMENOPTERA

Whether the orders here included constitute a monophyletic group of holometabolous insects or not will be a matter of opinion. Since holometabolism occurs in the unrelated Coccidae and Thysanoptera, some entomologists will contend that it may have arisen independently among other holometabolous orders. The modern larvae of the typical endopterygote insects differ from the nymphs of ametabolous insects and the larvae of hemimetabolous insects not only in being endopterous but also in several other respects. They lack eyes that are identical with the compound eyes of the adult, and usually they have independently developed simple larval eyes; the hypopharynx, when present, is more or less united with the labium; the body musculature differs from the typical adult musculature in varying degrees; and metamorphosis from larva to imago in all cases involves an intervening pupal stage.

Inasmuch as there can be little question that endopterygote insects have been evolved from exopterygote ancestors, the simplest and most reasonable view to take concerning the nature of the holometabolous endopterygote larva is that it represents in modified form the nymphal instars of ametabolous exopterygote insects. Both the larva and the nymph are the active juvenile stage of the insect during which the wings are developed. Whether the wings grow externally or internally, or may be retarded in their growth to a late instar, is a difference of no consequence. The larva as well as the nymph has wings in the course of development, and is not a "wingless" stage of ontogeny. If the legs also are developed beneath the cuticle, the larva for that reason is not "legless," and does not represent an apodous stage of ontogeny or phylogeny.

The principal problem concerning the origin of the endopterous holometabolous larva involves the question: For what way of life was the primary larva modified from an ordinary ametabolous nymph that led to the acquisition of its distinctive features and its holometabolous metamorphosis? The young cicada or the young stonefly clearly show how, by simple structural adaptations for environments different from those of the adult, a nymph might readily be converted into a hemimetabolous larva, but external modifications do not account for holometabolism.

The endopterous condition of the larva and the substitution of short-sighted simple eyes for long-sighted compound eyes were conceived by Lameere (1899) to have arisen as adaptations in a primary nymphlike juvenile form to boring into plant stems. The theory, however, does not take into consideration the facts that most present-day larvae of the boring type are specialized forms in their own orders, and that free-living forms give no evidence of having been reconstructed for life in the open from a primary boring type of larva. It is hard to believe, for example, that the antecedents of the aquatic *Corydalus* larva or the *Dytiscus* larva, or even those of terrestrial beetle larvae lived in plant stems. As for the change of eyes, it would seem that a boring larva would hardly need any eyes at all. Though the Lameere theory of larval origin is thus not convincing, it is the only theory that has been proposed to account specifically for the characteristic external features of modern endopterygote larvae.

We can readily imagine that the suppression of external wing pads during the nonfunctional period of their development would be a convenience to most any young insect regardless of its habitat. Wingless larvae, by comparison with winged nymphs, have certainly shown a great superiority in ability to adapt themselves to different environments and to different ways of living.

A theory concerning the nature of the endopterygote larva, elaborated by Jeschikov (1929), regards the larva as a free-living continuation of the embryo; the larva has even been defined as such (Henderson, 1949). First, we might ask, what animal is not a continuation of the embryo? The theory of Jeschikov, however, contends that the larva *is* an embryo, and that the nymphal stages of its ancestors are all condensed in the pupa. However, in no other insects are the wings developed in the embryo, at most they are represented only by differentiated groups of cells in the embryonic epidermis. The ametabolous and hemimetabolous Pterygota all show that wing development is a function of postembryonic life. Periodic moulting is common to both nymphs and larvae, but it would be quite exceptional in an embryo. If the larva is an embryo, cases of paedogenesis would really be embryogenesis, and larval heteromorphosis would be embryonic heteromorphosis; some embryos would take to the water on hatching, others would burrow into the ground, still others would climb trees, and finally we should have embryos spinning cocoons and transforming into pupae. These implications are rather too much for the theory. When the embryo comes out of the egg and takes on all the functions necessary for a free life, its embryonic stage is ended,

though of course what we now call it is merely a matter of conventional definition.

The endopterous condition of the larva very probably was not produced by a single mutation. In the simplest type of wing development among modern endopterygote insects, as shown by Tower (1903) in certain Coleoptera, the wing is first formed in the early pupa beneath the cuticle of the last larval instar, and is therefore exposed only at the moult to the pupa. If formed as a fold of the body wall at any earlier stage the wing rudiment would be exposed at the next larval moult. The first appearance of wing pads among exopterygote insects on different instars shows that the wing growth may be retarded. In the past history of those beetles in which the wing is not present as a fold until the early pupa, the external growth of the wing must have been first retarded and then suppressed until the end of larval life, and we may conclude, therefore, that the first step in attaining the endopterous condition was a retardation in the time of development of the wing rudiment. The formation of a wing fold is not the true beginning of the wing development; in earlier larval stages the alar rudiment is present in the form of a thickening or a differentiated group of cells in the epidermis, which is the wing in a state of suppressed growth.

On the other hand, in most of the endopterygote insects the development of the wings has been expedited by the early recession of the growing wing rudiments into pockets of the epidermis beneath the cuticle, which become closed and are thus not affected by the larval moults. Within these pockets the wings can grow without being exposed until they are everted at the moult to the pupa. According to Tower (1903) the wings develop in this manner among the Coleoptera in Scarabaeidae, Coccinellidae, and Chrysomelidae; Patay (1939) says the wings of *Leptinotarsa* develop in closed pockets toward the end of the third instar. A familiar example of the usual recessed type of wing development beginning in the second larval instar is that given by Mercer (1900) for *Pieris rapae*.

The endopterous condition in its evolution, therefore, has probably gone through two phases, both existing among modern insects. In the first phase the growth of the wings presumably was suppressed until the end of the juvenile period; in the second phase the wing rudiments developed again at an early larval stage, but now sank into the epidermis beneath the cuticle, thus still preserving the "wingless" state of the young insect. It must be evident, then, that there is no truly wingless larva of any winged insect; the wings exist in some

retarded stage of growth. The endopterygote larva, therefore, does not represent an apterous stage of ontogeny, and much less does it recapitulate an apterous stage of phylogeny.

Similarly, legless larvae are not truly apodous; the leg rudiments are present in some form, though they may be greatly reduced. In the honey bee, for example, Nelson (1915) has shown that external leg rudiments are present on the embryo, but at the time of hatching are reduced to discs in the epidermis, which later redevelop internally in the larva. The leg tissue, therefore, is continuously present, though it may not take the form of a leg bud until late in larval life.

The suppression of compound eyes during larval life, unlike the suppression of wing pads, would not seem to confer any advantage on a free-living young insect. The typical larval eyes are simple single eyes, usually only a few in a group on each side of the head. They are developed on the site of the future compound eyes and are connected with the same part of the brain; but generally at the end of larval life the larval eyes degenerate, and they never take any part in the formation of the definitive compound eyes. In the Culicidae and related Diptera it is shown by Constantineanu (1930) that the compound eyes begin their development in an early stage of the larva, and that the larval eyes, which are formed in the embryo, are retained in the adult. Yet the two remain as entirely distinct organs. In the larva of *Panorpa* there are 30 to 35 single eyes in a group on each side of the head, and, as described by Bierbrodt (1942), these panorpid larval eyes have attained the structure of ommatidia, and probably function as appositional compound eyes. However, the larval eyes and their nerves degenerate during the pupal metamorphosis and do not become the compound eyes of the adult. Here is a case, therefore, in which a larva has succeeded in reacquiring functional compound eyes, but these larval eyes, as those of other insects, give place to adult compound eyes newly developed in the pupa.

In discussing the origin and evolution of endopterygote larvae, Chen (1946) contends that the primary larva, derived from an exopterous nymph, was aquatic, and he cites the megalopterous larvae, particularly the larva of *Corydalus*, as being the closest modern representative of the primary larva. Though it may be conceded that the megalopterous larvae are relatively generalized modern forms, they are nevertheless superficially modified for aquatic life, and life in the water does not account for their more fundamental characters, which are those of endopterygote larvae in general. The stonefly, mayfly, and dragonfly larvae are all aquatic, and yet they have compound eyes and external wing pads, and they transform without a pupal stage.

If we assume that the primary endopterygote larva was a modified nymph, we might more reasonably expect it to be best represented among modern forms by some of the simpler terrestrial larvae, such as a raphidian larva (fig. 8 B), or coleopterous larvae in the families Carabidae, Staphylinidae (C), and Dermestidae (D). Such larvae live in the same general habitat as the adults, feed on the same kind

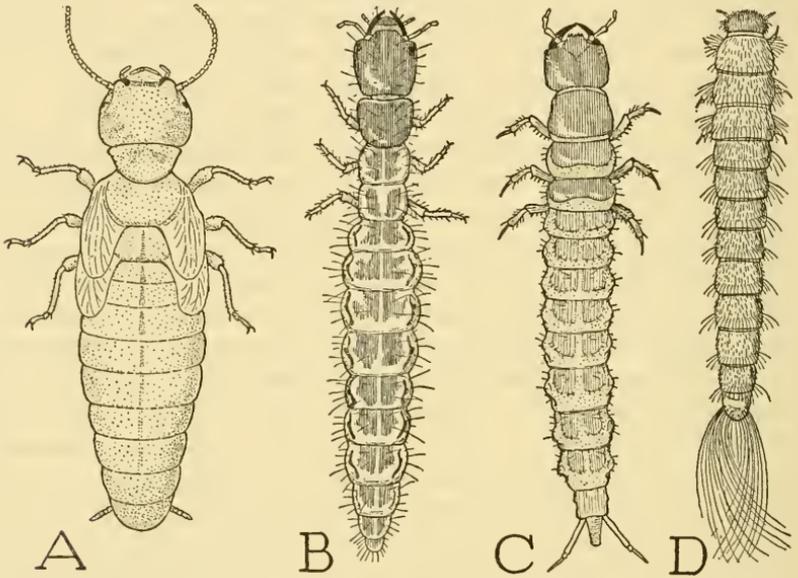


FIG. 8.—Examples of a generalized ametabolous nymph and of simple holometabolous larvae.

A, *Zootermopsis angusticollis* (Hagen), nymph of a winged termite. B, *Agulla adnixa* (Hagen), raphidian larva. C, *Creophilus maxillaris* Long, larva of a staphylinid beetle. D, *Attagenus piccus* Oliv., larva of a dermestid beetle.

of food with the same kind of mouth parts, and have no structural adaptations for any particular environment. Except for the lack of external wing pads and compound eyes they resemble an ametabolous nymph (A), and they differ least from the structure of the adults of their species.

The larvae of the lower endopterygote groups show their closer relation to the exopterygote insects in the possession of typical two-clawed pretarsi. Those with paired movable claws on the feet include the larvae of Megaloptera, Raphidioidea, most Neuroptera except Sisyridae, and the larvae of the coleopterous families Carabidae, Cicindellidae, Gyrinidae, Dytiscidae, Amphizoidae, and Noteridae. The two-clawed foot evidently is primitive among the winged insects ;

the single claw of the larva in the higher orders, therefore, is a secondary larval modification, and does not represent a primitive one-clawed pretarsus, or dactylopodite.

It would seem, therefore, that an unspecialized modern larva should best represent the primary endopterygote larva, since from such a larva evolution could more readily produce various specialized forms. Yet even the simplest of modern larvae gives us no suggestion of how or why it acquired its distinctive larval characters. The endopterygote holometabolous larva must, for the present, be accepted only as a fact; we have no evident explanation of its origin.

The reason for holometabolism, that is, for metamorphosis that involves the intervention of a pupal stage between the larva and the imago, is not to be found in the external characters of the larva. The young mayfly or the young dragonfly differ externally from their parents more than do the larvae of some endopterygote insects, but yet they transform without a pupal stage. The pupal transformation processes involve a variable degree of reconstruction of both external and internal larval tissues, but, so far as known, they always include at least a partial dissolution of the larval musculature accompanied by the formation of new muscles or of new muscle attachments for the imago. The cessation of muscular activity brings about the quiescence of the pupal stage. Since the lesser degrees of change in other internal organs might be accomplished direct from larva to imago, it appears to be the disparity in the muscular system between the young insect and the adult that constitutes the reason for holometabolism. As we have seen, this is true also for male Coccidae and the Thysanoptera. The external suppression of the wings, the absence of compound eyes, or the presence of abdominal appendages in the larva have nothing to do with the fact that the holometabolous larva has a muscular system that cannot go over entirely or directly into the adult musculature.

The somatic musculature of nearly all adult pterygote insects is built on the same fundamental plan, though some muscles may be reduced or eliminated in the thoracic segments of wingless species or in those having weak powers of flight. The musculature of exopterygote nymphs is essentially like that of the adults, but in holometabolous insects the musculature of the larva is usually very different from that of the adult. The pattern of the larval musculature is simpler in the less specialized larvae of each order, and it is least specialized in larvae that differ least from the adults. Hence, we may suppose that the simplification of the larval musculature in a primitive endopterygote

larva was an economy measure correlated with the reduction of the wings and the fewer abdominal movements that the larva had to make as compared with the adult. Whenever the difference between the larval musculature and the adult musculature reached a point where new attachments for imaginal muscles became necessary, a new moult had to intervene, and thus a pupal stage became interpolated between the larva and the imago. With the pupa once established as a reconstruction stage for the muscles, it served also increasingly for the transformation of other tissues.

In most of the major holometabolous orders the larval musculature becomes progressively more complex in the higher families. The wormlike form assumed by so many larvae, and the consequent necessity of a wormlike mechanism of movement readily accounts for the specialization of the musculature in all vermiform types of larvae. Since the insect larva, however, is not a worm, no matter how wormlike it may be, its musculature is never that of a worm, it merely serves mechanically to enable the larva to make wormlike movements.

Otherwise, the forms and structure of most modern specialized holometabolous larvae are clearly adaptations to specific environments or ways of living, usually different from those of the adult. Such larvae have thus taken on temporarily structures useful only to themselves, which must be discarded at the final transformation to the imago. The ordinary caterpillar with its short thoracic legs, its long abdomen supported on leglike props, its strong biting and chewing jaws and ample food tract is clearly made for feeding in the open and for the storage of food reserves. A boring larva, on the other hand, is unmistakably adapted to burrowing into wood or plant stems. The larvae of Diptera were probably in the first place aquatic, but their structure is readily adaptable to life in mud, fruit pulp, manure piles, and the bodies of other animals. The grubs of wasps and bees are incapable of self-support, but they are perfectly constructed for confinement in cells where they are furnished with food by their mothers or other adult attendants. Internal parasitic larvae are usually greatly simplified in structure because they have nothing to do but to feed on the food in which they are immersed.

The presence of paired appendicular organs on the abdomen of various endopterygote larvae has often been taken to be a retention from the embryo of a stage representing a primitive polypod condition in the ancestry of insects. Thus Chen (1946) says: "The primitive larvae are presumably of the campodeoid-polypod type, having three pairs of thoracic and ten pairs of abdominal legs; the latter bear each

a vesicle and a stylus." From this premise Chen concludes that the *Corydalus* larva is the closest modern representative of the primary larva, and that the latter was aquatic. In a former paper the writer (1931) reviewed the structure of the appendicular organs on the abdomen of endopterygote larvae, and suggested that these appendages represent the eversible vesicles and the styli of Thysanura.

Broad generalizations are always mentally comforting because they relieve the mind from the confusion of seemingly unrelated facts, for which reason also generalizations are prone to become wider than the evidence on which they are based. A closer comparison of the abdominal appendages of endopterygote larvae with the vesicles and styli of Thysanura shows that the two sets of organs are not identical in structure, which fact raises the suspicion that they may be in no way related. Furthermore, there is no valid reason for supposing that the primary endopterygote larva should have had thysanuran characters. Some exopterygote insects retain a single pair of styli on the abdomen, but none of them has abdominal vesicles or other abdominal appendages except cerci and the organs of copulation and egg laying, which are a common inheritance of Thysanura and both exopterous and endopterous Pterygota. Insects could not be encumbered with abdominal appendages after they acquired wings. The polypod progenitors of the insects are unknown; they probably became extinct when the primitive apterygotes became hexapods. As we have seen, even the Thysanura do not have true legs other than those of the thorax. Possible vestiges of abdominal legs are retained among the apterygotes only in the Protura and Collembola.

The adjectives "thysanuriform" and "campodeiform" as applied to the more simple types of endopterygote larva can have only a descriptive value. An endopterygote larva, no matter how thysanuriform it may be in appearance, is just as truly a winged insect as is an exopterygote nymph, and it is much farther removed than the nymph from its apterygote ancestors. Since it is hardly to be supposed that the exopterygote orders and the endopterygote orders represent two primary lines of divergence from primitive winged insects, the endopterygotes must have had a long line of exopterygote ancestry separating them from their apterygote progenitors. Exopterygote insects were already flourishing in Carboniferous times, endopterygotes appear in the Permian; the earliest apterygotes (Collembola) are known from the Devonian.

Larval abdominal appendages are most fully developed in the larva of *Corydalus* (fig. 9 A). Along each side of the abdomen on the first

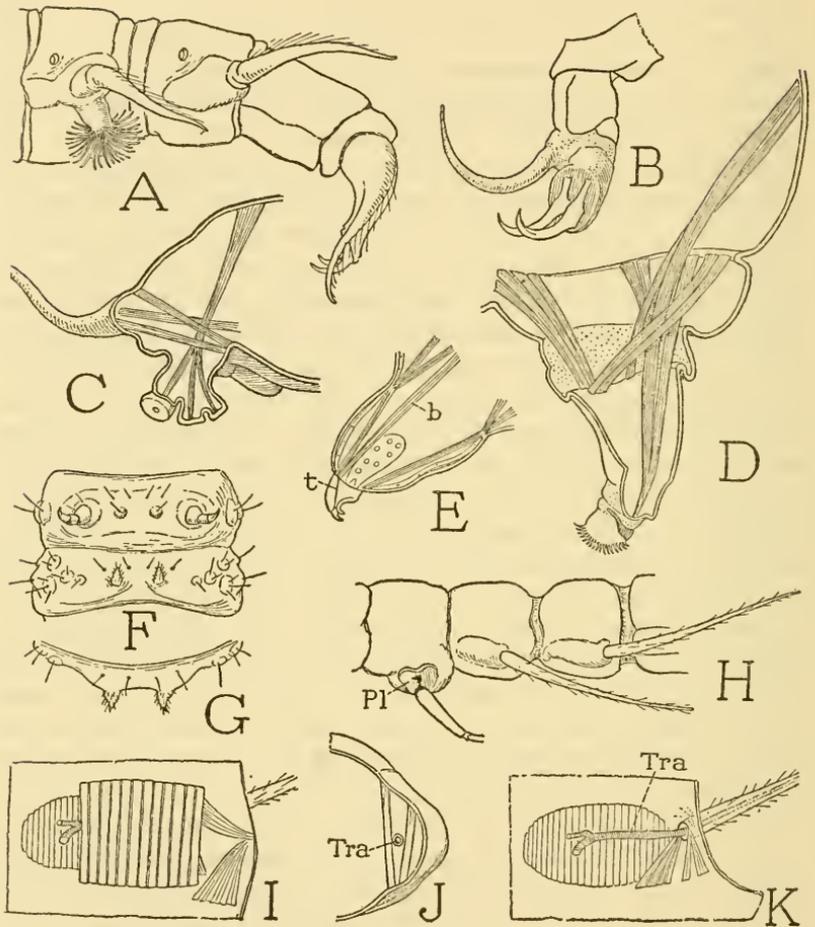


FIG. 9.—Abdominal appendicular organs of holometabolous larvae.

A, *Corydalus cornutus* (L.), posterior abdominal segments and appendages. B, same, terminal appendage of right side, mesal. C, same, cross section of gill-bearing segment. D, *Malacosoma americanum* (F.), a right abdominal leg cut open mesally to expose muscles. E, section of leg of a tardigrade, showing muscles (from Baumann, 1921). F, panorpid larva, under surface of meta-thorax and first abdominal segment. G, same, sternal arc of first abdominal segment, posterior. H, *Dineutes* sp., larva, metathorax and anterior abdominal segments. I, same, inner surface of an abdominal appendage-bearing lobe. J, same, section of left side of an abdominal segment. K, same as I with inner layer of muscles removed.

eight segments is a row of lobelike projections between the terga and sterna that fall in line with the bases of the thoracic legs. Each lobe bears a long, tapering lateral process, and each but the last a large ventral tubercle carrying a brush of gill filaments. On the tenth segment is a larger appendage (B) armed distally with a pair of strong claws, and bearing on its outer surface a slender process like that of the preceding appendages. In the larva of the related *Chauliodes* ventral tubercles are absent, but long, tapering lateral processes are present on the first eight abdominal segments, and the ninth segment bears a pair of appendages similar to those of *Corydalus*. Ventral tubercles are absent also in the *Sialis* larva (fig. 10 A), but long tapering lateral processes are present, each of which is distinctly divided into six segmentlike parts. The abdominal "legs" of caterpillars have a structure resembling so closely that of the gill tubercles of the *Corydalus* larva as to suggest that the two are homologous organs. The same is true of the abdominal "legs" of sawfly larvae, and of the apical appendages of trichopterous larvae, the structure of which has recently been reviewed by Pryor (1951).

The abdominal vesicles of Thysanura are retractile by short muscles arising on the supporting plates of the venter (fig. 2 C,D,E), and the styli are movable by muscles arising on these same plates (D,E). The plates are admittedly flattened remnants of abdominal limbs, and *Machilis* demonstrates that the styli are coxal appendages (B, *Sty*) acquired during postembryonic development. In the endopterygote larva the abdominal tubercles are likewise retractile, but the principal retractor is a long muscle taking its origin on the dorsal wall of the corresponding body segment (fig. 9 C,D). Whether this difference in the musculature of the thysanuran and larval organs is significant or not will be a matter of opinion, but the fact remains. On the other hand, the basal musculature of the tapering lateral processes of the megalopterous larvae (fig. 9 C) is quite comparable to that of a thysanuran stylus in that it arises from the supporting body lobe, which fact might therefore be taken as evidence that these processes truly represent styli.

When, however, we note the occurrence of similar abdominal processes in other unrelated larvae, the interpretation of any of them as primitive styli becomes doubtful. The aquatic larva of the gyrinid beetle *Dineutes* (fig. 10 B), for example, has a pair of long, tapering lateral filaments arising from each of the first eight abdominal segments and two pairs from the ninth segment. The single filaments are supported on lobes of the body (fig. 9 H) that lie in a line above

the level of the pleural plates (*Pl*) of the thorax. Each lobe is crossed internally by two layers of vertical muscle fibers (*I*) enclosing a large trachea between them (*J,K,Tra*) that runs out into the filament. The filament itself is movable by two antagonistic muscles, one mesal, the other lateral, attached on its base. Then there is the curious termitophilous tineid caterpillar, *Plastopolypus divisus* (fig. 10 C), first described by Silvestri (1920), which has long, slender, multiarticulate

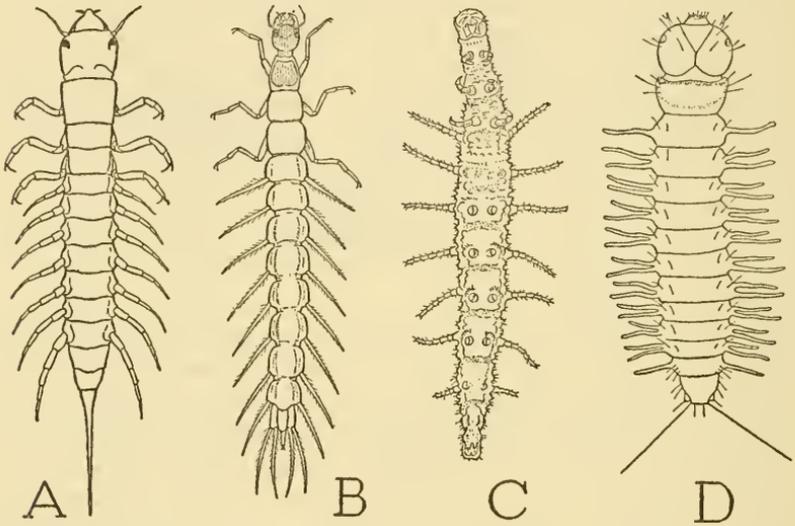


FIG. 10.—Examples of unrelated holometabolous larvae with lateral appendicular organs on the abdomen.

A, *Sialis* sp. Megaloptera. B, *Dinentes* sp. Coleoptera-Gyrinidae. C, *Plastopolypus divisus* Silv. Lepidoptera-Tineidae (from Hollande, Cachon, and Vaillant, 1951). D, *Nymphula maculalis* Clemens, Lepidoptera-Nymphulidae (from Welch, 1916).

processes projecting from the sides of the first seven segments of the abdomen. These appendicular structures have been shown by Hollande, Cachon, and Vaillant (1951) to be sensory and not exudatory organs, since they are covered with innervated setae and contain no glandular tissue; but these writers, and also Silvestri, find that each appendage is movable by a muscle inserted within its base. Must we, therefore, interpret all these structures as representative of thysanuran styli? Hollande, Cachon, and Vaillant contend that the abdominal appendages of the *Plastopolypus* caterpillar are merely secondary adaptations of the larva to life in the termite colony, as are also true exudatory lobes on the body of other termitophilous species.

Similar though nonmusculated processes are shown by Hollande, Cachon, and Vaillant to be present on a termitophilous fly larvae, but in this case two pairs are present on each body segment, one pair lateral, the other dorsal, and several other fly larvae associated with termites have simple nonarticulate lateral appendages, some very small, others large and club-shaped. Then there are the aquatic caterpillars with gill filaments along the sides of the abdomen (fig. 10 D), some of which are simple fingerlike processes and others elaborately branched filaments. The panorpidae larva is sometimes cited as an example of a larva having abdominal leg rudiments, but an examination of this larva shows that the supposed "legs" on the abdomen (fig. 9 G) do not fall in line with the thoracic legs, and correspond exactly in position with seta-bearing papillae on the thoracic venter between the legs (F).

All such examples of the presence of segmental appendicular structures on the larval abdomen only go to show the facility with which the young insect can develop special organs for various purposes of its own. As Pryor (1951) has pointed out, similarity of structure in nonsegmented organs of locomotion is not necessarily a criterion of homology. With respect to the abdominal "legs," he says, "there is in fact as much resemblance between a caterpillar and an onychophoran or a tardigrade as between a caterpillar and *Corydalus*." The tardigrade leg (fig. 9 E) has a long muscle (*b*) from the body wall, which, according to Baumann (1921), is connected with each claw by a slender tendon (*t*). Likewise in the Onychophora the plantar discs and claws of the legs are retractile in the same manner by muscles, some of which have their origins in the leg and others on the body wall. Such cases of similarity in musculature, as noted by Pryor, are evidently independent adaptations to the functional needs of locomotor organs having the same type of structure and action.

Ideas that can be neither proved nor disproved have to depend on circumstantial evidence for support, but when circumstantial evidence is not conclusive they had better be dropped, or held for further investigation. This principle applies to the musculated abdominal appendages of endopterygote larvae. If these appendages are related to the vesicles and styli of Thysanura, they are appurtenances of abdominal legs and not legs themselves. On the other hand, many insect embryos do have leg buds on the abdomen which usually disappear, but it is certainly quite possible that embryonic remnants of primitive legs might be retained and redeveloped in a new form for postembryonic use. We have only to consider the extraordinary elab-

oration of pleuropodia in the embryos of some insects to see the extent to which appendages presumably equivalent to legs can be modified for a new purpose. Eastham (1930) has shown that rudiments of abdominal appendages appear on the embryo of *Pieris rapae* in line with the rudiments of the thoracic legs, and that there is no evident reason for not regarding all these appendages as serially homologous organs. Many cases might be cited from other arthropods in which a leg rudiment develops into a very unleglike structure, and perhaps a very good example of this is to be seen in the external genital organs of insects.

The idea usually deduced from the presence of paired movable appendages on the abdomen of endopterygote larvae is that such larvae are recapitulations of a poly pod stage of insect ancestry. This idea, however, is not supported by other characters of these larvae. Take the caterpillar, for example; in no respect does it have a primitive organization. In the structure of its head, its mouth parts, and its muscular system the caterpillar is a highly specialized modern insect form, and, most important, it is a stage of postembryonic growth in which wings are in the course of development. The caterpillar has a poly pod status because its abdominal appendages were not suppressed in the embryo, but it does not represent a primitive poly pod stage of phylogeny. Wings certainly did not arise in a poly pod ancestor of the insects; a winged centipede is hardly to be visualized as a reality.

The holometabolous larva is an independent organism. It can depart to any extent from the structure of its parents, and it is under no compulsion to recapitulate its ancestral history. The independence of the larva begins with the embryo, which develops directly into the larval form whatever this may be. From the experimental work of Hegner (1911) on the eggs of *Leptinotarsa*, of Reith (1925) and of Pauli (1927) on the eggs of muscoid flies, and of Smreczynski (1938) on eggs of the beetle *Agelastica alni*, it is known that in these insects the larval structure is fully determined in the preblastoderm stage of the egg. Probably the same is true for many other holometabolous insects. A few hours later, however, as shown by Geigy (1931) in *Drosophila*, injury to the blastoderm causes defects in the adult fly. In this very early stage, therefore, the egg has the potentiality of producing both a larva and an imago, but the larval development takes precedence over the imaginal development. The primary business of the holometabolous embryo is to produce a larva; in so doing it may entirely ignore its own phylogenetic history, and needs

only to conserve enough undifferentiated material for the reconstruction of the adult in the pupal stage. The embryo and the larva thus become a single independent phase in the life history of the insect, but this fact is not a vindication of the idea that the larva is simply a continuation of the embryo leading a free life instead of being confined to an egg shell. The reverse more nearly expresses the truth; the specialized structure of the larva has been forced back on the embryo until the embryo becomes a preliminary larva. A phylogenetic significance, therefore, cannot be attributed either to the larva or the embryo of a holometabolous insect.

The insect larva owes its independence and its ability to take on characters of its own to its release from the necessity of inheriting special adult characters of its parents. The development of structures practical only to the winged imago must be inhibited throughout the embryonic and larval stages, and conversely, larval organs useful only to the larva may not be transmitted to the imago. In this way both the larva and the adult are free to become more and more specialized in different directions, but the greater their divergence, the greater becomes the degree of reconstruction required of the pupa. Yet the larva, no matter how divergent it may become from the line of adult phylogeny, must carry the adult inheritance as well as its own. The potency for redeveloping the parent form either resides in the ability of larval tissues to be transformed into imaginal tissues, or it is carried by undifferentiated embryonic cells of the larva, which resume the imaginal development in the pupa. In the more intense degrees of pupal metamorphosis, as Tiegs (1922) has said, the changes amount at times to an absolute death of the larva, the tissues of which go into almost complete dissolution, and if imaginal reconstruction cells were not present the larva would be left to decompose.

#### X. LARVAL HETEROMORPHOSIS

Heteromorphosis of the larva, commonly called hypermetamorphosis, is of frequent occurrence among predaceous and parasitic species of insects, examples being known in Neuroptera, Coleoptera, Strepsiptera, Lepidoptera, Hymenoptera, and Diptera. It seems remarkable that a larva can assume two or more distinct forms during its life history, and the fact that it may do so raises the question as to how the juvenile hormone is able to control a succession of different forms. However, since this hormone is nonspecific with regard to related species of insects, it should be nonspecific with regard to different larval forms of any one species. The hormone has nothing

to do with determining the structure of the young insect; this is the work of hereditary factors. The hormone simply maintains the integrity of the juvenile form, whatever this may be, against the forces of further development.

The ability of the embryo to develop into a larval form that has no relation to the form of its parents is strange enough, but it is passing strange that this same larva can change its form several times during its larval life and still finally revert to the adult structure. The fact of heteromorphosis appears to demonstrate the plasticity of larval tissues, which seemingly can be molded and remolded by the growth organizer to produce a succession of adaptive forms. The histological changes that may take place in larval metamorphosis, however, as well as the role of hormones remain yet to be investigated.

Two categories of heteromorphosis in parasitic larvae are to be distinguished according as the adult female lays her eggs in the open, or on or within the body or egg of the prospective host of the larva. In the first case the newly hatched larva must be able by its own activity either to find its appropriate host, or to attach itself to a carrier that will transport it to the nest wherein are the host eggs or larvae on which it is destined to feed. A first-instar larva of this type, therefore, is constructed for an active life, and has been termed a *planidium* (little wanderer), but its structure, of course, will depend on the insect order to which its parents belong. After entry into the nest or body of the host, however, the planidium transforms into a second-stage larva of much simplified form and structure adapted to a sedentary life of parasitism. With those species, on the other hand, in which the eggs are attached on, or inserted into, the body of the host, the young larva begins at once its parasitic existence; it has no need for an active stage, and develops directly from the embryo into a form adapted only for life and feeding usually within the host, and accordingly in many species it is greatly reduced and simplified in structure. During later instars, however, the simple larva takes on a form more typical of the usual larva of its order.

#### PARASITES WITH A PLANIDIAL STAGE

The term *planidium* has a functional rather than a structural significance, but it is remarkable how larvae in different orders have taken on similar characters in adaptation to the requirements of planidial life.

*Coleoptera*.—Larval heteromorphosis among the Coleoptera occurs in the Carabidae, Staphylinidae, Meloidae, and Rhipiphoridae. Most

familiar are the life histories of the blister beetles, Meloidae, some of which feed on the eggs of grasshoppers, others infest the nests of bees. The transformations of species of the American *Epicauta* are well known from the early work of Riley (1876) and later papers by Ingram and Douglas (1932) and Horsfall (1941). The European *Mylabris variabilis* is described and fully illustrated by Paoli (1938).

The adult females of *Epicauta* and *Mylabris* deposit their eggs in the ground where grasshoppers are likely to be, but not necessarily

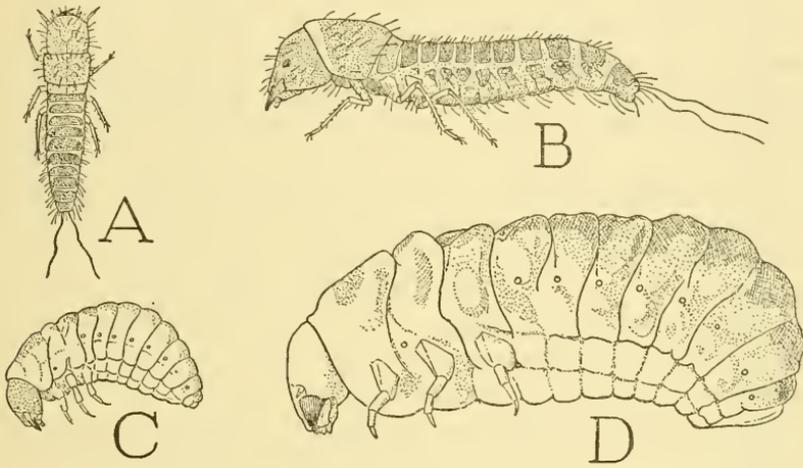


FIG. 11.—Three larval stages of a meloid beetle, *Mylabris variabilis* Pall. (from Paoli, 1938).

A, first instar, planidium. B, same, more enlarged. C, second instar. D, fourth instar, similar to third and fifth instars.

close to a grasshopper's nest. The first-stage larva is a planidium having the form of an active generalized coleopterous larva with long slender legs (fig. 11 A,B). It is commonly termed a "triungulin," though two of its pretarsal "claws" are merely strong spines. The planidium runs actively about and burrows into the ground until it finds the egg nest of an acridid. After feeding on a few eggs, it moults and transforms into a more simple short-legged, soft-bodied second instar (C). This larva resumes feeding, grows, and goes through two more stages in which it becomes a thick scarabaeoid grub (D). The next instar, which is the fifth, resembles the preceding, but it comes out of the egg nest and burrows downward a short distance into the ground. This larva in *Mylabris*, according to Paoli, does not feed, and transforms into a sixth larva, in which the integument is thick, rigid, and dark-colored, and the mandibles and legs are much

reduced. This sixth larva, the "ipnotica" of Paoli, is immobile and passes the winter in a dormant condition. In the spring it sheds its tough, protective integument. The seventh larva that emerges resembles the fourth and fifth instars; it is again active, though it does not feed, and burrows upward to near the surface of the ground, where it transforms into the pupa, from which finally the adult emerges.

The life history of *Epicauta* is essentially the same as that of *Mylabris*, though according to Horsfall (1941) the fifth larva of *E. pennsylvanica* feeds to repletion before it burrows down into the ground. Moreover, this fifth larva in species of *Epicauta* may transform directly into the pupa, thus eliminating the hibernating form and the seventh instar. Pupation following the fifth instar is said by Ingram and Douglas (1932) to take place with individuals of *Epicauta lemniscata* that complete the fifth stage in the spring, while those maturing in the fall or under unfavorable weather conditions go over into the hibernating stage, which is followed by the active seventh instar. Horsfall (1941) reports the same thing for *Epicauta pennsylvanica*. A notable feature in the metamorphosis of these meloid larvae is its reversibility, as shown by the transformation of the hibernating larva into an active burrowing form like that which preceded it, though geotropically one is positive and the other negative.

Other species of Meloidae are parasites in the nests of bees in the families Megachilidae and Andrenidae. The life history and larval stages of one of these, *Tricrania sanguinipennis*, infesting the underground nests of the andrenid *Colletes rufithorax* is fully described by Parker and Böving (1925). The female of *Tricrania* deposits her eggs under small objects lying on the ground in the vicinity of the nesting places of the bees. The newly hatched larvae are slender planidia, tapering at each end, with long legs and well-sclerotized body segments. It would appear that they might find their way directly into the nest of a prospective host, but observations show that generally they attach themselves to a male bee seeking a female and are thus carried into the nest. Within the brood cell the intruder first devours the egg of the bee, thus making sure of no competition from the bee larva that might otherwise hatch. At the first moult the planidium transforms into a soft, smooth larva having a boat-shaped form with the spiracles on the back, an adaptation that enables the larva to float on the food mass of honey and pollen in the cell, which constitutes its food from now on. At later stages, however, as the larva grows larger and the food mass shrinks, the larva becomes a fat scarabaeoid grub. In all, the *Tricrania* larva goes through six

instars, but, except for a shortening of the legs and other minor modifications, it makes no radical change of form after the second moult. There is no hibernating larval stage in the life of *Tricrania*, but the fifth and sixth instars remain within the unbroken fourth and fifth skins, which serve also as a covering for the pupa. The adult beetles are formed in the fall, but remain within the bee's nest until the following spring.

The metamorphosis of the carabid *Lebia scapularis*, which is predaceous on the larvae of the elm leaf beetle, *Galerucella luteola*, is described by Silvestri (1904) as follows. The young *Lebia* is a slender, elongate larva of the planidium type, having legs adapted to running, well-developed mandibles, and a pair of long, jointed apical processes on the abdomen. It attacks a *Galerucella* larva and feeds on the viscera until its growing body becomes so large and loaded with fat to such an extent that it can no longer move actively about. In this condition it might fall an easy prey to other insects, but the *Lebia* larva now encloses itself in a cocoon spun of silk threads from the Malpighian tubules, and finally includes its prey in the cocoon. When finished with feeding, and having attained its maximum development, this first larva moults into a second form having a general pale color, mouth parts unadapted to feeding, the legs and antennae reduced to small conical stumps, and the caudal processes suppressed. From this second, nonfeeding instar the larva goes into a prepupal stage, in which the head takes on adult characters, and wing rudiments are present on both the mesothorax and the metathorax. After another moult the prepupa becomes a pupa. Silvestri makes no comment on the unusual occurrence in the Coleoptera of a prepupa, which evidently belongs to the pupal stage of the insect. Heteromorphosis in *Lebia*, therefore, appears to affect the pupa as well as the larva.

Heteromorphosis again occurs in several genera of Staphylinidae in which the larvae are parasitic on the pupae of Diptera within the puparium. Wadsworth (1915) gives a good account of the life history and larval stages of *Aleochara bilineata*, a parasite of the cabbage fly, *Chortophila brassicae*. The newly hatched larva is an active thysanuriform planidium that must seek in the ground the puparium of the cabbage fly. Having found a puparium it gnaws a hole in the latter and feeds on the outside of the pupa from a puncture in the pupal integument until it becomes much swollen. The second instar of the larva is quite different from the first; the cuticle is soft and white, the antennae and mouth parts are altered, the legs reduced to vestiges, the claws are lost, and the caudal spines disappear. The third

larva resembles the second except for its larger size. Both the second and the third larvae lie lengthwise on the back of the thorax of the fly pupa, and obtain their food by suction. Pupation takes place in the fly puparium, and the adult beetle gnaws its way out.

The larval heteromorphosis of the Rhipiphoridae is too well known to need more than a brief notice. Species of *Rhipidius* are internal parasites in all larval stages on cockroaches. Other species attacking wasps and bees are endoparasitic in the first instar but take an external position in later instars. The first larva of one of these species is an active planidium which must find and attach itself to a carrier that will transport it to the nest of a prospective host. Here it enters the host larva as an internal parasite. When fully grown in the first instar, however, it leaves the body of the host through a puncture, moults, and in the second stage takes a position across the back of the host larva on the first or second thoracic segment. The external larva loses the features of the first instar and becomes a grublike parasite, some species being characterized by the presence of large tubercles on the back.

*Neuroptera*.—Among the Neuroptera the larvae of nearly all species are predaceous, their prey being mostly other insects which they attack in the open. The larvae of some Mantispidae, however, feed on spider eggs within the spider's cocoon. The mantispid eggs being laid on trees or bushes, the young larva must actively find its food. The life history of *Mantispa styriaca* has long been known from the work of Brauer (1869). The newly hatched *Mantispa* is a simple, slender neuropteroid larva with relatively small mandibles and no distinctive specialization. Hatched in the fall, it hibernates through the winter; in the spring it finds a spider's cocoon and cuts its way through the silken wall. With feeding in the first instar, the abdomen becomes greatly enlarged, but at the first moult the larva changes to a fat grub with a small head and greatly reduced legs. This change of the active first-stage mantispid larva to a sedentary grub is certainly not a reversion to any ancestral larval form among the Neuroptera; it is an individual secondary adaptation to the life of ease and plenty the larva is to lead from now on in the protection of the spider's cocoon, within which it finally pupates.

*Strepsiptera*.—The Strepsiptera are notable for the heteromorphosis of the parasitic larval stages of both sexes, and also for the fact that in most species the sexually mature female retains the larval form, though with a greatly modified reproductive system, and remains within the body of the host. In the genera *Eoxenos* and *Mengenilla*, however, the female leaves the host and in the adult stage is found

in the open, either free or enclosed in the last larval skin. The females of these species are much less modified in structure than are the females of species that remain in the hosts. The males of all species are free, fully winged insects.

The adult female of *Eoxenos laboulbenei*, as described by Parker and Smith (1933), is broadly oval, with a distinct head and thorax and a 10-segmented abdomen; wings are absent, but the legs are relatively long and segmented, mandibles are present though simple, and spiracles occur on each of the first seven abdominal segments. At the posterior border of the seventh abdominal segment is a genital aperture leading into a short, open, median oviduct, but otherwise nothing is to be seen of the reproductive system; in the mature female the entire abdominal cavity is full of eggs. Females of *Eoxenos* found within the last larval skin are enveloped also in a thin pupal cuticle, showing that, in this genus at least, the female is a true imago. In mating, as observed by Parker and Smith (1934), the male of *Eoxenos* curves his abdomen beneath that of the female, but the aedeagus pierces the integument of the female instead of entering the genital aperture. The eggs hatch within the body of the female and the young planidial larvae escape through the open inner end of the oviduct. The host of *Eoxenos laboulbenei* was for a long time unknown, but Carpentier (1939) finally discovered the parasitic stage of the larva in the body of a lepismatid, *Lepisma aurea*.

In other strepsipteran genera, parasitic in Orthoptera, Pentatomidae, Fulgoridae, Cicadellidae, and particularly in Hymenoptera of many families, both the female and the male develop to sexual maturity within the body of the host. The female remains within the host, and retains the form of the mature larva, having a large, soft abdomen and a short, cylindrical, darkly sclerotized cephalothorax (fig. 12 G), which latter alone is thrust out of the abdomen of the host. Mandibles are present in some species, absent in others, but the female is always wingless and legless. She remains enclosed in the last larval skin, and the parasitic females are not known to have a pupal stage. It is questionable, therefore, whether the egg-producing parasitic female is a true adult or a sexually precocious last-stage larva. As noted above, Parker and Smith found evidence of a pupal stage in the nonparasitic female of *Eoxenos laboulbenei*.

The reproductive organs of the parasitic females are greatly reduced, and the abdomen is filled with a great mass of eggs. The development of the eggs free in the body cavity is described by Brues (1903) in *Xenos peckii*. Between the ventral surface of the body of the female and the enveloping larval skin is a free space, or brood

chamber, which opens anteriorly at the base of the cephalothorax by a median slit, or in some species by a pair of apertures. The brood chamber is in communication with the body cavity of the female by several funnel-shaped tubes. During mating, according to Perkins (1918), the male of *Stylops aterrima* inserts the aedeagus into the anterior opening of the brood chamber; in *Acroschismus wheeleri*, Schrader (1924) says the spermatozoa, after being discharged into the brood chamber, find their way through the ventral ducts of the female's abdomen into the body cavity, where they disperse, penetrate the egg membranes, and effect fertilization. Silvestri (1940), however, has apparently demonstrated that the male of *Halictophagus tettigometrae*, in inserting the aedeagus through the ventral membrane between the head and thorax, penetrates the body wall of the female and discharges the spermatozoa directly into the haemocoel, whence they finally migrate to the posterior extremity of the abdomen. The young larvae on hatching from the eggs escape from the body of the female through the ventral funnels into the brood chamber, and gain the exterior by way of the anterior opening of the chamber.

The male strepsipteron develops also inside the body of the host, and before emergence as an adult he is enveloped by the last larval skin. Unlike the female, however, the male goes through a pupal stage before transforming into a free-winged insect, leaving the pupal cuticle behind within the larval skin.

For a good example of the larval stages of a typical strepsipteron we may refer to the well-illustrated account by Kirkpatrick (1937) of the life history of *Corioxenos antestiae*, a parasite of Pentatomidae infesting coffee plants in East Africa. The first-instar larva is a planidium (fig. 12 A) of coleopterous type of structure, and attaches itself (B) to an immature pentatomid of the genus *Antestia*. The parasite remains motionless on the host until the latter moults, when it bores into the body through the soft new skin. At its own first moult the planidium transforms into a simple, soft-bodied, legless scarabaeoid grub (C), in which even body segmentation is not visible. With succeeding moults the larva goes through four more instars (D,E,F), without any radical change of form except for the development of a row of eight processes along the back of the abdomen. The larva apparently feeds by the absorption of body liquids of the host through its skin, and the dorsal protuberances are supposed to increase the absorptive area. During the later larval stages (F) the body becomes differentiated into a slender cephalothorax and a large abdomen; extrusion of the cephalothorax from the host takes place in the

seventh instar, after which the female larva moults to the final form (G) within the last larval skin. The larval instars of the male resemble those of the female, but the male goes through a pupal stage before issuing as a winged adult.

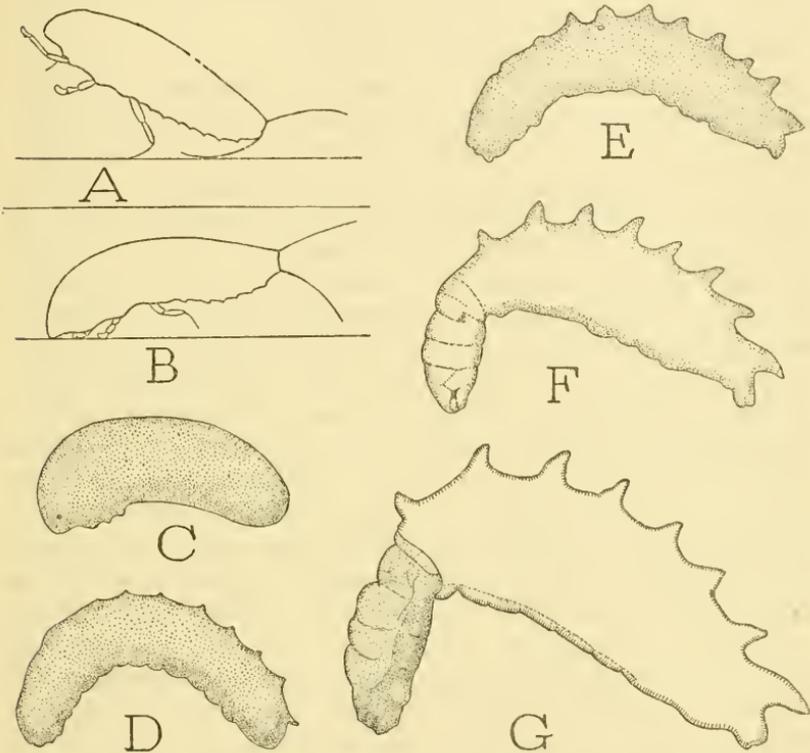


FIG. 12.—Developmental stages of a strepsipteron, *Corioxenos antestiae* Blair (from Kirkpatrick, 1937).

A, first instar, planidium in waiting attitude (length 0.25-0.27 mm.). B, same, in position of attachment on host. C, first parasitic instar (length 0.4 mm.). D, second parasitic instar, female. E, third parasitic instar, female. F, fifth parasitic instar, female. G, mature female, unfertilized (length 3 mm.).

Extrusion of the cephalothorax of *Corioxenos antestiae*, Kirkpatrick says, is always between the back plates of the third and fourth segments of the host, the male in the middle and the female on one side. In this species the female has a pair of openings into the brood pouch, one right, the other left, a provision to insure that one or the other will not be covered by a wing of the host. The body of the mature larva and also of the adult female lies in the body of the host with the ventral side of the abdomen uppermost and the cephalothorax

bent posteriorly, so that the dorsal surface of the exposed cephalothorax is uppermost when extruded. In this position of the female copulation with a free male takes place.

An even more detailed account of the biology, life history, and anatomy of a strepsipteron will be found in the paper by Silvestri (1940) on *Halictophagus tettigometrae* Silv.

*Lepidoptera*.—The caterpillar in its body form is the most conservative of all holometabolous larvae, even predaceous species in general preserve the eruciform type of structure. In the Epipyropidae, however, the larvae of which are external parasites on Homoptera, particularly Fulgoridae, there is a pronounced structural adaptation of the larva to parasitic life and even a heteromorphosis. Since the adult female deposits her eggs not on a prospective host but on vegetation, the first-stage larvae must attain a host by their own efforts, and they resemble, as much as a caterpillar might, the planidia of other parasites with similar habits. The newly hatched larva of *Agamopsycha threnodes* is described by Perkins (1905) as a minute, slender creature, tapering to the caudal extremity, and provided with legs unusually long for a caterpillar; it is clearly adapted for the active life of a young predaceous insect that must find a host for itself. The later instars, which feed on the back of the abdomen of the host, are very different from the first. In the mature stage the head is extremely small, the legs reduced, the mandibles minute; the body becomes contracted to an oval form, and the larva takes on a superficial resemblance to a mealy bug, accentuated by the presence of a waxy covering. A description of all the stages of *Epipyrops eurybrachydīs* Fletcher is given by Krishnamurti (1933). Among the Lepidoptera various leaf-mining species also undergo a change of form during larval life, being at first flattened for feeding within the leaf, and later, on emergence from the mine, taking on the usual caterpillar form for cocoon spinning.

*Diptera*.—Parasitic dipterous larvae, of which the first instar is of planidium type, and which, therefore, are heteromorphic, are said by Clausen (1940) to occur generally in the Acroceridae (Cyrtidae), Bombyliidae, and Nemestrinidae, frequently in the Tachinidae, and in a few species of Sarcophagidae.

The Acroceridae (Cyrtidae, Oncodidae) are parasitic in their larval stages on spiders. The female deposits her eggs on bushes or trees, and the young larvae by their own efforts must attach themselves to spiders that chance to come their way, if they are to survive. The larval stages of *Oncodes pallipes* as described by Millot (1938) may be taken as typical of the family. The newly hatched planidium (fig.

13 I) is not over 0.4 mm. in length, slender and elongate, with a small head and 11 body segments. The body segments are sclerotized dorsally and ventrally and are armed with strong spines, a pair on the last segment being particularly long. The mouth armature includes a median sharp-pointed process and a pair of lateral hooks. The last abdominal segment terminates in an attachment apparatus consisting of three strong central hooks and a ventral semicircle of small spines. The larva at this stage is metapneustic, having a pair of spiracles only on the last segment. After hatching, the larva stands vertically by means of the attachment structure on the end of its abdomen, but it is capable of locomotion either by looping movements like those of a measuring worm, or by small leaps of a few millimeters made by suddenly straightening the curved body. If a young spider happens to pass close by, the planidium springs upon it and penetrates into its interior; otherwise the prospective parasite will die in the course of a few days. The parasite passes the winter without change in the body of the spider. In the spring it moults into a second instar and later again into a third instar (J). In these instars the larva is simply a small fly maggot; the body is indistinctly segmented, tapering anteriorly, enlarged posteriorly, and ends with a small apical cone. There are now two pairs of spiracles but those of the prothorax are not functional. The infested spider remains alive and normally active almost to the end, but at last the parasite consumes the vital organs of its host and comes out to pupate, leaving nothing of the spider but the empty skin.

The planidium of *Pterodontia flavipes* (fig. 13 H), another acrocerid parasite of spiders, described by King (1916), resembles that of *Oncodes*, but the body ends with a small adhesive disc between the bases of a pair of long, slender spines. This larva, according to King, progresses either by looping in the manner of a leech, or by jumping. Preparatory to making a leap, the larva stands erect on the attachment disc with the caudal spines extended backward; by a sudden downward pressure of the spines the larva then throws itself a distance of five or six millimeters. When on moist surfaces, however, King says, the larva progresses by extending and contracting its body. This last observation is of particular interest because it shows that the planidium still retains the common mode of locomotion of a fly maggot. In its subsequent stages the *Pterodontia* larva returns to the form of a simple, smooth-skinned maggot, which, when mature, emerges from the body of the spider.

For another example of larval heteromorphosis among the Diptera, we may refer to the paper by Clausen (1928) on *Hyperalonia oeno-*

*maus*, a bombyliid larval parasite of the scoliid *Tiphia*, which itself is parasitic on grubs of the scarabaeid genus *Anomala*. The eggs of *Hyperalonia* are deposited on the ground or dropped there by the female in flight. The first larva (fig. 13 G) on hatching is a slender, vermiform planidium 0.9 mm. in length, with a strongly sclerotized head and 12 uniform body segments; the thoracic segments bear each a pair of long, slender lateral spines, and on the apical segment of the abdomen is a pair of similar but longer spines directed posteriorly. This larva has to search through the ground for the buried cocoons of *Tiphia*; after entering a cocoon it feeds on the thoracic region of the *Tiphia* larva. At the first moult the planidium changes into a much simpler larval form, which lacks the body spines and the strong sclerotization of the head, and is characterized by deep intersegmental constrictions. In the third stage (F) the larva becomes thick-bodied and grublike, but is not essentially different from the second larva; it passes the winter in the cocoon of the host, and pupates the following spring. The same species attacks also other scoliid genera, and the Bombyliidae in general, according to Clausen, are parasitic on Orthoptera (egg cases), Coleoptera, Lepidoptera, Diptera, and Hymenoptera.

*Hymenoptera*.—Among the Hymenoptera, larval heteromorphosis following a first-stage planidium occurs in the parasitic Perilampidae and Eucharidae. The females in these families lay the eggs apart from the host, and the young larvae are provided with a strongly sclerotized integument which allows them to live a relatively long time without desiccating and without feeding. By means of a caudal sucker and long tail bristles the planidium is able to stand erect and to spring at a prospective host.

The following account of the planidium of a species of *Perilampus* parasitic on larvae of *Chrysopa* is given by H. S. Smith (1917). The eggs are laid on the leaves of plants where the *Chrysopa* larvae are looking for aphids. From the egg hatches an active planidium (fig. 13 A), which at first crawls rapidly about, but soon attaches itself to the leaf by its caudal sucker and stands up at a right angle to the leaf surface. In this position it may remain motionless for days at a time until some insect comes within its reach. Then suddenly the planidium becomes "frantically active, reaching and swaying back and forth in its attempt to attach itself to the prospective host." If a *Chrysopa* larva comes too near, "the planidium attaches itself with lightning-like quickness to a hair or bristle of the host. It then leisurely crawls down the hair to the host's body and attaches itself by its mouth hooks." When the *Chrysopa* larva spins its cocoon and pupates, the

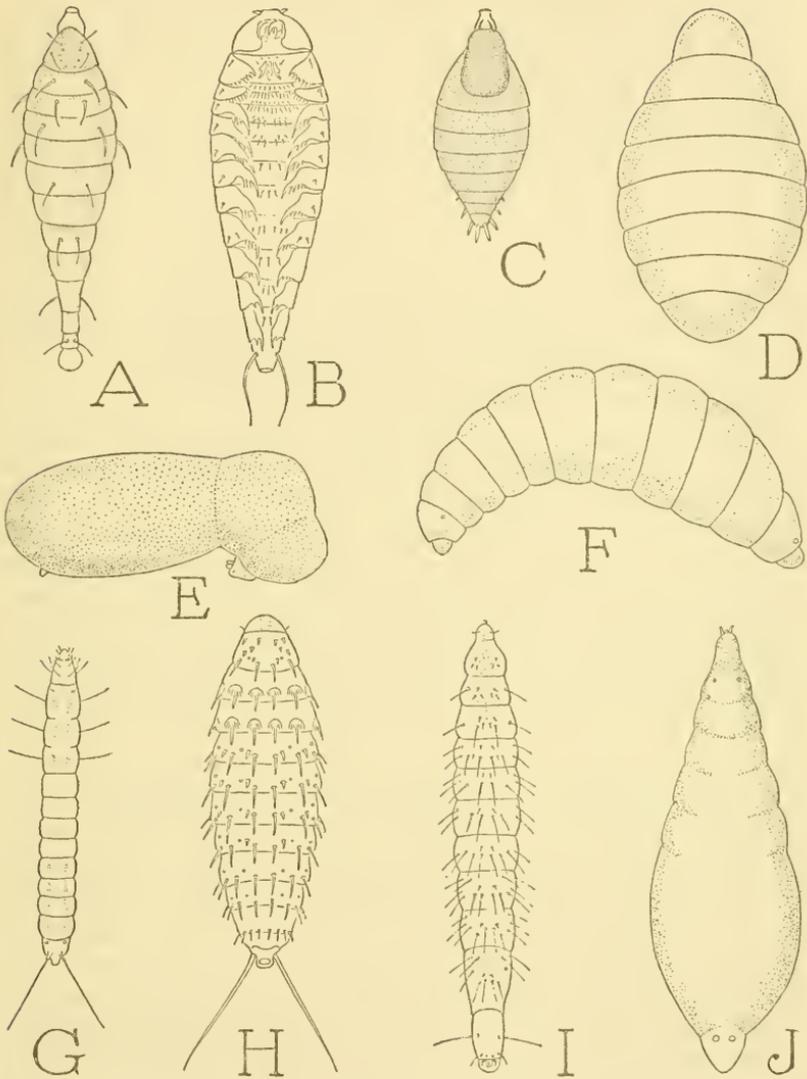


FIG. 13.—Examples of hymenopterous and dipterous parasitic larvae with a planidial first instar.

A, *Perilampus chrysopae* Crawford, planidium (from Smith, 1912). B, *Perilampus hyalinus* Say, planidium (from Smith, 1912). C, *Schizaspidia tenuicornis* Ashm., planidium (from Clausen, 1923). D, same, second instar (from Clausen, 1923). E, same, third instar (from Clausen, 1928). F, *Hyperolonia oenomaus* Rond., third instar (from Clausen, 1928). G, same, first instar (from Clausen, 1928). H, *Pterodontia flavipes* Say, first instar (from King, 1916). I, *Oncodes pallipes* Latr., first instar (from Millot, 1938). J, same, third instar (from Millot, 1938).

planidium feeds as an external parasite on the pupa. Often, however, the parasite attaches itself to the stalk of a *Chrysope* egg, in which case the young chrysoptid falls a sure victim to the *Perilampus* planidium in wait for it.

Another species of *Perilampus* described by H. S. Smith (1912) is a secondary parasite on the fall webworm, *Hyphantria cunea*. The planidium (fig. 13 B) enters the body of the caterpillar through the skin and searches for the larva of a primary parasite, including both dipterous and hymenopterous species. At the first moult the perilampid larva loses the characteristic features of the planidium and changes into an ordinary hymenopterous grub, in which form it remains through subsequent instars with only slight modifications.

The description by Clausen (1923) of the life history of a Japanese eucharid, *Schizaspidia tenuicornis* Ashm., parasitic on ant larvae, will serve as a good example of the nature of the planidium and the heteromorphosis of the larva in the Eucharidae. The eggs of this species are laid by the females during the later part of summer in the buds of trees and hatch the following spring. The newly emerged larva (fig. 13 C) is a planidium scarcely more than one-tenth of a millimeter in length, having suctorial mouth parts and a pair of sharp mandibles, and is provided with a small adhesive disc at the posterior end of the abdomen, which is armed with strong spines. Locomotion is accomplished by successive loopings and extensions of the body as the latter is held to the support alternately by the mouth and the caudal disc. When awaiting the chance arrival of a prospective host, however, the planidium stands up at an angle of 45 degrees on its caudal sucker, and then, when opportunity offers, it attaches itself by its mandibles to a passing ant, and is thus transported to the ant's nest. Here the parasite is brushed off from its carrier and now attaches itself by its jaws to an ant larva. At the first moult the special characters of the planidium, together with the mandibles, are cast off with the exuviae.

The second instar of the parasite is a simple, thick, grublike larva (fig. 13 D) having only suctorial mouth parts; it maintains its hold on the host by the mandibles of its own cast skin. When now the ant larva becomes a pupa, the parasite frees itself from the larval exuviae of the ant and by means of its oral sucker attaches itself to the pupa. It then moults to its third instar (E), in which the body segmentation is lost and the mouth is armed with a short stiletto for puncturing the skin of the pupa. The ant pupa is now sucked dry and soon dies, after which the fully fed parasite pupates. Though the *Schizaspidia* larva assumes a characteristically different form in each of its three instars, the pupa is typically hymenopteran.

The larval history of *Schizaspidia tenuicornis* shows how complex the life of a parasite may be, and how both in its structure and its instincts the young insect must become adapted in each instar to conform with the particular conditions that confront it. As noted by Clausen, the *Schizaspidia* larva, in losing its mandibles, breaks with all other hymenopterous parasites, in which the mandibles are retained in all stages.

#### PARASITES WITHOUT A PLANIDIAL STAGE

Finally we come to those dipterous and hymenopterous parasites of which the female deposits her eggs directly on or in the body of the host or in the host egg. In these species the young larva on hatching finds itself in immediate contact with its food supply, and there is hence no need of an active stage in its life history. The larva is structurally adapted during its embryonic development for life in the body of the host, and in many cases, especially with hymenopterous parasites, the adaptive modifications result in a greatly simplified larval form.

*Diptera*.—Among the Diptera, modifications or special structural developments of endoparasitic larvae appear to be related principally to the function of respiration, but they may be superposed on a state of simplification in which most of the usual vital organs are not yet developed.

An extreme case of reduction or of delayed development accompanied by specialization in the first-stage larva of Diptera is seen in the agromyzid *Cryptochaetum*, parasitic in scale insects, described by Thorpe (1931, 1941). The eggs of the fly are inserted into the body of a half-grown scale before the body wall has become hardened. The first-stage larva of *C. iceryae*, according to Thorpe (1931), is little more than a transparent cylindrical sac (fig. 14A), 0.3 to 0.4 of a millimeter in length. There is no mouth or sclerotized mouth parts, no somatic muscles, no spiracles, tracheal system, or heart. The alimentary canal is complete, but the stomodaeum and the proctodaeum are not open into the mesenteron, and no food is present in the tract; the parasite evidently absorbs nutriment through its integument from the body liquid of the host. A special feature of the larva is the presence of a pair of large, fingerlike diverticula containing blood projecting from the posterior end of the body. In the second-stage larva (B) the body becomes distinctly segmented, and the posterior segments are ringed with short spines; the mouth is open and strongly sclerotized mouth parts are present; there is a tracheal system but no

spiracles, and a few longitudinal muscles have been developed. The caudal diverticula of the first instar have lengthened into a pair of tails nearly half the length of the body, and fine tracheal branches later penetrate into their open basal parts. In the third stage the body preserves the general form and structure of the second stage, but the tails have increased greatly in length, being one and a half times or more the length of the body. In its fourth stage (C) the larva

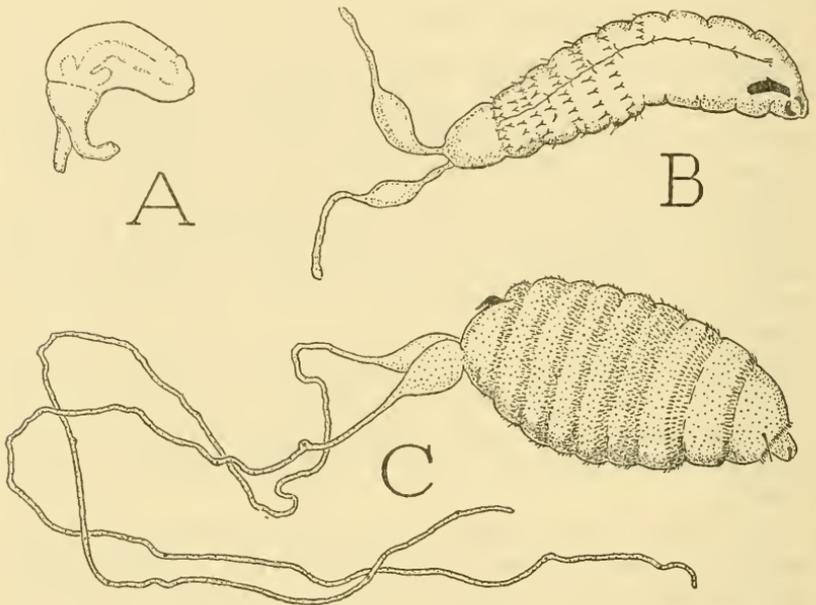


FIG. 14.—Three larval stages of an agromyzid dipteran, *Cryptochaetum iceryae* (Will.), parasitic in the coccid *Icerya purchasi* Maskell (from Thorpe, 1931).

A, first instar. B, second instar. C, fourth instar.

becomes an ovoid, yellowish-white maggot composed of a head and 10 body segments; the tails are greatly lengthened, slender filaments, but have become brittle and are easily broken. Each body segment has a belt of minute spines around its anterior end, anterior and posterior spiracles are now present, but the hooklike posterior spiracles are still closed, the alimentary canal is open, the muscular system is fully developed.

In *Cryptochaetum striatum* (Thorpe, 1941) the larval stages are said to be much the same as in *C. iceryae*, but in the third stage the respiratory tails are 10 times the length of the body and are filled for at least two-thirds of their length with fine tracheal branches.

In contemplating a larva of such incomplete structure as that of

the first instar of *Cryptochaetum*, the question comes up as to how it got that way. The usual answer to the question is that the embryo hatched at an early immature stage. Concerning the "early hatching" idea, Thorpe (1931) says: "The theory obviously cannot be pushed too far, for there are many truly adaptive characters which arise *de novo* in insect larvae, and cannot in any way be described as embryonic." There is no question that "adaptive characters" may include the suppression of structures that are temporarily useless, as well as the development of new structures that are only temporarily useful. Nature is always economical where there is no need of prodigality. A larva living in the midst of liquid food which it absorbs through its skin has no use for a mouth, feeding organs, or a functional alimentary canal, and no need of a locomotor muscular system. If also it can get sufficient oxygen by absorption from the medium in which it lives, there is no immediate need of a tracheal system. All these negative conditions might be supposed to have been acquired by the simple expedient of early hatching, but the larva, if so produced, is not a normal early-stage embryo. The retarded state of development very probably was early determined in the egg, and the larva must then be what it is regardless of when it hatches. The principal *new* structures of the *Cryptochaetum* larva, Thorpe points out, are the respiratory tails. Otherwise the larva simply develops the other organs when they are needed. The delay in development is a mere economy, and numerous examples of various degrees of economy might be cited from other species.

*Hymenoptera*.—In the Hymenoptera endoparasitic first-stage larvae often have such strange forms that they would hardly be known for young insects if their development had not been followed. Clausen (1940) distinguishes, describes, and illustrates 14 different types of first-stage parasitic larvae in the Hymenoptera, nearly all of which but the planidium are endoparasitic. The eggs of some species are deposited on the outside of the host, of others in the body cavity of the host, and of still others in the host egg. The so-called "egg parasites," however, Clausen observes, are truly larval parasites, since they feed on the larva and "their development is primarily at the expense of that stage." In the present discussion we are concerned entirely with the forms of these first-instar larvae, which later take on the more conservative structure of typical hymenopterous grubs. The species are therefore heteromorphic, though their heteromorphism affects principally the first instar. The change to the final form may take place at the first moult, but often the second instar is intermediate in form between the first and the following instars. As with

the parasitic larvae of Diptera, these aberrant hymenopterous parasites present various special developments in combination with different degrees of undevelopment of usual organs. Whatever their form or structure may be, however, we must assume that in some way it is fitting to the life these larvae live.

As an example of greatly simplified and specialized first-stage larval structure in the Hymenoptera we may take the braconid *Helorimorpha antestiae*, an internal parasite of the pentatomid *Antestia*, described by Kirkpatrick (1937), or the similar larva of the ichneumonid *Limmerium validum*, endoparasitic in the fall webworm, described by Timberlake (1912). In each of these species the first-instar larva (fig. 15 C) has an enormous "head" on a relatively small, simple, unsegmented body ending in a long tapering tail. The only appendages present are a pair of slender, incurved, sharp-pointed mandibles. An even simpler larva of the same type is that of *Platygaster marchali* (E).

In the second stage the *Limmerium* larva takes on a verniform type of structure with a small head and 12 body segments, the tail of the first instar being greatly shortened. The third instar, as also that of *Helorimorpha antestiae* (fig. 15 D), is a typical hymenopterous larva. The heteromorphosis of these species, therefore, results from the extreme modification of the first instar; in its subsequent changes the larva merely returns to the usual form.

A somewhat more specialized type of first-instar larva occurs among the Platygasteridae, examples of which are here illustrated at A, B, F, and I of figure 15. The large anterior part of the body carries the mandibles, antennal rudiments, and a pair of simple posterior appendages. This headlike part of the larva has been shown by Marchal (1906) to be a cephalothorax bearing the antennae, mouth parts, and the prothoracic legs. The body region behind the cephalothorax is partly or entirely segmented, and may end with tail appendages of various patterns. In their development these larvae eventually attain the form and structure of an ordinary hymenopterous grub.

A curious type of first instar larva is characteristic of the Scelionida; it is classed by Clausen (1940) as the "teleaform" type of larva, but in form it suggests the embryo of a mouse (fig. 15 J). *Hadronotus ajax*, an egg parasite of the squash bug, *Anasa tristis*, furnishes a good example. The newly hatched larva (J) as described by Schell (1943) is a slender creature with a sharp, tail-like caudal horn curved anteriorly. The body is constricted between a large anterior part, probably a cephalothorax, and an elongate posterior part,

but is unsegmented. The cephalothorax bears anteriorly a pair of large, soft mandibles, and posteriorly a "labial projection." The caudal horn is a feeding accessory. This larva grows by a great increase in the size of the abdomen only. In the second stage the larva takes on an oval saclike form, still without segmentation. The third instar, however, is a fully segmented, typical hymenopterous larva (K).

Finally, we must note that not all parasitic hymenopterous larvae take on queer forms in the first instar. Among the Proctotrypoidea the larva of *Phaenoserphus viator*, parasitic on a carabid beetle larva, as described by Eastham (1929), hatches in the form of a simple grub (fig. 15 H), in which the abdomen becomes fully segmented during the first instar. The only special character of this larva is the presence of small paired ventral papillae on the eight body segments following the prothorax. On the head, according to Eastham, are a labrum, a pair of antennal papillae, a pair of sickle-shaped mandibles, a pair of simple maxillary lobes, a small labium, and a sclerotized ring supporting the mouth parts.

Advocates of the Berlese "early hatching" theory would explain the simplicity of these first-instar parasitic larvae as products of immature eclosion of the embryo. Thus Chen (1946), who discredits the theory as applied to other larvae, says: "The precocious types are confined to parasitic Hymenoptera and appear to have been independently acquired by the different groups." He then distinguishes among these first-stage larvae a "vermiform polypod" type (fig. 15 H), an "oligomeric protopod" type (A), and a "polymerous protopod" type (F), supposedly representing successively earlier stages of embryonic development. The usual implication of this theory is that the different types of larvae correspond with phylogenetic stages presumed to be recapitulated in embryonic development.

The presence of apparent abdominal appendages on the first-instar larva of *Phaenoserphus viator* (fig. 15 H) gives this larva a polypod appearance, but Eastham (1929) says the abdominal papillae may be merely adaptive structures. He notes that the difficulty of ascribing such a larva to a primitive embryonic stage "lies in comparing the whole larva at any one stage in its life with any single embryonic state." The presence on the head of fully developed, typical hymenopterous larval mouth parts does not harmonize with the idea that the larva represents an early polypod stage of the embryo. The presence of mandibles on such a simplified larva as that of *Helorimorpha* (C) likewise shows that the form of this larva has no embryonic or phylo-

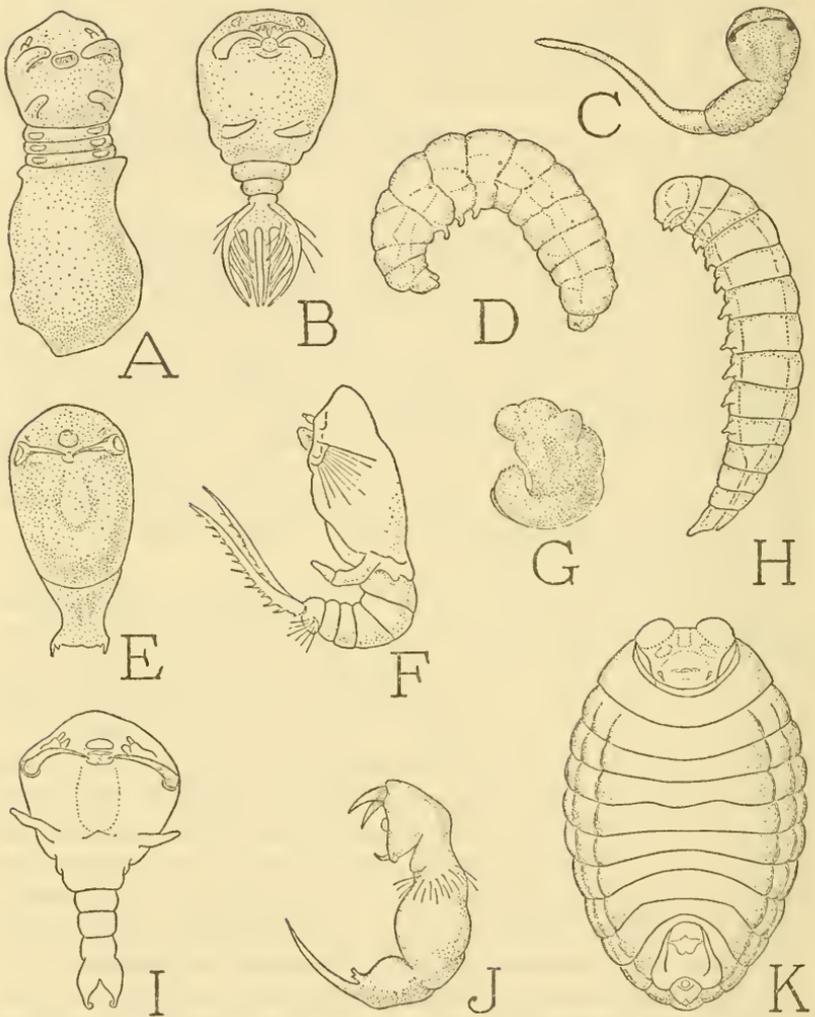


FIG. 15.—Examples of hymenopterous parasitic larvae without a planidial first instar.

A, *Platygaster herrickii* Packard, first instar (from Kulagin, 1898). B, *Platygaster intricator* Kulagin, first instar (from Kulagin, 1898). C, *Helorimorpha* sp., first instar (from Kirkpatrick, 1937). D, same, mature larva (from Kirkpatrick, 1937). E, *Platygaster marchali* Kieffer, first instar (from Marchal, 1906). F, *Synopeas* sp., first instar (from Marchal, 1906). G, same, embryo (from Marchal, 1906). H, *Phaenoserphus viator* Hal., first instar (from Eastham, 1929). I, *Tricacus remulus* (Walker), first instar (outline from Marchal, 1906). J, *Hadronotus ajax* Girault, first instar (from Schell, 1943). K, same, third instar (from Schell, 1943).

genetic significance. The other appendages have simply been suppressed as needless.

The same may be said of the so-called "oligomerous" and "polymerous protopod" larvae (fig. 15 A,B,F,I). They do not *as a whole* have the structure of any one stage in ordinary embryonic development, and none of them is suggestive of being a primitive embryo. An embryo develops continuously, but these larvae maintain the form and structure they have at hatching until the first moult, as does any ordinary larva. In short, there is no reason for regarding them as embryos. Just as a free, active, first-stage larva, or planidium, is adapted to the predatory life it must lead, so these internal parasitic larvae are adapted to an endoparasitic life. They are specialized both in the forms they have, and in the developmental retardation of organs they do not have and do not need. The principle of economy is invoked here just as with the simplified dipterous larvae.

In the first-stage *Hadronotus* larva (fig. 15 J) we see again an example of early specialization in form accompanied by retardation in the development of organs not immediately needed. If we consider the numerous other forms of first-instar larva among the parasitic Platygasteridae and Scelionidae, illustrations of which are assembled by Clausen (1940, figs. 108-111, 113), it is clear there is no evident logic in picking out any one form as representing a particular stage of ordinary embryonic development. The development of *Synopeus rhanis* within the egg from the blastula to the first larva (F), as illustrated by Marchal (1906, pl. 17), shows that the embryo (G) develops directly from the beginning into the platygasterid larval form, without going through any stages suggestive of those of an embryo that develops into a typical free-living larva. Evidently the larval form is determined in the egg, and the embryo, thus relieved from phylogenetic influences, develops into a larva of the platygaster type. The time of hatching has nothing to do with it.

An example of heteromorphosis affecting the first larval stage very similar to that in the parasitic Hymenoptera occurs in the pseudoscorpion (Barrois, 1896; Vachon, 1938). The eggs at an early stage of development are discharged into a brood pouch suspended below the genital aperture of the female and are here nourished on a secretion from the ovaries. On hatching, the larva breaks through both the chorion and the wall of the brood pouch, but remains attached to the outside of the latter by its ventral surface and the mouth region. It is now nourished, as were the eggs, by the ovarian secretion discharged into the brood pouch. At this stage the young pseudoscorpion is a simple saclike creature with rudimentary appendages, but without

body segmentation or internal organs. A deep muscled invagination on its ventral surface was regraded by Barrois as a sucking organ, but Vachon has questioned this function. However, in some manner the larva absorbs the ovarian secretion from the brood pouch and completes its development in one instar. At the next moult it takes on at once the adult structure in miniature. The so-called larva might be regarded as a second embryo, but clearly it is an adaptive form quite unlike any early stage in ordinary arachnid development.

The frequency with which larval heteromorphosis occurs among unrelated insects shows that the larval organization is highly unstable and that mutations make it readily responsive to the need of environmental adaptation. A case of heteromorphosis among the vertebrates would be most astonishing; with the insects heteromorphosis is commonplace. The adaptational changes in the structure of heteromorphic larvae from one instar to the next is good evidence that homomorphic larvae are themselves merely juvenile adaptations to their various modes of living. The ease with which the insect larva assumes a form compatible with its living conditions is well illustrated by the difference between a free-living planidium of one parasitic species and the endoparasitic first larva of another related species. The planidium is equipped for activity, for finding and attacking its prospective host; the endoparasite is reduced to the bare essentials needed for feeding on an ambient food supply and for mere existence otherwise. It may be noted here, also, that simplification of structure often occurs in the second or following instars, as with species having a planidial first larva, in which case "early hatching" cannot be invoked to account for it. Whatever form the early larva may take on, however, it is incumbent on the larva eventually to return to its parental form, and this it does by first reverting in its later stages to the larval form typical of its order or family.

## XI. THE PUPAL TRANSFORMATION

The insect pupa is one of the most remarkable things in animate nature; within it are intimately mingled the processes of both life and death. With the shedding of the last larval skin the fully formed pupa appears as a rough sketch of the future adult. The visible pupa, however, is only an external shell; inside of it the larval tissues and organs are being replaced by those of the imago. The juvenile hormone no longer maintains the larval organization, and in consequence the tissues of the larva have either gone into a state of dissolution, or, under the influence of the developmental hormones, are being recon-

structed into imaginal organs, while other organs of the imago are being formed anew from undifferentiated living cells whose development had been repressed by the juvenile hormone. Though hormones control or regulate the transformation processes, there resides in the pupa some mysterious organizing force that builds up the imago from the larval material or from special cells that have been carried by the larva from the embryo. When the imaginal structure is accomplished, the pupal skin is shed and the insect now reappears in the parental form that produced the fertilized egg from which the larva was hatched. The life cycle is thus completed, only to be indefinitely repeated.

Various investigators have observed that the cells of tissues, particularly the epidermis, undergoing metamorphosis discharge dark-staining globules from the nuclei. These globules are commonly termed *chromatic droplets*. Earlier writers, as Pérez (1910) and Poyarkoff (1910), regarded their discharge as a sign of "rejuvenation" in the larval cells; by the rejection of the droplets the cells were supposed to discard their larval ingredients and to be thus prepared for a new growth. The same globules, however, are observed to result from the dissolution of nuclei, and Wigglesworth (1942), from a review of the evidence, concluded that the droplets are always formed in this way. He noted that they are present in the epidermis during the moults of *Rhodnius*, and in greatest numbers where nuclei appeared to be formed in excess of the need for new cells. Nuclei become superfluous, he says, "either because they belong to specialized larval structures that are being discarded, or because the exuberance of cell division has led to their production in greater numbers than are needed." Several writers have observed chromatic droplets also in the growing tissues of the embryo.

*The epidermis.*—Since the newly exposed pupa appears to be already perfectly formed and does not thereafter change externally, it is the ectoderm that undergoes the first reconstruction. The change to the pupal form, however, is not as sudden as it appears to be, since long before the larval skin is cast off the transformation processes had begun in the so-called prepupal stage of the larva, just as each larval stage begins within the unbroken cuticle of the preceding instar. Moulting and ecdysis, therefore, are not synchronous, and the two terms are not synonymous.

The method by which the pupal epidermis is formed is not the same in all insects. In various families of the Coleoptera in particular it appears that the cells of the larval epidermis retain a faculty for renewed and differential growth, and that in these insects most of the

larval epidermis goes over, with changes, directly into the pupal epidermis. At the other extreme, in the higher orders the larval cells enter a state of degeneration and are thrown into the body cavity, while the entire pupal epidermis is generated anew from small groups of cells, the imaginal discs, that have remained undifferentiated from the embryo. Imaginal discs of undeveloped appendages, however, are present in all cases, and represent adult structures whose growth is continued during the larval life.

In the beetle *Sitophilus (Calandra) oryza* Murray and Tiegs (1935) say it is usually possible to distinguish in the epidermis even of the very young larva groups of small, more basophile cells that will form the appendages, rostrum, and copulatory organs of the adult, but that there is no distinct imaginal tissue to form the main part of the body wall. Also in *Leptinotarsa*, according to Patay (1939), the larval epidermis simply undergoes a renewal of developmental activity by which it is transformed into the pupal epidermis without any process of dissolution of its cells. Again, in the chrysomelid *Galerucella*, Poyarkoff (1910) finds little evidence of destruction of larval cells in the transformation of the epidermis from the larva to the pupa.

On the other hand, in Hymenoptera and Diptera there may be a complete renewal of the epidermis from imaginal discs of the larva, accompanied by a destruction of the larval cells. In the thorax the imaginal discs of the appendages not only form the appendages themselves, but they spread outward on all sides to furnish new epidermis for the thorax, and in the abdomen the pupal epidermis is likewise proliferated from abdominal discs. As the new epithelium spreads from the regeneration centers, the old cells of the larval epidermis go into a state of dissolution and are forced into the body cavity where they dissolve or are consumed by phagocytes.

According to Anglas (1901), in *Vespa* and *Apis* as the pupal epidermis spreads from the proliferation centers, the old epidermis becomes vacuolated and separated from the basement membrane. The new tissue advances by incorporating what remains of the larval cells, the protoplasm of which is absorbed, digested, and assimilated by the multiplying imaginal cells. The new epidermis is at first plastic, allowing the modeling of the pupal form, but later it becomes fixed by the hardening of the new cuticle. Anglas reports there is no phagocytosis of the disintegrating larval cells, such as described in some other insects.

In the chalcid *Nasonia*, Tiegs (1922) says that in the newly hatched larva the ectoderm consists of large cells which constitute the greater part of the integument, and of strips of small embryonic

cells which are the imaginal discs of the future pupal integument. In the last part of the final larval instar the larval cells go into a state of cytoplasmic disintegration, which is partly chemical and partly due to the action of phagocytes. At the same time the cells of the imaginal discs of the epidermis multiply and spread out, replacing the disintegrating larval cells, until they re-form the entire body wall, including such internal parts of it as the tendons of muscles, the tentorium, and the thoracic phragmata.

The regeneration of the integument in Diptera from imaginal discs has been described by various writers. Wahl (1901) gives a full account of the epidermal regeneration centers in the larva of *Eristalis*, which on the thorax include the discs of the pupal respiratory trumpets, the wings, the halteres, and the legs, and on the abdomen epithelial thickenings formed of embryonic cells. Pérez (1910) says the newly generated epidermis of *Calliphora* on the thorax grows over the larval epidermis, the cells of which are thus rejected into the body cavity and phagocytized. In the abdomen the epidermal renovation is progressive and slow, but here also the old cells are thrown into the body cavity where they become the prey of phagocytes.

Finally, we may quote from the more recent paper by Robertson (1936) on the epidermal regeneration in *Drosophila*. At an early larval period the rudiments of the legs, wings, and halteres, Robertson says, are masses of embryonic cells sunken into pockets of the ectoderm, which remain open through hollow stalks. These pockets are the imaginal discs which will regenerate the thoracic epidermis. As development proceeds, the mouths of the stalks become wider and the peripheral parts of the discs expand into the surrounding epidermis, the cells of which gradually retreat and are sloughed off into the body cavity, where they are taken up by phagocytes. The imaginal discs continue to expand by cells multiplication until finally they unite and thus replace the entire larval epidermis of the thorax with a new epidermal epithelium, which is that of the pupa and the adult. On the abdomen likewise the larval epithelium is replaced by a new epidermis generated from islands of undifferentiated cells. On most of the abdominal segments there are two pairs of these imaginal discs, one pair dorsal, the other ventral, but the spiracles also are centers of regeneration, making thus six discs on each spiracle-bearing segment. On the last segment, however, there is only a single, ventral histoblast. During the early part of the pupal stage the cells of the abdominal discs multiply and spread out, displacing the larval cells, which are rejected into the body cavity and there phagocytized. At

about the thirty-sixth hour of pupal development in *Drosophila* the imaginal epidermis is complete.

That the body setae may also undergo a metamorphosis is shown by the studies of Krumins (1952) on *Galleria mellonella*, the wax moth. The setal apparatus consists of the three usual cells, the trichogen, the tormogen, and a sense cell. In all larval instars except the first, the setae are slender and hairlike and are re-formed at each moult, but in some cases the sense cell is subepidermal and in others it is intraepidermal. At the moult to the pupa only those larval setae having intraepidermal sense cells are re-formed on the pupa, and these pupal setae are replaced on the imago by conical setae. The adult, however, acquires also smaller conical setae not represented on the pupa.

*The appendages.*—In the lower orders of holometabolous insects in which the adult mouth parts are not essentially different from those of the larva, and the larval legs are functional external organs, the corresponding pupal appendages are formed simply within the cuticle of the larval appendages. If the adult appendages are to be much longer than the larval appendages, the growing organs become folded beneath the larval cuticle until they can straighten out at the pupal ecdysis. In some cases, however, the lengthening organs push back into pockets of the pupal integument, but if the imaginal organ begins its growth during larval stages it will be accommodated in a pocket of the larval integument. Eassa (1953) very precisely describes the growth of the imaginal antennae of *Pieris brassicae*, which have their inception in the first larval stage. Each imaginal antennal rudiment is differentiated around the sense cells and trichogenes at the base of the corresponding short larval antenna; as it increases in size it recedes into a pocket of the head wall, and becomes folded upon itself. During the fifth (last) instar the antennal pocket of the forming pupal head is open by a long slit under the yet unshed larval cuticle, from which the antenna will be everted at the ecdysis of the pupa. On the pupal head, however, the antenna has taken a much higher position than that of the larval antenna. The intervening part of the head wall, Eassa shows, is newly generated from the unfolding wall of the antennal pocket.

The growth of the antenna and the reconstruction of the head in *Pieris* is very similar to that which takes place in lower Diptera, except that in the latter the antennal pouches may include the rudiments of the compound eyes. In the cyclorrhaphous flies the antennae and eyes are developed in pouches of the larval head commonly known as the "frontal sacs," which are ingrowths behind the frons (not "in-

vaginations of the pharynx" as they are often said to be). With the formation of the pupa the two postfrontal pouches unite, and when everted their walls form a large part of the imaginal head bearing the eyes and the antennae (see Snodgrass, 1953).

The imaginal legs of holometabolous insects, in which the larva has external legs, are formed in the usual manner within the larval legs and find space to grow beneath the larval cuticle. If the larva is externally legless, however, the rudiments of the adult legs, which may appear early in larval life, grow within peripodial pockets of the larval epidermis, and are not everted until the moulting of the last larval skin. In the same manner are developed the wings of all endopterous insects. In the higher orders the everting leg and wing pouches contribute to the formation of the thoracic wall of the pupa.

*The alimentary canal.*—Of the three constituent parts of the alimentary tract of an insect, the stomodaeum and the proctodaeum are unquestionably ectodermal since they are formed in the embryo as ingrowths of the body wall. The embryonic mesenteron, however, is ordinarily generated from cells proliferated at the inner ends of the stomodaeum and proctodaeum, which, growing respectively rearward and forward, envelop the yolk in a sac, which is the definitive mesenteron, or functional stomach of the insect known as the ventriculus. Because of the mode of its embryonic origin, some writers have insisted that the insect stomach also must be ectodermal. That this interpretation is entirely unnecessary and evidently erroneous, however, has been shown by Henson (1946), who points out that the tissue at the inner ends of the stomodaeum and the proctodaeum represents the anterior and the posterior lips of the closed blastopore, which, according to the rules of embryogeny, should normally generate ectoderm outwardly and endoderm inwardly. The writer (1935) has explained the matter in essentially the same way in showing that the anterior and posterior mesenteron rudiments are remnants of an originally invaginated endoderm that regenerate the mesenteron. As already noted in the introduction, the embryonic method of forming the stomach is an adaptation to life in the egg. Inasmuch as the embryo cannot take its food into its stomach in the manner of its free-living ancestors, the embryonic stomach grows around the food stored as yolk in the egg. The insect stomach, therefore, begins its history with a metamorphic process, but it does not violate the germ-layer theory.

Since the diet of an adult insect is often very different from that of the larva, the alimentary canal in most holometabolous insects undergoes a very considerable alteration during the pupal transforma-

tion, the change affecting not only the form and relative size of its several parts, but also the nature of the epithelial wall. The degree of reconstruction that takes place in the stomodaeum and proctodaeum varies in different insects, but the mesenteron epithelium is probably always renewed from the larva to the pupa, and in some cases it undergoes a second renewal from the pupa to the adult. An interesting feature in the metamorphosis of the alimentary canal, however, is that the reconstructive changes do not proceed in the same manner in all insects.

The stomodaeum and proctodaeum being of ectodermal origin, their changes in the pupal metamorphosis are similar to those of the epidermis. They may be merely remodeled by a renewal of activity in their cells without any cell destruction, or they may be partly or wholly regenerated from proliferation centers, accompanied by a degeneration and elimination of the old larval cells, which are thrown off into the body cavity. Where the proliferation centers are best differentiated they take the form of circular bands of cells at the inner end of the stomodaeum and the proctodaeum, termed the anterior and posterior *imaginal rings*.

Reconstruction of the stomodaeal and proctodaeal epithelium by a general renewal of developmental activity of the larval cells, without accompanying cell destruction, has been described in some Coleoptera, as in *Galerucella* by Poyarkoff (1910), *Leptinotarsa* by Patay (1939), and *Sitophilus* by Murray and Tiegs (1935). In *Tenebrio*, according to Rengel (1897), the remodeling of the stomodaeum and proctodaeum proceeds from their inner ends, but there are no specific imaginal rings clearly differentiated. The old larval epithelium appears to be absorbed by the advancing newly formed cells. Dobrovsky (1951) follows in great detail the anatomical alterations that take place in the digestive tract of the honey bee during postembryonic development. The stomodaeum and proctodaeum apparently are remodeled into the adult structure by a new growth of the larval cells. In the wasp, according to Anglas (1901), the cells at the posterior end of the stomodaeum and the anterior end of the proctodaeum begin at the time of pupation an active proliferation extending respectively backward and forward; the advancing new cells absorb the old and thus renew the epithelium.

In Trichoptera, Lübben (1907) describes the remodeling of the stomodaeum and proctodaeum by new growth of the larval cells. Russ (1908), however, says that in *Anabolia laevis* imaginal rings are present, though of little importance. The anterior ring serves only for the lengthening of the stomodaeum and the formation of the

stomodaeal valve; the posterior ring is but weakly developed and plays no important role in the reconstruction of the proctodaeum. A part of the rectal region is regenerated from a circumanal zone of proliferation.

The regeneration of the stomodaeum and proctodaeum from imaginal rings is said by Tiegs (1922) to take place in the hymenopteron *Nasonia*, but it is particularly in Lepidoptera and Diptera that these proliferation centers have been observed. In the silkworm, according to Verson (1905), the cells of the imaginal rings become active at the change to the pupa, but they are merely centers of enlargement of the stomodaeum and proctodaeum. Newly formed cells are added to the larval cells already present, pushing the latter farther away without replacing them. Otherwise the stomodaeum and proctodaeum, though they undergo great changes in form, are remodeled by renewed activity of the larval cells. Likewise in *Malacosoma*, Deegener (1908) says the imaginal rings form only small additions to the larval stomodaeum and proctodaeum, and there is no degeneration or emission of larval cells. The larval cells remain, forming the pupal epithelium by reconstructive growth.

The imaginal rings of *Calliphora erythrocephala* are very precisely described by Pérez (1910). The anterior ring is a circle of small cells in the alimentary epithelium surrounding the base of the stomodaeal valve, and therefore on the dividing line between stomodaeum and mesenteron. The posterior ring is a narrow circle of cells in the intestinal wall just behind the bases of the Malpighian tubules. Cellular proliferation from the imaginal rings is said by Pérez to regenerate most of the stomodaeal and proctodaeal epithelium in *Calliphora*, but the terminal parts are formed from anterior and posterior centers of ectodermal proliferation. The degenerating replaced larval cells are thrown off into the body cavity. In *Calliphora vomitoria*, according to Van Rees (1889), there is only a partial regeneration of the stomodaeum and proctodaeum from imaginal rings; the anterior part of the stomodaeum is remodeled by transformation of the larval cells, and in the proctodaeum the rectum is regenerated from behind forward. In *Drosophila* the stomodaeal epithelium is described by Robertson (1936) as being mostly regenerated from the anterior imaginal ring, but regeneration in the pharyngeal region proceeds from the buds of the labium. "As the new epithelium forms, the old larval cells are displaced into the body cavity where they are devoured by phagocytes." The proctodaeal epithelium of *Drosophila* is likewise regenerated in its anterior part from the posterior imaginal ring, and

posteriorly by forward proliferation from the ectodermal imaginal disc of the last body segment.

From these samples of the reconstruction processes that convert the stomodaeum and the proctodaeum of the larva into the corresponding parts of the adult, we may conclude that in the majority of insects the larval cells of the ectodermal parts of the alimentary canal retain the potentiality of rejuvenation. When released from the inhibition of the juvenile hormone they proceed by renewed division and differentiation with the formation of the adult organs. As with the epidermis, however, there is a tendency for certain groups of cells to assume more and more of the work of reconstruction, and these cells finally take the form of specific regeneration centers, the so-called imaginal rings. It is to be noted that the degenerating larval cells of the stomodaeal and proctodaeal epithelia are thrown out into the body cavity, as are those of the epidermis; the discarded epithelium of the mesenteron, on the other hand, is ejected into the stomach lumen.

The mesenteron in its function is more specifically physiological than are the ectodermal parts of the food tract, since it is the seat of digestion and absorption, while the stomodaeum and proctodaeum serve rather in a mechanical way for ingestion, storage, and elimination. The mesenteron, therefore, undergoes a more thorough renovation during the pupal metamorphosis, since it must radically alter its functional activities in response to the usual change of diet from larva to adult. Probably in all holometabolous insects there is a complete renewal of the mesenteron epithelium, but here again, as with the epidermis, the stomodaeum and the proctodaeum, we find that the method of renewal is not the same in all insects.

The larval epithelium of the mesenteron consists typically of two sets of cells. Those of one set are the functional cells concerned with secretion and absorption; those of the other are small cells next to the basement membrane between the bases of the functional cells, known as *replacement cells* because by multiplying they form new functional cells to take the place of those that have become exhausted and which in a degenerating condition are thrown out into the lumen of the stomach. In the majority of insects it is these replacement cells that form also the entire epithelium of the pupal mesenteron, but some Coleoptera appear to repeat the embryonic method of forming the stomach, since they regenerate the mesenteron epithelium from cells at the inner end of the stomodaeum.

According to Mansour (1934) the mesenteron epithelium is regenerated from the posterior end of the stomodaeum in representatives of the following coleopterous families: Cucujidae, Chrysomelidae,

Curculionidae, and Scolytidae. In *Galerucella* Poyarkoff (1910) says the larval epithelium of the mesenteron is rejected in toto, including the basement membrane, and that there is then formed a provisional pupal epithelium derived from cells of the posterior face of the stomodaeal valve. The cells of the new pupal epithelium become differentiated into ordinary epithelial cells and small replacement cells. The pupal epithelium, however, is in turn replaced by an imaginal epithelium formed by the pupal replacement cells, but the imaginal epithelium is thus also derived primarily from the stomodaeum. In *Sitophilus (Calandra) oryza* Mansour (1927) says that about three days before the pupal moult, the larval epithelium of the mesenteron collapses and degenerates, and together with the replacement cells is thrown off into the lumen. The adult epithelium is then derived in *S. oryza* and in other rhynchophorous species from the posterior end of the transforming stomodaeum. According to Murray and Tiegs (1935), however, the larval replacement cells of *S. oryza* are not discharged with the old epithelium, but remain as a layer of scattered cells on the outer surface of the new epithelium and eventually form the mesenteron caeca.

The regeneration of the mesenteron of *Leptinotarsa decimlineata* is described by Patay (1939) as follows. When the larva is ready for transformation, the stomodaeal valve becomes the seat of an intense proliferation, forming numerous fusiform cells of an embryonic character. The basement membrane behind the valve soon breaks, and the larval epithelium turns inward and rearward while the newly formed cells from the valve extend over its outer surface. The larval epithelium, including the replacement cells, is then soon rejected into the lumen. The valve cells construct an entire new epithelium, including islands of replacement cells and a basement membrane. Thus is formed the pupal epithelium, but again at the moult to the imago the pupal epithelium is rejected and the replacement cells reconstruct an imaginal epithelium. The metamorphosis of the mesenteron of *Leptinotarsa* as given by Patay is thus the same as that in *Galerucella* as described by Poyarkoff.

Statements that the mesenteron is formed from cells of the posterior end of the stomodaeum are not to be understood to mean that these cells are ectodermal; as already noted, Henson (1946) has shown that corresponding cells in the embryo represent the anterior end of the blastopore, and therefore properly generate endoderm inward. The imaginal ring of the larva, as said by Henson, "is not an imaginal rudiment but a reactivated blastopore."

The formation of the pupal mesenteron epithelium from replacement cells of the larva is widespread among the insects, and is too well known to need an extensive review here. According to Mansour (1927) this method of epithelial regeneration is known to occur among Coleoptera in Tenebrionidae, Histeridae, Hydrophilidae, Bostrychidae, Elateridae, Scarabidae, Buprestidae, Anoboliidae, Dytiscidae, and Lucanidae. It is the only method of replacement that has been observed in Trichoptera, Lepidoptera, Hymenoptera, and Diptera. At the beginning of metamorphosis in these insects, the digestive cells of the larval epithelium go into a state of degeneration, while the replacement cells enter a phase of active division, proliferating new cells that spread out under the old epithelium and eventually replace it. The degenerating larval cells are cast off into the stomach lumen, where they form a disintegrating mass of material known as the "yellow body."

Of particular interest are those cases in which the pupal epithelium of the mesenteron is said to be replaced by a special imaginal epithelium. However, without any renewal of the pupal epithelium, the imaginal mesenteron may undergo changes of form and relative size. Deegener (1904) described in *Cybister* the formation of a separate epithelium for the pupa differing from that both of the larva and the imago, the function of which he said is to digest the yellow body resulting from the dissolution of the larval epithelium. Both the pupal epithelium and the imaginal epithelium are generated from replacement cells. We have already noted that Poyarkoff (1910) reports the formation of a provisional pupal epithelium in *Galerucella*, which is replaced by an imaginal epithelium generated from the replacement cells of the pupal epithelium. Poyarkoff, however, contends that the pupal epithelium of *Galerucella* is never functional because in the pupal stage the mesenteron is closed at both ends. In the same way in *Leptinotarsa*, according to Patay (1939), the pupal epithelium of the mesenteron derived from the inner end of the stomodaeum is replaced by an imaginal epithelium regenerated from the pupal replacement cells. In the coleopteron *Acanthoscelides obtectus* as described by Bushnell (1936), the pupal epithelium formed from the larval replacement cells is later cast off into the stomach lumen, leaving only a basal layer of cytoplasm containing the smaller nuclei, from which there is then regenerated the definitive imaginal epithelium. The degenerating material from the larval epithelium, Bushnell says, is probably digested and absorbed by the pupal epithelium, which is then itself cast off and gives place to the imaginal epithelium. Lastly, we may note that Tieg (1922) says the pupal epithelium of the chalcid

*Nasonia*, which is formed from larval replacement cells, proceeds to digest and absorb the detritus from the rejected larval epithelium, after which it degenerates, but from its posterior part is formed the definitive mesenteron of the adult.

Deegener (1904) contended that the presence of separate pupal and imaginal epithelia in the mesenteron of many insects is evidence that the pupa represents a former actively feeding stage in the life history of holometabolous insects. Most students of insect metamorphosis, however, have seen a physiological reason for the formation of a specific pupal mesenteron epithelium in the fact that the pupal stomach must digest the disintegrating tissue of the larval mesenteron thrown into it, in order that this material may be reutilized by the developing imaginal organs. In this case the physiological requirements of the adult stomach will be very different from those of the pupal stomach, and it is therefore but a physiological necessity that the epithelium should be renewed for the purposes of the adult. Deegener (1908) himself notes that there is no formation of a new imaginal epithelium in *Malacosoma*; the pupal epithelium persists and goes over directly into the epithelium of the imaginal mesenteron, but with many changes in its cytological structure.

That there is a complete regeneration of the mesenteron epithelium at the moults of the larva, as described by Möbusz (1897) in *Anthrenus*, has not generally been observed, but there is nothing improbable in Möbusz's claim, since the replacement cells are active at all times in renewing the depleted functional epithelium. According to Henson (1929) the mesenteron epithelium of *Vanessa* is renovated at each larval moult by the addition of new cells. It would be of interest to know if any such change takes place in the successive forms of heteromorphic larvae.

*The Malpighian tubules.*—In some insects the Malpighian tubules go over from the larva to the adult without any essential change, in others their walls are regenerated from replacement cells while the old cells degenerate, in still others the larval tubes completely disappear and the imaginal organs grow out in their place as a new set of tubes.

It is still an open question, or at least a disputed one, as to whether the Malpighian tubules of insects are ectodermal or endodermal in origin. Most investigators claim that they arise from the inner end of the proctodaeum, others state as positively that they are outgrowths of the posterior part of the mesenteron. In the embryo of the honey bee Nelson (1915) says the rudiments of the tubules are formed prior to the ingrowth of the proctodaeum as invaginations of the ectoderm

around the point where the proctodaeum is to appear. For a short time, therefore, the tubules "open directly on the external surface of the embryo." A similar condition, according to Nelson, is known otherwise only in *Chalicodoma*. If it occurred more widely we might suspect that the Malpighian tubules were originally circumanal glands of the integument, and that they have secondarily been carried inward with the ingrowing proctodaeum.

The larval tubes of Hymenoptera that have been studied degenerate and disappear, the imaginal tubes are formed anew. In the honey bee Oertel (1930) says the larval tubes disappear apparently by chemical means, not by phagocytosis. The imaginal tubes are then formed as budlike outgrowths from the extreme anterior end of the proctodaeum. According to Dobrovsky (1951) the ring of buds of the imaginal tubes of the bee appear on the surface of the pylorus a short distance behind the inner fold, or "diaphragm," that separates the lumen of the larval mesenteron from that of the proctodaeum. These observations agree with those of Anglas (1901) that the larval tubes of the wasp and bee arise from the front end of the proctodaeum, disappear at metamorphosis, and are replaced by imaginal tubes that grow out just behind their bases. In the same manner, according to Tiegs (1922), are formed the imaginal tubules of the chalcid *Nasonia*, though there are no larval tubules.

The developing imaginal Malpighian tubules of the beetle *Leptinotarsa* are described and distinctly illustrated by Patay (1939) as diverticula from the anterior end of the proctodaeum. At the beginning of pupation their cells take on an appearance of degeneration, the cytoplasm becoming vacuolated and the nuclei irregular, but after the moult to the imago they soon again assume the aspect of normal functional cells, and without destruction or cell division the persisting larval tubules become the organs of the imago. In some other Coleoptera, however, the imaginal tubules are said to be regenerated from small replacement cells in the walls of the larval organs. Poyarkoff (1910) describes the imaginal tubules of *Galerucella* as being formed in this manner, and Murray and Tiegs (1935) say the cells of the larval tubules in *Sitophilus* (*Calandra*) degenerate in the pupa, while new imaginal cells are proliferated by active mitosis of the replacement cells until they form a new tube. The detritus of the larval cells is not discharged but slowly absorbed.

A detailed account of the transformation of the Malpighian tubules from the larva to the adult without dissolution or cell destruction is given by Samson (1908) for the lepidopteron *Heterogenea limacodes*. During the long prepupal stage of this species the Malpighian tubules

go into a degenerative state to such an extent that they appear to be on their way to complete dissolution; at the moult to the pupa, however, reconstructive changes begin that lead to the reformation of the tubules into the organs of the imago. The imaginal tubules retain the form of the larval tubules, but they have undergone an entire change in their histological structure, which, Samson suggests, is correlated with the change of food from the larva to the moth.

In the Diptera the Malpighian tubules, so far as observed, undergo no essential change from larva to adult. Pérez (1910) says that the cells of the tubules in Muscidae simply go into a resting condition during the pupal period, and then again resume functional activity in the imago. Robertson (1936) notes simply that the cell structure of the tubules in *Drosophila* appears to be the same in the larva and the imago. The tubules of *Drosophila*, Robertson says, open into the digestive tract just *in front* of the posterior imaginal ring that regenerates the proctodaeum, from which fact it would appear "that the Malpighian tubules of *Drosophila* belong to the mesenteron." Henson (1946) finds likewise in *Calliphora* that the Malpighian tubules grow out in front of the posterior imaginal ring, so that not only the tubules but also the pyloric region from which they arise are of endodermal origin, and he believes that the same condition prevails in other insects.

*The fat body.*—The so-called fat body of the insect is a physiological tissue; the changes its cells undergo from larva to imago are merely the accompaniments or results of functional activities and are not of the nature of a true metamorphosis. In the larva the fat cells elaborate and store nutritive materials in the form of fat, albuminoids, and glycogen, which are utilized mostly in the pupal reconstruction, but may be carried over into the adult. In some insects there is little or no destruction of the fat cells during metamorphosis, in others most of the cells disintegrate in the pupa to liberate their stored products, while a few are carried over intact to generate the fat body of the adult. Insects such as most Coleoptera in which the pupal transformation is less intense, and which feed amply in the adult stage, have less need of larval food reserves, and show the least change in the larval fat cells during metamorphosis. On the other hand, with insects in which there is an extensive breakdown of larval tissues and an almost complete reconstruction of adult tissues in the pupa, the food material stored in the larval fat cells is of vital importance for the reconstruction of new imaginal tissues. It is in such insects that the fat cells most abundantly give up their contents to the pupal blood, and perish in so doing, leaving only a few to go over into the adult to form the imaginal fat body.

In the Muscidae, it is said by Pérez (1910), the larval fat cells disintegrate completely in the pupa and their remains are devoured by phagocytes. The imaginal fat body, according to Pérez, is then redeveloped from mesenchymatous cells on the inner surface of the epidermis, the abdominal fat tissue being derived from mesenchyme on the inner surfaces of the imaginal discs of the epidermis. If the imaginal fat body is renewed in this manner in the higher Diptera, its formation from mesenchyme is paralleled by the renewal of the muscles from free myoblasts in the same insects.

*The oenocytes.*—The oenocytes are specialized ectodermal cells developed from the epidermis in the neighborhood of the spiracles, mostly in the abdomen. In some insects the oenocytes remain in the epidermis, but usually they are liberated into the body cavity, where they occur either in groups connected with the spiracular tracheae, or freely scattered in association with the fat cells. Most students of insect metamorphosis report that the oenocytes are renewed at the pupal transformation, and Wigglesworth (1933) says there is in the hemipteron *Rhodnius* a new generation of oenocytes formed at each nymphal moult, though some of the old oenocytes persist. According to Albro (1930) the larval oenocytes of the beetle *Galeruella nymphaeae* persist very definitely up to the pupal period, but then they undergo degeneration and histolysis. The smaller imaginal oenocytes appear later newly proliferated from the epidermis. In *Sitophilus* (*Calandra*) the larval oenocytes are said by Murray and Tieg (1935) to begin a slow disintegration in the prepupal stage, some being attacked by leucocytes, but the majority later disappear without phagocytosis. The imaginal oenocytes are independently developed from the epidermis of the abdomen close to the spiracles, but in the imago they are mostly dispersed among the cells of the fat body. No budding of imaginal oenocytes from larval oenocytes was observed by Murray and Tieg, such as described by some earlier writers. In *Leptinotarsa*, Patay (1939) observes that the imaginal oenocytes scatter in the body cavity by amoeboid movements.

The function of the oenocytes is still not exactly known, though the cells are now thought to be secretory organs of some kind. It has commonly been observed that the appearance of secretory activity in the cells is greatest at the times of moulting, and Albro (1930) expressed a common opinion in her statement that secretion by the oenocytes "is in some way, directly or indirectly, correlated with the phenomenon of moulting seems highly probable." Wigglesworth (1933), however, finds that the oenocytes of *Rhodnius* show their greatest activity *after* the new epidermis is complete. He concludes, therefore, that the oeno-

cytes are concerned with the formation of the new cuticle, "that they synthesize, and secrete into the blood, materials which go to form a part of the cuticle." This conclusion receives support also from the fact that the oenocytes are specialized epidermal cells. For a good, well-documented review of the present status of the oenocyte question, see Richards (1951).

*The tracheal system.*—In most holometabolous insects the tracheal system of the larva is carried over to the adult with little change other than the development of new branches to accommodate the particular needs of the imago, and the elimination of tracheae needed only by the larva. As with other parts of the ectoderm, however, more complex reconstructive processes take place in the tracheal tubes of some insects, involving a dissolution of the larval epithelium and the regeneration of a new imaginal epithelium. According to Anglas (1901) the tracheal system of the bee undergoes no true metamorphosis, the only change being one of growth and extension by proliferation from the ends of branches, and the enlargement of certain tubes to form the air sacs of the adult. In the curculionid beetle *Sitophilus (Calandra)*, Murray and Tiegs (1935) say that the tracheal system of the adult differs from that of the larva principally in the elaboration of the thoracic tracheae. The larval tracheae are directly converted into the adult tracheae, accompanied by cell division in the epithelium, but only rarely is there any disintegration of the cells. Even terminal branches within the metamorphosing larval muscles remain intact and become reassociated with the newly forming imaginal fibers.

On the other hand, in the chalcid *Nasonia*, Tiegs (1922) finds that there is an extensive reconstruction of imaginal tracheae from replacement cells in the basal parts of the larval spiracle trunks. Partly by disintegration and partly by phagocytosis, he says, the entire larval tracheal system disappears, but regeneration of the imaginal epithelium keeps pace with the destruction of the larval cells, so that there is no discontinuity in the tracheal system itself. Pérez (1910) gives a detailed account of the tracheal metamorphosis in *Calliphora erythrocephala*. Though the greater part of the larval system of the fly persists into the imago with more or less extensive remodeling, certain parts of it are destined to be totally destroyed by phagocytes, and to be replaced by newly generated tissue. The tracheal regeneration centers, or histoblasts, are groups of small cells distributed through the walls of the larval tubes; they give rise to new branching trunks, and replace the larval epithelial cells of those parts that have been destroyed by phagocytes. The presence of histoblastic centers of regeneration in the tracheal system, as in other parts of the ectoderm,

thus appears to be a specialized condition developed in only certain groups of insects.

*The dorsal blood vessel.*—From the descriptions of most writers on the internal metamorphosis of insects it would appear that the heart and aorta undergo little change from larva to adult during the pupal transformation, and it has been observed in various insects that the heart continues to beat throughout the pupal stage. In the wasp, Anglas (1901) says the dorsal vessel undergoes no metamorphosis except a change of form. According to Murray and Tiegs (1935) the cells of the heart and aorta of *Sitophilus* increase in size during the larval stage, but they do not divide, and they survive the period of metamorphosis intact; the alary muscles of the heart go over with little change into the imago. In *Leptinotarsa* about the only change in the heart described by Patay (1939) is the formation during the pupal stage of the pulsatile vesicle in the mesothorax of the imago. Robertson (1936) says of *Drosophila* that “the dorsal vessel of the larva seems to pass over directly into the adult,” and that “the alar muscles either disappear and are re-formed in the late pupa, or they are somewhat altered, being much more delicate in the imago than in the prepupa.”

In contrast to these accounts, Tiegs (1922) reports that the heart of *Nasonia* undergoes a profound metamorphosis, beginning at the time of larval defaecation. Just prior to this the cells of the heart and the pericardium undergo a granular degeneration. The imaginal heart is then regenerated mainly from scattered embryonic cells in the heart wall. A new pericardium is formed from a mass of embryonic cells lying below the larval pericardium, from which proliferating cells extend forward, absorbing the elements of the larval pericardium as they grow. Eight hours after defaecation, Tiegs says, the heart tube of *Nasonia* has been completely regenerated, and below it is the regenerated pericardium.

It seems probable that further studies on the heart of other insects during metamorphosis will reveal greater changes than have heretofore been reported, unless there is some special reason for the renovation of the organ in *Nasonia*. On the other hand, if reorganization in the structure of the heart is of common occurrence, it is difficult to explain how a regular heartbeat is maintained during the pupal stage. In the larva the heart beats continuously in a forward direction, but it has been shown by Gerould (1924) and other investigators that during the pupal and adult life in many insects there is a periodic reversal in the direction of the beat. Gerould (1933) records the occurrence of periodic heartbeat reversal in the pupa and imago of representatives

of Coleoptera, Lepidoptera, Hymenoptera, and Diptera. "In general," he says, "normal reversal occurs independently of the central nervous system and is essentially myogenic." For a bibliography of the subject, and a description of the structure and action of the heart in the pupa and imago of *Bombyx mori*, see Gerould (1938).

*The nervous system.*—It is well known that changes in the gross structure of the central nervous system commonly take place between the larva and the adult. Ganglia are drawn forward or condensed by a shortening of the connectives in both the thorax and the abdomen, with the result that ganglionic masses on the nerve cords are fewer and individual ganglia are displaced from their proper segments. On the other hand, condensation of ganglia may be present in the larva, as in the higher Diptera, in which all the body ganglia are united in a large thoracic nerve mass closely connected with the brain. The significance of these gross changes in the nervous system is not clear, but concentration and anterior displacement of ganglia is always found in the more specialized insects.

The internal reorganization of the nervous system during the pupal transformation has been less studied than that of other tissues. Bauer (1904) has shown that a reconstruction of the brain and the development of the optic lobes of the adult proceeds from neuroblasts in the larval brain, and, though he apparently made no special study of reorganization in the other ganglia, he says that scarcely any other organ system of the insects undergoes such a thorough metamorphosis as does the central nervous system.

In their account of the metamorphosis of *Sitophilus (Calandra) oryza*, Murray and Tiegs (1935) say that "no direct observations have been made on the manner in which the nervous system of an insect like *Calandra* becomes readjusted during metamorphosis to meet the needs of the highly specialized imaginal musculature," but they add that "many new motor neurons doubtless develop from neuroblasts." However, "disintegration of larval cells occurs but rarely, and consequently degenerating nerve trunks are never found, as in many other insects." In contrast to this Tiegs (1922) finds in the chalcid *Nasonia* that the larval cells of the nerve cord degenerate, while the imaginal neuroblasts begin to divide and multiply, growing at the expense of the larval cells on which they nourish themselves. In the larval brain there is a distinct layer of nonfunctioning neuroblasts outside the central mass of functional cells. At the time of defaecation by the larva the larval brain cells go into dissolution as do the nerve fibers, while the neuroblasts become active and give rise particularly to the complex

optic lobes of the compound eyes and to the centers of the imaginal ocelli and antennae.

A study of the developing innervation of the pupal legs of *Tenebrio molitor* has been made by Sorokina-Agafonowa (1924), who describes an elaborate definitive branching of motor and sensory nerves growing out from the main leg nerve of the larva. The sensory branches go to the epidermis and end in bipolar nerve cells. In a later part of the pupal stage these end cells divide each into several cells until there are hundreds of them which become connected with small setae of the cuticle. The author points out that the connection between the nerve cells and the receptor organs thus appears to be secondary and not primary. It is generally said, however, that the sense cell of a setal sense organ is a division product of a cell in the epidermis, and that the sensory axon grows centrally from it (see Wigglesworth, 1953b).

A complete analysis of insect metamorphosis certainly should include a study of differences in the neuromuscular mechanisms between larva and adult that form the basis of difference in sensory reactions and instincts. It would seem that in many cases there must take place in the pupa an extensive rearrangement of both sensory and motor nerves and an almost complete reorganization of the neuron associations in the central nervous system to account for the behavioristic differences between the larva and the adult. Since we cannot attribute any degree of intelligence to a larva, the common act of spinning a cocoon must be supposed to depend on some special pattern of structure in the larval nervous system that would be entirely useless to the adult. Van der Kloot and Williams (1953a, 1953b) have made an interesting analysis of the role of both external and internal stimuli in the spinning of the cocoon by the *Cecropia* caterpillar.

A good example of a complex larval instinct is seen in the manner by which the caterpillar of the bagworm moth, *Thyridopteryx ephemeraeformis* constructs its portable bag. Several hundred tiny larvae may hatch out at the same time from the eggs of a single female moth. After a period of dispersal they all settle down and proceed by identical methods to enclose themselves in conical bags. Each little caterpillar first with its mandibles cuts out a number of small oval pieces of leaf epidermis (cork or blotting paper will do just as well), and then strings them together in a band with threads of its silk attached to the leaf at each end (fig. 16 A). This done, instead of crawling beneath the band, the caterpillar turns a complete somersault, going head first over and under the band (B), landing on its back in reversed direction (C). Then, righting itself (D), it cuts out more leaf bits and makes a ventral band (E) continuous with the one over its back. It now has a

complete girdle about its thorax. Next, elevating its abdomen (F) it lengthens the girdle downward until only its head and feet are exposed below (G). Finally, when the bag encloses the whole body, the anchoring threads break loose and the now fully clothed young caterpillar walks away (H) to take its first meal on the leaf. As the cater-

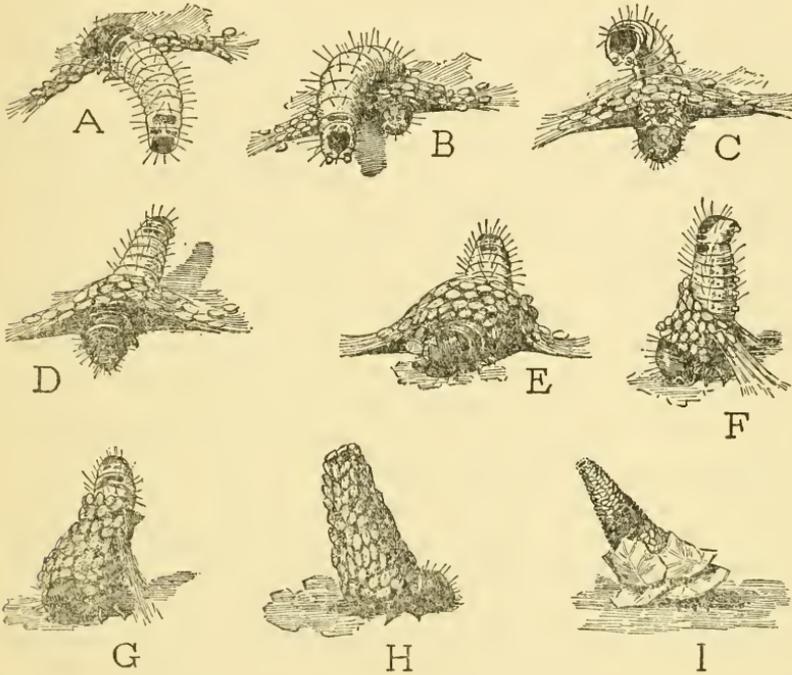


FIG. 16.—Construction of a bag by a newly hatched bagworm, *Thyridopteryx ephemeraeformis* (Haw.).

A-H, consecutive acts of an individual larva making its bag from bits of leaf epidermis cut out with its mandibles. I, an older specimen with later additions to the bag, less enlarged.

pillar grows it merely enlarges the bag by leafy additions to the lower edge (I). Such instinctive skill and methodical procedure as this of the newly hatched bagworm must depend on the presence of a highly developed mechanism for coordinated sensory and motor chain reactions in the central nervous system.

*The muscular system.*—In considering the metamorphosis of the muscular system it must first be noted that all the muscles of all holometabolous insects do not undergo the same degree of change. Five categories may be distinguished: (1) Larval muscles that go over unchanged into the adult, (2) larval muscles that are reconstructed into

imaginal muscles, (3) larval muscles that are destroyed and not replaced, (4) muscles newly formed for the imago replacing larval muscles that have been completely destroyed, (5) newly formed muscles not represented in the larva or which are as yet undeveloped in the larval stage.

The histolysis and histogenesis of the muscles have been described by many writers for various insects. The accounts are not all in entire agreement as to the details of the processes, but a chief point of difference relates to the part that phagocytes may play in the destruction of the larval muscles, a question which is of no concern to us in the present discussion, and is fully reviewed by Oertel (1930). The most important matter is the apparently well-established fact that in different insects the muscles are regenerated in different ways. In the more generalized orders, such as Coleoptera, the histogenesis of a reorganized muscle or of a replacement muscle is said to proceed from small nuclei *within* the tissue of the larval muscle itself. On the other hand, in the more specialized orders, particularly in the higher Diptera, such muscles are remodeled or replaced by myoblasts originating *outside* the larval muscles, probably generated from mesoderm in the embryo. Muscles of appendages that are undeveloped in the larva are in all cases derived from free myoblasts.

The degenerative processes in larval muscles are always pretty much the same. The complete histolysis of a thoracic muscle of *Ephestia kühniella* is described as follows by Blaustein (1935). The advent of degeneration appears at the beginning of the prepupal period with the disappearance of cross striation in the muscle fibers. Lymphocytes now enter the muscle through the sarcolemma and penetrate between the fiber bundles, which lose their connections and separate from one another. The sarcolemma is next broken, admitting increasing numbers of lymphocytes, and is finally ruptured on all sides. The lymphocytes, however, Blaustein says, probably do not at this time have a phagocytic action on the muscle tissue. At the end of the third day of pupal life the muscle nuclei begin to degenerate in large numbers, and dissolve as the nuclear membranes disappear. The degenerating muscle tissue is now attacked by phagocytic lymphocytes that penetrate between the dissociated fibrillae. By the end of the fourth day of the pupa the histolysis of the muscle is complete, and there remains in the place of the muscle only a great number of phagocytes engorged with muscle fragments.

Essentially the same process of muscle degeneration has been described by other writers for other insects. Some earlier writers regarded the lymphocytes penetrating the muscles as phagocytes, but it

is now generally agreed that phagocytes do not initiate the destruction of the muscles. They devour the products of the muscle disintegration, and the greatly enlarged, engorged phagocytes may become extremely numerous throughout the body cavity of the pupa, as in higher *Diptera*, in which they have been called "spherules of granules," or "Körnchenkügeln."

The reconstruction of the muscular system was thought by Berlese (1902) to proceed from the nuclei of the larval muscles, which, being set free in small masses of cytoplasm, became myocytes and were carried to the places where imaginal muscles were to be formed. More recent writers, however, find that in those insects in which the muscles are reconstructed from intrinsic elements, the larval muscles contain two sets of nuclei. Those of one set are the functional larval nuclei, which are destroyed; those of the other set are converted into myocytes, which form the new muscle in place of the degenerated larval muscle. In the beetle *Galerucella*, for example, Poyarkoff (1910) says that the larval muscles contain large nuclei that multiply by amitosis, and small nuclei that multiply by mitosis. The first are the larval nuclei, and will disappear; the small nuclei are the regenerative elements of the imaginal muscles. These mitotic nuclei become enclosed in small masses of sarcoplasm to form myocytes, which associate in long strands that eventually become the fibers of the new or reconstructed imaginal muscle. The regeneration of muscles in *Sitophilus* (*Calandra*) is similarly described by Murray and Tiegs (1935). The small nuclei are at first scattered in the sarcoplasm of the larval fibers, but as the muscle degenerates they migrate into the body of the muscle, which becomes crowded with them. Here these nuclei form myocytes, which unite into columns of cells that finally become the imaginal fibers. Likewise the formation of adult muscles that replace degenerating larval muscles is said by Patay (1939) in *Leptinotarsa* to proceed from small peripheral nuclei within the tissue of the larval muscles.

In the honey bee, Terre (1899) very concisely describes two sets of nuclei in the larval muscles; those of one set are large nuclei in the body of the muscle, the others are small nuclei mostly arranged in longitudinal rows at the surfaces of the fibers. After the larva has finished spinning its cocoon, the muscle substance degenerates and is penetrated by the small nuclei, while the large nuclei dissolve and disappear. The small nuclei become surrounded by masses of myoplasm and thus become the myocytes that reconstruct the muscle for the imago. On the other hand, in the account of the metamorphosis of the muscles of the honey bee given by Oertel (1930) it would appear that

the myoblasts invade the muscle from the outside. Oertel does not discuss the genesis of the free myoblasts, but he says "it is commonly believed that the myoblasts are of mesodermal origin." In the regenerating abdominal muscles he notes that the fibers in some cases are completely covered by myoblasts, and, in connection with the thoracic muscles, that nuclei present in the larva before sealing of the comb cell become incorporated into the new muscles. In the wasp *Polistes*, according to Pérez (1912), the larval muscles have two sets of nuclei, large larval nuclei in the body of the muscle, and small embryonic nuclei attached to the *outside* of the muscles. The muscles undergo a degeneration and reconstruction without being entirely destroyed, but the larval nuclei are mostly eliminated as the imaginal nuclei take their places in the regenerating muscle. In comparing the muscle metamorphosis of the vespids with that of the muscid flies Pérez says the only difference is that in the muscids the imaginal myoblasts are at first exterior to the muscles, while in the wasps the myoblasts are attached on the muscles they are to reconstruct and later become free in order to proliferate outside the muscle.

In the chalcid *Nasonia*, according to Tiegs (1922), the adult muscles are all formed from free mesodermal myoblasts, which are present in the earliest larva. During the larval period the myoblasts are small embryonic cells scattered in the body cavity close to the muscles. As the larval muscles degenerate the neighboring myoblasts become active, multiply by mitosis, penetrate the sarcolemma, and move about in the disintegrating myoplasm by amoeboid movements. Eventually the whole larval fiber, including the sarcolemma, disappears and the invading myocytes take its place, becoming arranged in rows that finally form the new imaginal fibers.

The description by Blaustein (1935) of the muscle transformation in the lepidopteron *Ephestia kühniella* is not explicit as to the origin of the myoblasts, but this author says that where a prospective muscle is to be formed very small embryonic cells are first laid down. By mitotic division they multiply, and by fusion with one another they form long strands that become the imaginal muscle fibers.

The histogenesis of the muscles of the dipteran *Psychoda alternata* is described by Schmidt (1929), but here again it is not clear whether the myoblasts are intrinsic or extrinsic with relation to the larval muscles. The dorsal longitudinal muscles of the metathorax of the larva while undergoing degeneration lose their cross striation and the sarcolemma disappears, the contractile substance and the plasma blend into a homogeneous mass in which are imbedded many small nuclei, which are the myoblast nuclei that will regenerate the imaginal muscles.

In the higher Diptera there appears to be no doubt that the imaginal myoblasts are primitive embryonic cells at first *free* in the body cavity of the larva. As examples of the process of muscle formation in the higher Diptera we may cite from the paper by Pérez (1910) on the metamorphosis of Muscidae, and from that by Robertson (1936) on *Drosophila*. Both authors describe the myoblasts of the imaginal muscles as originating *outside* the larval muscles. According to Pérez the myocytes are mesodermal cells preexisting in the body cavity, more or less in the vicinity of the epidermal histoblasts, but they are not of ectodermal origin. They represent the precocious rudiments of the imaginal musculature in a state of dissociation. These free myocytes, Pérez asserts, are the homologues of the small regenerative nuclei in the larval muscles of those insects in which the muscles are re-formed from intrinsic elements. However, he does not suggest how the free myocytes became dissociated from the larval muscles. Robertson does not discuss the origin of the free myocytes in *Drosophila*.

The adult muscles of Muscidae, according to Pérez, excepting those that are exclusively imaginal, are mostly muscles that have been re-constructed in the pupa from larval muscles. The larval muscle degenerates into a homogeneous mass, which is then penetrated from the outside by the myoblasts, which reconstruct the larval muscle tissue into a muscle for the adult. The imaginal muscles of the muscids, Pérez says, are thus formed from two different sources, the remains of the larval muscles, and the embryonic myoblasts, the two being combined in different proportions in different muscles. On the other hand, Robertson says, "Practically all muscles of *Drosophila* are destroyed by histolysis and consumed by phagocytes during the prepupal and early pupal instars." Thoracic muscles, which in *Calliphora* Pérez believed were remodeled into imaginal muscles, according to Robertson simply undergo a long-delayed histolysis. Myocytes of the longitudinal thoracic muscles appear in the dorsal part of the pupa of *Drosophila* as early as the fifth hour of the pupal period. They surround the persisting larval muscles and increase greatly in numbers. The larval muscles degenerate completely and disappear, leaving in their place the myocytes, which spread out in the position of the future imaginal muscles. Differentiation then proceeds anteriorly and posteriorly from the central mass of myocytes until a new muscle is fully formed.

Muscles newly generated in the pupa, having no representatives in the larval musculature, are for the most part the muscles of appendages that are undeveloped in the larva, including the mouth parts, the antennae, the legs, and the external reproductive organs. These mus-

cles necessarily are generated from unorganized groups of myoblasts of mesodermal origin that are adventitious on the inner surfaces of the ectodermal histoblasts of the appendages. If, however, an appendage is functionally developed in the larva, it has its own normal larval muscles, and these muscles will undergo a metamorphosis of the type characteristic of the species. In the larva of the beetle *Thymalus*, for example, Breed (1903) says the leg muscles go into a state of degeneration until they reach a structureless condition, but this condition is of short duration and is followed by a phase of reconstruction.

The reason for the metamorphosis of the muscular system is not hard to see; it is the difference between the musculature of the larva and that of the imago. Breed (1903) argued that the larval musculature must undergo a reconstruction because of the specialized condition of the adult musculature in winged insects. The truth, however, is clearly just the reverse. The adult musculature is essentially the same in all insects from Ephemeroptera to Diptera, except that the thoracic musculature is uniquely specialized in Odonata and is simplified in Blattidae, Mantidae, and Isoptera. The musculature of an adult holometabolous insect, therefore, is in general no more specialized than that of a winged adult ametabolous or hemimetabolous insect. It is the musculature of the holometabolous larva that has become specialized for purposes of the larva. Its specialization was at first perhaps one of simplification, but with the larval evolution the larval musculature increases in complexity along patterns that have little or no relation to the imaginal musculature because it becomes adapted to the entirely different mechanism of movement in the larva. The more different a larva becomes from the adult of its species, the more specialized its musculature must be, and, therefore, it is in such insects as Lepidoptera, Hymenoptera, and Diptera that the greatest degree of muscle reconstruction occurs between larva and imago.

It is evident that the pupal transformation of the muscles is not entirely comparable to the regeneration of any of the other tissues. The formation of imaginal muscles from special nuclei within the larval muscles might be likened to the regeneration of ectodermal parts from histoblasts within the ectoderm, but the construction of muscles from myoblasts scattered in the larval body has no counterpart in the regeneration of other tissues. Furthermore, it is difficult to understand how the free myocytes in one case, as Pérez contends, can be homologues of the regenerative nuclei in the other, and it is quite mysterious how mesodermal cells lying idle throughout embryonic and larval life can be assembled in the pupa and induced to form new muscles for

the imago. Yet there seems to be no doubt that they do this very thing. The essence of holometabolism is the muscle transformation.

## XII. MUSCLE ATTACHMENTS AND THE NATURE OF THE PUPA

The somatic muscles of arthropods for mechanical reasons are necessarily attached on the cuticle of the integument. The attachment is by means of fine fibrils called tonofibrillae, which traverse the epidermis from the cuticle and are attached to the muscle fibrillae; their outer ends in some cases appear to be embedded in the inner part of the endocuticle. The nature of the tonofibrillae and the manner of their formation have been discussed for half a century, and are still not definitely known; a review of opinion is given by Richards (1951) and need not be repeated here. Probably the best explanation of the tonofibrillae is that they are cuticular filaments formed by the epidermal cells where a muscle comes into contact with the integument; if their outer ends are embedded in the cuticle we may assume that the inner layer of the endocuticle was laid down subsequent to the formation of the tonofibrillae. The connection with the muscle fibrillae is said to be formed by a splitting of the inner ends of the cuticular fibers, which are thus "spliced" to the muscle fibrillae so that the two become mechanically continuous.

It is well known that homologous muscles may have their attachments at different places on the body wall in different insects. The shift is generally attributed to "migration" of the muscles in the phylogenetic history of the insects; but in embryonic development and in metamorphosis the muscles become attached where their ends come in contact with the epidermis. It seems probable, therefore, that the formation of tonofibrillae by the epidermis is evoked by the muscle contact. A necessary condition for muscle attachments on the cuticle is that the latter must be established when the epidermal cells are physiologically active and thus able to produce tonofibrillae while the cuticle is in a formative state. Since most of the adult muscles of holometabolous insects undergo a prolonged period of reconstruction in the pupa, they do not make their final attachments until the end of the pupal period when the imaginal cuticle is being formed. On the other hand, if a muscle is ready for attachment at an early stage, as in hemimetabolous insects, it can be attached at once on the imaginal cuticle at the end of the larval stage.

The nature of the pupa has been a subject of much difference of opinion. Perhaps the most common interpretation is that the holometabolous pupa represents the last nymphal stage of insects without

metamorphosis, which would mean either that the pupa is simply a modified last larval instar, or that the juvenile specialization that produced the larva stopped at the penultimate moult, so that the pupa is a reversion to a nymphal stage with incompletely developed external wings. The nymphal theory of the pupa is carried still further by Jeschikov (1929), who contends that the larva is merely a free-living stage of the embryo and that the pupa represents the whole period of ancestral postembryonic development, "sie erscheint als Resultat des Zusammenfließens aller nymphalen Altersstufen." The pupa itself sufficiently refutes this theory; it gives no evidence of being a composite stadium since its external structure once formed remains unchanged. (See also p. 49.)

A more reasonable theory concerning the nature of the pupa is that of Poyarkoff (1914), which holds that the pupa is a preliminary imaginal stage that has been separated from the final adult by an extra moult in order to furnish a new cuticle for the attachment of muscles reconstructed or newly formed in the pupa. Furthermore, Poyarkoff adds, the pupa as a preliminary adult serves as a necessary mold for the muscles forming within it, since in the larva these muscles could not attain the size and the points of attachment appropriate for the adult. It is only after the insect has assumed the external imaginal form in the pupal stage that new muscles can be completed, but even then they are still incapable of functioning because of the lack of attachments. They cannot be attached at the beginning of pupation since they are not yet formed, and they are not able to attach on the pupal cuticle after the latter is hardened. Hence a new moult is necessary to furnish the only condition in which tonofibrillae can be formed for anchoring the muscles on the cuticle. Hinton (1948) strongly advocates the views of Poyarkoff concerning the nature of the holometabolous pupa. If the larval muscles had not departed from the plan of the adult musculature, the larva might go over directly into the adult. The pupal moult is the solution on the part of the insect to the problem of attaching new or reconstructed muscles. The only evidence against this interpretation of the pupa that might arise would be the discovery in some insect with a pupal stage that no new muscle attachments are formed. At present no such condition is known.

There can be no question that in its general form and structure the pupa is an unfinished adult. The likeness to the adult is strikingly seen in the relatively generalized raphidian pupa (fig. 17 B), which has distinctly imaginal characters in the shape of the head, the long, slender legs, the subsegmented tarsi, and the large, paired movable

claws on each foot (D). When this pupa is ready to transform it leaves the winter nest of the larva and crawls to a suitable place on the bark of twigs of the tree, to which it tightly clings with its claws

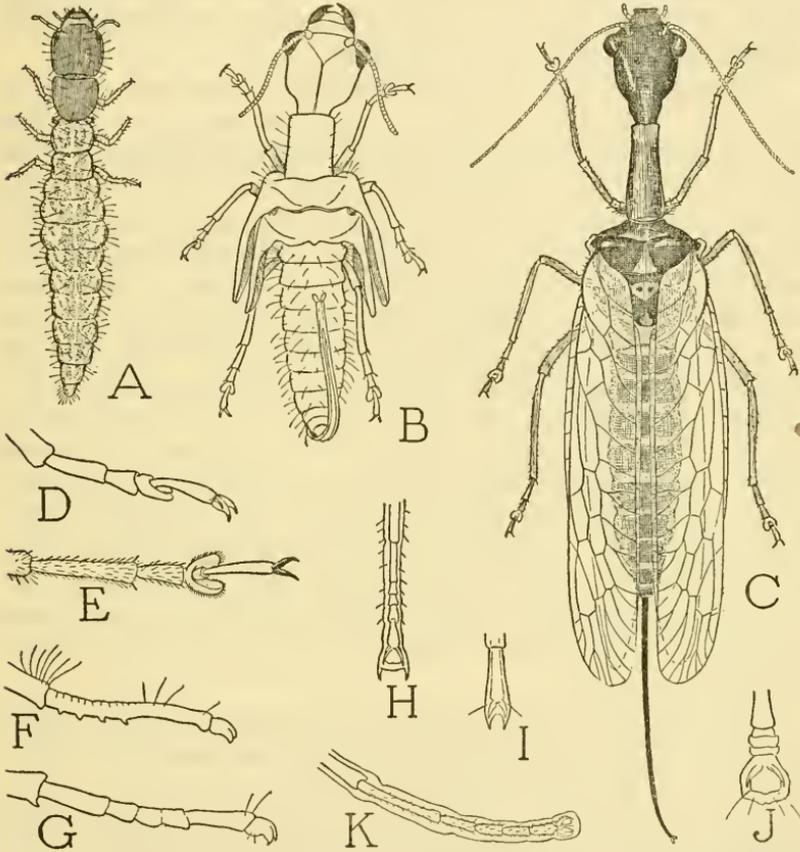


FIG. 17.—Larva, pupa, and adult of a raphidian, and examples of pupal tarsi.

A, *Agulla adnixa* (Hagen), larva. B, same, pupa. C, same, adult female. D, same, pupal tarsus. E, same, tarsus of adult. F, myrmelionid pupal tarsus. G, *Corydalus cornutus* (L.), pupal tarsus. H, chrysopid pupal tarsus. I, *Boreus* sp., pupal tarsus. J, *Mantispa* sp., pupal tarsus. K, *Musca domestica* (L.), pupal tarsus.

(see Stein, 1838, Kästner, 1934). The pupa of the megalopteron *Nigronia serricornis* (Say) also has paired claws, but in most of the other neuropteroid families the end segment of the pupal leg is merely split into two apical points (F, G), or it bears two small clawlike teeth (H, I) within which the paired claws of the adult are formed. In a

mantispid (J), however, the pupal tarsus ends with a simple expansion, and in the higher insect orders, whether the larval leg is one-clawed or two-clawed, the end of the pupal leg (K) is a simple lobe ensheathing the pretarsus of the adult. The clawless pupal leg in the higher orders, therefore, is a result of secondary simplification in an appendage not yet needed for locomotion.

That the pupa is a part of the imaginal phase of the insect can be deduced from other lines of evidence. In the ametabolous or hemimetabolous insects the juvenile hormone maintains the nymphal or larval status up to the transformation to the imago; in the holometabolous insects the same hormone carries the larval form only up to the pupa. Furthermore, the histoblasts of the larva, or imaginal discs, form directly not the organs of the adult but those of the pupa. The dividing line that separates the holometabolous pupa from the larva, therefore, is the same as that which separates the ametabolous imago from the nymph. The holometabolous pupa and adult thus equate as a unit with the ametabolous imago. Williams (1952) has shown that the same hormone system, namely, that of the brain and the thoracic glands, controls both pupation of the larva and the adult development of the pupa. Finally, when we consider that all the internal organs of the pupa are the adult organs in a state of being completed, the pupa can hardly be regarded as anything else than a preliminary adult. At the last larval moult, as Poyarkoff has said, the insect changes into an imago, but the state of its internal organs does not permit it to become at once an adult.

The occurrence of a moult in the imaginal stage, as Hinton (1948) points out, is not limited to the holometabolous insects; it regularly takes place in most Ephemeroptera, while in the apterygote insects and the other arthropods moulting is usual throughout life. Hinton suggests, therefore, that the pupa is equivalent to the ephemeropterid subimago. However, it would hardly seem that there can be any real relation between the imaginal moult of the mayfly and the moult of the pupa in the very distantly related holometabolous insects. More probably the pupal moult was a secondary, independently developed moult in the ancestors of the present holometabolous insects, rather than a "throwback" to a time when adult moulting was a regular event. It has been shown by Burks (1953) that the subimagines of Ephemeroptera are sexually mature; their sperm and eggs mixed in normal saline solution produce fertilized eggs, from which larvae may be hatched. Some species, therefore, have simply eliminated the second moult.

## REFERENCES

- ADAMS, J. A.  
1933. The early instars of the firebrat, *Thermobia domestica* (Packard). (Thysanura.) Proc. Iowa Acad. Sci., vol. 40, pp. 217-219.
- ALBRO, HELEN T.  
1930. A cytological study of the changes occurring in the oenocytes of *Galerucella nymphacae* L. during the larval and pupal periods of development. Journ. Morph., vol. 50, pp. 527-567, 8 pls.
- ANGLAS, J.  
1901. Observations sur les métamorphoses internes de la gûepe et de l'abeille. Bull. Sci. France et Belgique, vol. 34, pp. 363-473.
- BARROIS, J.  
1896. Mémoire sur le développement des *Chelifer*. Rev. Suisse Zool., vol. 3, pp. 461-498, 2 pls.
- BAUER, V.  
1904. Zur innern Metamorphose des Centralnervensystems der Insekten. Zool. Jahrb., Anat., vol. 20, pp. 123-152, 7 text figs., 1 pl.
- BAUMANN, H.  
1921. Beitrag zur Kenntnis der Anatomie der Tardigraden (*Macrobiotus Hufelandii*). Zeitschr. wiss. Zool., vol. 118, pp. 637-652, 10 figs.
- BERLESE, A.  
1896. Le Cocciniglie Italiane viventi sugli agrumi. Parte III. I Diaspitti. Riv. Patol. Veg., vol. 4, pp. 203-477.  
1902. Osservazioni su fenomeni che avvengono durante la ninfosi degli insetti metabolici. Parte II. Tessuto muscolare. Riv. Patol. Veg., vol. 10, pp. 1-120, 32 figs.
- BICKLEY, W. E.  
1942. On the stomodaeal nervous system of insects. Ann. Ent. Soc. Amer., vol. 35, pp. 343-354, 2 pls.
- BIERBRODT, ERIKA.  
1942. Der Larvenkopf von *Panorpa communis* L. und seine Verwandlung, mit besonderer Berücksichtigung des Gehirns und der Augen. Zool. Jahrb., Anat., vol. 68, pp. 51-136, 33 text figs., 1 pl.
- BLAUSTEIN, W.  
1935. Histologische Untersuchungen über die Metamorphose der Mehlmotte *Ephestia kühniella* Zeller. Zeitschr. Morph. Ökol. Tiere, vol. 30, pp. 333-354, 15 figs.
- BODENSTEIN, D.  
1943. Hormones and tissue competence in the development of *Drosophila*. Biol. Bull., vol. 84, pp. 34-58, 2 pls.  
1944. The induction of larval molts in *Drosophila*. Biol. Bull., vol. 86, pp. 113-124, 1 pl.  
1950. The postembryonic development of *Drosophila*. In Demerec, Biology of *Drosophila*, Chap. 4, pp. 275-367, 33 figs.  
1953a. Endocrine control of metamorphosis with special reference to Holometabola. Trans. IX Internat. Congr. Ent., Amsterdam, vol. 2, pp. 58-62.  
1953b. The role of hormones in molting and metamorphosis. In Roeder, Insect physiology, pp. 879-931, fig. 244-257.

BOUNHIOL, J. J.

1938. Recherches expérimentales sur le déterminisme de la métamorphose chez les Lépidoptères. Bull. Biol. France et Belgique, Suppl. 24, 199 pp., 34 text figs., 2 pls.

1953. Rôle du corpus allatum dans la métamorphose des insectes. Trans. IX Internat. Congr. Ent., Amsterdam, vol. 2, pp. 63-72.

BRAUER, F.

1869. Beschreibung der Verwandlungsgeschichte der *Mantispa styriaca*, Poda. Verhandl. Zool.-Bot. Ges. Wien, vol. 19, pp. 831-840, 1 pl.

BREED, R. S.

1903. The changes which occur in the muscles of a beetle, *Thymalus marginicollis* Chev., during metamorphosis. Bull. Mus. Comp. Zool., vol. 40, pp. 317-382, 7 pls.

BRUES, C. T.

1903. A contribution to our knowledge of the Stylopidae. Zool. Jahrb., Anat., vol. 18, pp. 241-270, 3 text figs., 2 pls.

BURKS, B. D.

1953. The mayflies, or Ephemeroptera, of Illinois. Bull. Illinois Nat. Hist. Surv., vol. 26, 216 pp., 395 figs.

BURTT, E. T.

1938. On the corpora allata of dipterous insects. II. Proc. Roy. Soc. London, ser. B, vol. 126, pp. 210-223, 3 figs.

BUSHNELL, R. J.

1936. The development and metamorphosis of the mid-intestinal epithelium of *Acanthoscelides obtectus* (Say) (Coleoptera). Journ. Morph., vol. 60, pp. 221-241, 2 pls.

BUTLER, HORTENSE.

1904. The labium of the Odonata. Trans. Amer. Ent. Soc., vol. 30, pp. 111-133, 6 pls.

CALVERT, P. P.

1898. The first filling of the tracheae with air in Odonata. Ent. News, vol. 9, p. 73.

1911. Studies on Costa Rican Odonata, I. The larva of *Cora*. Ent. News, vol. 22, pp. 49-64, 2 pls.

1928. The significance of odonate larvae for insect phylogeny. Proc. IV Internat. Congr. Ent., vol. 1, pp. 919-925, 7 figs.

CARPENTIER, F.

1939. Sur le parasitisme de la deuxième forme larvaire de *Eoxenos laboulbenei* Peyer. Bull. Ann. Soc. Ent. Belgique, vol. 79, pp. 451-468, 12 figs.

CAZAL, P.

1948. Les glandes endocrines rétro-cérébrales des insectes (étude morphologique). Bull. Biol. France et Belgique, Suppl. 32, 227 pp., 186 figs.

CHAUDONNERET, J.

1949. A propos du corps jugal des Thysanoures. Bull. Soc. Zool. France, vol. 74, pp. 164-167, 1 fig.

CHEN, S. H.

1946. Evolution of the insect larva. Trans. Roy. Ent. Soc. London, vol. 97, pp. 381-404, 6 figs.

## CHINA, W. E.

1931. A remarkable mirid larva from Cuba, apparently belonging to a new species of the genus *Paracarnus* Dist. (Hemiptera, Miridae). *Ann. Mag. Nat. Hist.*, ser. 10, vol. 8, pp. 283-288, 2 figs.

## CLAASSEN, P. W.

1931. Plecoptera nymphs of America (north of Mexico). *Thomas Say Foundation*, vol. 3, 199 pp., 35 pls.

## CLAUSEN, C. P.

1923. The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. *Ann. Ent. Soc. Amer.*, vol. 16, pp. 195-217, 2 pls.
1928. *Hyperalonia oenomaus* Rond., a parasite of *Tiphia* larvae (Dip., Bombyliidae). *Ann. Ent. Soc. Amer.*, vol. 21, pp. 642-659, 1 pl.
1940. *Entomophagous insects*, 688 pp., 257 figs. New York.

## CONSTANTINEANU, M. J.

1930. Der Aufbau der Sehorgane bei den in Süßwasser belebenden Dipterenlarven und bei Puppen und Imagines von *Culex*. *Zool. Jahrb., Anat.*, vol. 52, pp. 253-346, 25 text figs., 12 pls.

## CORBET, P. S.

1951. The development of the labium of *Sympetrum striolatum* (Charp.) (Odonata). *Ent. Month. Mag.*, vol. 87, pp. 289-296, 21 figs.

## DAY, M. F.

1943. The corpus allatum of the sheep ked, *Melophagus ovinus* L. *Psyche*, vol. 50, pp. 1-7, 1 pl.

## DEEGENER, P.

1904. Die Entwicklung des Darmcanals der Insekten während der Metamorphose, Teil I. *Cybister roeseli* Curtis. *Zool. Jahrb., Anat.*, vol. 20, pp. 499-676, 11 pls.
1908. Die Entwicklung des Darmcanals der Insekten, während der Metamorphose, Teil II. *Malacosoma castrensis* L. *Zool. Jahrb., Anat.*, vol. 26, pp. 45-182, 5 pls.

## DE LERMA, B.

1937. Osservazioni sul sistema endocrino degli insetti (corpora allata e corpi faringei). *Arch. Zool. Italiano*, vol. 24, pp. 339-368, 17 figs.

## DEMEREK, M.

1950. *Biology of Drosophila*, 632 pp. New York and London.

## DOBROVSKY, T. M.

1951. Postembryonic changes in the digestive tract of the worker honeybee (*Apis mellifera* L.). *Cornell Univ. Agr. Exp. Stat., Mem.* 301, 45 pp., 12 pls.

## EASSA, Y. E. E.

1953. The development of imaginal buds in the head of *Pieris brassicae* Linn. (Lepidoptera). *Trans. Roy. Ent. Soc. London*, vol. 104, pp. 39-50, 3 text figs., 1 pl.

## EASTHAM, L. E. S.

1929. The post-embryonic development of *Phaenoserphus viator* Hal. (Proctotrypoidea), a parasite of the larva of *Pterostichus niger* (Carabidae), with notes on the anatomy of the larva. *Parasitology*, vol. 21, pp. 1-21, 3 pls.
1930. The embryology of *Pieris rapae*.—Organogeny. *Philosoph. Trans. Roy. Soc. London*, ser. B, vol. 219, pp. 1-50, 9 pls.

1938. Movements of the gills of ephemerid nymphs in relation to the water currents produced by them. Journ. Queckett Micr. Club, ser. 4, vol. 1, pp. 1-5.
1939. Gill movements of nymphal *Ephemera danica* (Ephemeroptera) and the water currents caused by them. Journ. Exp. Biol., vol. 16, pp. 18-33, 8 figs.
- FORD, E. B.
1937. Problems of heredity in the Lepidoptera. Biol. Rev., vol. 12, pp. 461-503.
- GEIGY, R.
1931. Erzeugung rein imaginaler Defekte durch ultraviolette Eibestrahlung bei *Drosophila melanogaster*. Roux' Arch. Entw.-Mech., vol. 125, pp. 406-447, 47 figs.
- GEROULD, J. H.
1924. Periodic reversal of heart-beat in a chrysalis. Science, vol. 60, pp. 570-572.
1933. Orders of insects with heart-beat reversal. Biol. Bull., vol. 64, pp. 424-431.
1938. Structure and action of the heart of *Bombyx mori* and other insects. Acta Zoologica, Internat. Tidskr. Zool. (Stockholm), vol. 19, pp. 297-352, 37 figs.
- GRANDI, M.
1950. Contributi allo studio dei Plecotteri. II. Morphologia comparata del torace di alcuni specie de Plecotteri. Boll. Ist. Ent. Univ. Bologna, vol. 18, pp. 30-57, 17 figs.
- HEGNER, R. W.
1911. Experiments with chrysomelid beetles. III. The effects of killing parts of the eggs of *Leptinotarsa decemlineata*. Biol. Bull., vol. 20, pp. 237-251, 17 figs.
- HENDERSON, I. F.
1949. A dictionary of scientific terms, 4th ed., 480 pp. Edinburgh and London.
- HENSON, H.
1929. On the development of the mid-gut in the larval stages of *Vanessa urticae* (Lepidoptera). Quart. Journ. Micr. Sci., vol. 73, pp. 87-105, 1 pl.
1946. The theoretical aspect of insect metamorphosis. Biol. Rev., vol. 21, pp. 1-14, 4 figs.
- HEYMONS, R.
1897. Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L. Zeitschr. wiss. Zool., vol. 62, pp. 583-631, 3 text figs., 2 pls.
1904. Die Hinterleibsanhänge der Libellen und ihrer Larven. Ann. K. K. Naturhist. Hofmus., Wien., vol. 19, pp. 21-58, 11 text figs., 1 pl.
1906. Über die ersten Jugendformen von *Machilis alternata* Silv. Sitzb. Ges. nat. Freunde Berlin, Jahrg. 1906, pp. 253-259.
- HINTON, H. E.
1948. On the origin and function of the pupal stage. Trans. Roy. Ent. Soc. London, vol. 99, pp. 395-409, 1 fig.
1951. The structure and function of the endocrine glands of the Lepidoptera. Proc. South London Ent. and Nat. Hist. Soc. for 1950-51, pp. 124-160, 19 figs.

- HOLLANDE, A., CACHON, J., AND VAILLANT, F.  
1951. Recherches sur quelques larves d'insectes termitophile. *Ann. Sci. Nat.*, ser. 11, Zool., vol. 13, pp. 365-396, 30 figs.
- HORSFALL, W. R.  
1941. Biology of the black blister beetle (Coleoptera: Meloidae). *Ann. Ent. Soc. Amer.*, vol. 34, pp. 114-126, 1 pl.
- HORTON, J. R.  
1918. The citrus thrips. U. S. Dept. Agr. Bull. 616, 42 pp., 10 figs.
- IDE, F. P.  
1935. Post embryological development of Ephemeroptera (mayflies). *Canadian Journ. Res.*, vol. 12, pp. 433-478, 13 figs.
- INGRAM, J. W., AND DOUGLAS, W. A.  
1932. Notes on the life history of the striped blister beetle in southern Louisiana. *Journ. Econ. Ent.*, vol. 25, pp. 71-74.
- JESCHIKOV, J.  
1929. Zur Frage über die Entstehung der vollkommenen Verwandlung. *Zool. Jahrb., Anat.*, vol. 50, pp. 601-652.
- JOBLING, B.  
1939. On the African Streblidae (Diptera Acalypterae) including the morphology of the genus *Ascodipteron* Adens., and a description of a new species. *Parasitology*, vol. 31, pp. 147-165, 4 figs.
- JOLY, N.  
1872. Note sur un nouveau cas d'hypermetamorphose constaté chez le *Palingenia virgo* a l'état de larve. *Ann. Sci. Nat.*, ser. 5, Zool., vol. 15, 5 pp.
- KÄSTNER, A.  
1934. Zur Lebensweise der Kamelhalsfliegen (Raphidiina). *Zool. Anz.*, vol. 108, pp. 1-11, 6 figs.
- KING, J. L.  
1916. Observations on the life history of *Pterodontia flavipes* Gray. (Diptera.) *Ann. Ent. Soc. Amer.*, vol. 9, pp. 309-321, 2 pls.
- KIRKPATRICK, T. W.  
1937. Studies on the ecology of coffee plantations in East Africa. II. The autecology of *Antestia* spp. (Pentatomidae) with a particular account of a strepsipterous parasite. *Trans. Roy. Ent. Soc. London*, vol. 86, pt. 14, pp. 247-343, 40 figs.
- KRISHNAMURTI, B.  
1933. On the biology and morphology of *Epipyrops eurybrachydīs* Fletcher. *Journ. Bombay Nat. Hist. Soc.*, vol. 36, No. 4, pp. 944-949, 1 pl.
- KRUMIŇŠ, R.  
1952. Die Borstenentwicklung bei der Wachsmotte *Galleria mellonella* L. *Biol. Zentralbl.*, vol. 71, pp. 183-210, 13 figs.
- KULAGIN, N.  
1898. Beiträge zur Kenntnis der Entwicklungsgeschichte von *Platygaster*. *Zeitschr. wiss. Zool.*, vol. 63, pp. 195-235, 2 pls.
- LA BAUME, VON W.  
1909. Über die Metamorphose der Ephemeriden. *Sitzb. Ges. nat. Freunde Berlin*, Jahrg. 1909, pp. 137-153, 3 figs.
- LAMEERE, A.  
1899. La raison d'être des métamorphoses chez les insectes. *Ann. Soc. Ent. Belgique*, vol. 43, pp. 619-636.

LAUTERBORN, R.

1903. Tracheenkiemen an der Beine einer Perliden-Larve (*Taeniopteryx nebulosa* L.). Zool. Anz., vol. 26, pp. 637-642, 2 figs.

LEE, HELEN TSUI-YING.

1948. A comparative morphological study of the prothoracic glandular bands of some lepidopterous larvae, with special reference to their innervation. Ann. Ent. Soc. Amer., vol. 41, pp. 200-205, 1 pl.

LINDSAY, EDER.

1939. The biology of the silverfish *Ctenolepisma longicaudata* Esch., with particular reference to its feeding habits. Proc. Roy. Soc. Victoria, vol. 52, pp. 35-83, 12 text figs., 2 pls.

LÜBBEN, H.

1907. Über die innere Metamorphose der Trichopteren. Zool. Jahrb., Anat., vol. 24, pp. 71-128, 3 pls.

MÄKEL, MARIA.

1942. Metamorphose und Morphologie des *Pseudococcus*-Männchens mit besonderer Berücksichtigung des Skelettmuskelsystems. Zool. Jahrb., Anat., vol. 67, pp. 461-588, 24 figs.

MANSOUR, K.

1927. The development of the larval and adult mid-gut of *Calandra oryzae* (Linn.): The rice weevil. Quart. Journ. Micr. Sci., vol. 71, pp. 313-352, 5 pls.

1934. The development of the adult mid-gut of coleopterous insects and its bearing on systematics and embryology. Bull. Fac. Sci. Egyptian Univ., No. 2, 34 pp., 5 pls.

MARCHAL, P.

1906. Recherches sur la biologie et le développement des Hyménoptères parasites. Les Platygasteres. Arch. Zool. Exp. Gén., ser. 4, vol. 4, pp. 485-640, 8 pls.

MARLATT, C. L.

1923. The periodical cicada. U.S. Bur. Ent. Bull. 71, 183 pp., 68 figs.

MATHEV, A. P.

1948. Nutrition in the advanced embryo of the scorpion: *Palamnaeus scaber* Thorell. Proc. Indian Acad. Sci., B, vol. 27, pp. 111-118, 6 figs.

MELANDER, A. L.

1903. Notes on the structure and development of *Embia texana*. Biol. Bull., vol. 4, pp. 99-118, 6 figs.

MELIS, A.

1935. Tisanotteri Italiana. Studio anatomico-morfologico e biologico del Liottripide dell'olivo ("*Liothrips oleae*" Costa). Redia, vol. 21, pp. 1-188, 44 text figs., 8 pls.

MERCER, W. F.

1900. The development of the wings in the Lepidoptera. Journ. New York Ent. Soc., vol. 8, pp. 1-20, 5 pls.

MILLOT, J.

1938. Le développement et la biologie larvaire des Oncodidés (Cyrtidés), diptères parasites d'araignés. Bull. Soc. Zool. France, vol. 63, pp. 162-181, 183-197, 14 figs.

MÖBUSZ, A.

1897. Ueber den Darmkanal der *Anthrenus*-Larve, nebst Bemerkungen zur Epithelregeneration. Arch. Naturg., Jahrg. 63, vol. 1, pp. 89-128, 3 pls.

MÜLLER, K.

1927. Beiträge zur Biologie, Anatomie, Histologie und inneren Metamorphose der Thrips-Larven. Zeitschr. wiss. Zool., vol. 130, pp. 251-303, 27 text figs., 1 pl.

MUNSCHEID, LILI.

1933. Die Metamorphose des Labiums der Odonaten. Zeitschr. wiss. Zool., vol. 143, pp. 201-240, 44 figs.

MURPHY, HELEN E.

1922. The metamorphosis of may-fly mouth parts. Bull. Lloyd Library, No. 22, Ent. Ser. No. 2, 39 pp., 6 pls.

MURRAY, FLORENCE V., AND TIEGS, O. W.

1935. The metamorphosis of *Calandra oryzae*. Quart. Journ. Micr. Sci., vol. 77, pp. 405-495, 20 text figs., 5 pls.

NABERT, A.

1913. Die Corpora allata der Insekten. Zeitschr. wiss. Zool., vol. 104, pp. 181-358, 8 text figs., 5 pls.

NEEDHAM, J. G.

1911. Descriptions of dragonfly nymphs of the subfamily Calopteryginae. Ent. News, vol. 22, pp. 145-154, 2 pls.

NELSON, J. A.

1915. The embryology of the honey bee, 282 pp., 95 text figs., 6 pls. Princeton.

NESBITT, H. H. J.

1941. A comparative morphological study of the nervous system of the Orthoptera and related orders. Ann. Ent. Soc. Amer., vol. 34, pp. 51-81, 8 pls.

OERTEL, E.

1930. Metamorphosis of the honeybee. Journ. Morph., vol. 50, pp. 295-339, 4 pls.

PAOLI, G.

1938. Note sulla biologia e sulla filogenesi dei Meloidi (Coleoptera). Mem. Soc. Ent. Italia, vol. 16, pp. 71-96, 6 figs.

PARKER, H. L., AND SMITH, H. D.

1933. Additional notes on the strepsipteron *Eoxenos laboulbenei* Peyerimhoff. Ann. Ent. Soc. Amer., vol. 26, pp. 217-233, 2 pls.

1934. Further notes on *Eoxenos laboulbenei* Peyerimhoff with a description of the male. Ann. Ent. Soc. Amer., vol. 27, pp. 468-477.

PARKER, J. B., AND BÖVING, A. G.

1925. The blister beetle, *Tricrania sanguinipennis*—Biology, description of different stages and systematic relationship. Proc. U. S. Nat. Mus., vol. 64, 40 pp., 5 pls.

PATAY, R.

1939. Contribution a l'étude d'un Coleoptère [*Leptinotarsa decimlineata* (Say)]. Évolution des organes au cours du développement. 145 pp., 59 figs. Rennes.

- PAULI, M. E.  
 1927. Die Entwicklung geschnürter und zentrifugierter Eier von *Calliphora vomitoria* und *Musca domestica*. Zeitschr. wiss. Zool., vol. 129, pp. 483-540, 64 figs.
- PÉREZ, C.  
 1901. Histolyse des tubes de Malpighi et des glandes sericigènes chez la fourmi rousse. Bull. Soc. Ent. France for 1901, pp. 307-309.  
 1910. Recherches histologiques sur la métamorphose des Muscides, *Calliphora erythrocephala* Mg. Arch. Zool. Exp. Gén., ser. 5, vol. 4, pp. 1-274, 62 text figs., 16 pls.  
 1912. Observations sur l'histolyse et l'histogénèse dans la métamorphose des Vespides (*Polistes gallica* L.). Acad. Roy. Belgique, Mém., ser. 2, vol. 3, 101 pp., 10 pls.
- PERKINS, R. C. L.  
 1905. Leaf-hoppers and their natural enemies (Epipyropidae). Bull. Hawaii Sugar Planters' Assoc. Exp. Stat., vol. 1, pt. 2, pp. 75-85.  
 1918. The assembling and pairing of *Stylops*. Ent. Month. Mag., vol. 54, pp. 121-191.
- PETERSON, A.  
 1951. Larvae of insects, Part II, 416 pp., 104 pls. Columbus, Ohio.
- PFEIFFER, ISABELLE WEED.  
 1939. Experimental study of the function of the corpora allata in the grasshopper, *Melanoplus differentialis*. Journ. Exp. Zool., vol. 82, pp. 439-461.  
 1942. Suppression of metamorphosis in the grasshopper, *Melanoplus differentialis*. Anat. Rec., vol. 84, p. 486.  
 1945. Effect of the corpora allata on the metabolism of adult female grasshoppers. Journ. Exp. Zool., vol. 99, pp. 183-233.
- PFLUGFELDER, O.  
 1937. Bau, Entwicklung und Funktion der Corpora allata und cardiaca von *Dixippus morosus* Br. Zeitschr. wiss. Zool., vol. 149, pp. 477-512.  
 1938. Weitere experimentelle Untersuchungen über die Funktion der Corpora allata von *Dixippus morosus* Br. Zeitschr. wiss. Zool., vol. 151, pp. 149-191, 30 figs.  
 1947. Über die Ventraldrüsen und einige andere inkretorische Organe des Insektenkopfes. Biol. Zentralbl., vol. 66, pp. 211-235, 32 figs.
- PICKLES, A.  
 1931. On the metamorphosis of the alimentary canal in certain Ephemeroptera. Trans. Roy. Ent. Soc. London, vol. 79, pp. 263-279, 2 pls.
- POSSOMPÈS, B.  
 1950. Rôle de cerveau au cours de la métamorphose de *Calliphora erythrocephala* Meig. C. R. Acad. Sci., Paris, vol. 231, pp. 594-596.
- POULSON, D. F.  
 1950. Development of the ring gland in *Drosophila*. In Demerec, Biology of *Drosophila*, pp. 234-238.
- POYARKOFF, E.  
 1910. Recherches histologiques sur la métamorphose d'un Coléoptère (La galéruque de l'orme). Arch. Anat. Micr., vol. 12, pp. 333-474, 69 figs.  
 1914. Essai d'une théorie de la nymphe des insectes holomelaboles. Arch. Zool. Exp. Gén., vol. 54, pp. 221-265.

- PRIESNER, H.  
1926. Die Thysanopteren Europas, 755 pp., 5 pls. Wien.
- PRYOR, M. G. M.  
1951. On the abdominal appendages of larvae of Trichoptera, Neuroptera, and Lepidoptera, and the origins of jointed limbs. *Quart. Journ. Micr. Sci.*, vol. 92, pp. 351-376, 30 figs.
- REITH, F.  
1925. Die Entwicklung des *Musca*-Eies nach Ausschaltung verschiedener Eibereiche. *Zeitschr. wiss. Zool.*, vol. 126, pp. 181-238, 39 figs.
- RENGEL, C.  
1897. Über die Veränderung des Darmepithels bei *Tenebrio molitor* während der Metamorphose. *Zeitschr. wiss. Zool.*, vol. 62, pp. 1-60, 1 pl.  
1898. Über die periodische Abstossung und Neubildung des gesammten Mitteldarmepithels bei *Hydrophilus*, *Hydrous* und *Hydrobius*. *Zeitschr. wiss. Zool.*, vol. 63, pp. 440-455, 1 pl.
- RICHARDS, A. G.  
1951. The integument of arthropods, 411 pp., 65 figs. Minneapolis.
- RILEY, C. V.  
1876. On the larval characters and habits of the blister-beetles belonging to the genera *Macrobasis* Lec. and *Epicauta* Fabr., with remarks on other species of the family Meloidae. *Trans. Acad. Sci. St. Louis*, vol. 3, pp. 544-562.
- ROBERTSON, C. W.  
1936. The metamorphosis of *Drosophila melanogaster*, including an accurately timed account of the principal morphological changes. *Journ. Morph.*, vol. 59, pp. 351-399, 4 pls.
- ROEDER, K. D.  
1953. *Insect physiology*, 1100 pp., 257 figs. New York and London.
- RUSS, E. A. L.  
1908. Die postembryonale Entwicklung des Darmkanals bei den Trichopteren (*Anabolia laevis* Zett.). *Zool. Jahrb., Anat.*, vol. 25, pp. 675-770, 4 pls.
- SAMSON, KATHARINA.  
1908. Über das Verhalten der Vasa Malpighii und die excretorische Funktion der Fettzellen während der Metamorphose von *Heterogenea limacodes* Hufn. *Zool. Jahrb., Anat.*, vol. 26, pp. 403-422, 2 pls.
- SCHARRER, BERTA.  
1946a. The role of the corpora allata in the development of *Leucophaea maderae* (Orthoptera). *Endocrinology*, vol. 38, pp. 35-45, 4 figs.  
1946b. The relationship between corpora allata and reproductive organs in adult *Leucophaea maderae* (Orthoptera). *Endocrinology*, vol. 38, pp. 46-55, 4 figs.
- SCHARRER, BERTA, AND SCHARRER, E.  
1944. Neurosecretion. VI. Comparison between the intercerebralis-cardiacum-allatum system of the insects and the hypothalamo-hypophyseal system of the vertebrates. *Biol. Bull.*, vol. 87, pp. 242-251.
- SHELL, S. C.  
1943. The biology of *Hadronotus ajax* Girault (Hymenoptera-Scelionidae), a parasite in the eggs of the squash-bug (*Anasa tristis* De Geer). *Ann. Ent. Soc. Amer.*, vol. 36, pp. 625-635, 2 pls.

## SCHMIDT, ELSE.

1929. Die Histolyse und Histogenese der Muskulatur von *Psychoda alternata* Say. Zeitschr. Morph. Ökol. Tiere, vol. 13, pp. 117-143, 8 figs.

## SCHOENEMUND, E.

1912. Zur Biologie und Morphologie einiger *Perla*-Arten. Zool. Jahrb., Anat., vol. 34, pp. 1-56.

## SCHRADER, SALLY H.

1924. Reproduction in *Acroschismus wheeleri* Pierce. Journ. Morph., vol. 39, pp. 157-205, 4 pls.

## SILVESTRI, F.

1904. Contribuzione alla conoscenza della metamorfosi e dei costumi della *Lcbia scapularis* Fourc. Redia, vol. 2, pp. 68-84, 5 pls.
1920. Contribuzione alla conoscenza dei Termitidi e Termitofili dell'Africa Occidentale. II. Termitofili. Boll. Lab. Zool. Gen. e Agr. R. Scuola Sup. Agr. in Portici, vol. 14, pp. 265-319.
1940. Studi sugli "Strepsiptera." (Insecta.) II. Descrizione, biologia e sviluppo postembryonale dell' *Halictophagus tettigometrae* Silv. Boll. Lab. Zool. Gen. e Agr. Fac. Agr. Portici, vol. 32, pp. 11-48, 34 figs.

## SMITH, H. S.

1912. The chalcidoid genus *Perilampus* and its relation to the problem of parasite introduction. U. S. Bur. Ent., Techn. Ser., Bull. 19, pt. 4, pp. 33-69, 8 figs.
1917. The habit of leaf-oviposition among the parasitic Hymenoptera. Psyche, vol. 24, pp. 63-68, 4 figs.

## SMITH, LUCY W.

1913. The biology of *Perla immarginata* Say. Ann. Ent. Soc. Amer., vol. 6, pp. 203-212.

## SMRECYNSKI, S.

1938. Entwicklungsmechanische Untersuchungen am Ei des Käfers *Agelastica abni* L. Zool. Jahrb., Zool. Physiol., vol. 59, pp. 1-58, 21 figs.

## SNODGRASS, R. E.

1931. Morphology of the insect abdomen. Part I. General structure of the abdomen and its appendages. Smithsonian Misc. Coll., vol. 85, No. 6, 128 pp., 46 figs.
1935. The history of an insect's stomach. Ann. Rep. Smithsonian Inst. for 1933, pp. 363-387, 15 figs.
1953. The metamorphosis of a fly's head. Smithsonian Misc. Coll., vol. 122, No. 3, 25 pp., 7 figs.

## SOROKINA-AGAFONOWA, MARIE.

1924. Das Verhalten des peripheren Nervensystems der Insekten in der Metamorphose. Zeitschr. Anat. und Entwickl., vol. 74, pp. 318-337, 2 pls.

## SPIETH, H. T.

1933. The phylogeny of some mayfly genera. Journ. New York Ent. Soc., vol. 41, pp. 55-86, 327-390, 14 pls.

## STEIN, F.

1838. Entwicklungs-Geschichte mehrerer Insectengattungen aus der Ordnung Neuropteren. Arch. Naturg., vol. 4, pp. 315-333, 1 pl.

## SUTER, P.

1932. Untersuchungen über Körperbau, Entwicklungsgang und Rassendifferenzierung der Kommaschildlaus, *Lepidosaphes ulmi* L. Mitt. Schweiz. ent. Ges., vol. 15, pp. 347-420, 64 figs.

## SWEETMAN, H. L., AND WHITTEMORE, F. W.

1937. The number of molts of the firebrat (Lepismatidae, Thysanura). Bull. Brooklyn Ent. Soc., vol. 32, pp. 117-120.

## TERRE, L.

1899. Contribution a l'étude de l'histolyse et de l'histogénese du tissu musculaire chez l'abeille. C. R. Soc. Biol. Paris, vol. 51, pp. 896-898.

## THOMSEN, ELLEN.

1940. Relation between corpus allatum and ovaries in adult flies (Muscidae). Nature, vol. 145, pp. 28-29.
1942. An experimental and anatomical study of the corpus allatum in the blow-fly *Calliphora erythrocephala* Meig. Vidensk. Medd. Dansk Naturhist. Foren., vol. 106, pp. 317-405, 4 text figs., 12 pls.
1948. Effect of removal of neurosecretory cells in the brain of adult *Calliphora erythrocephala* Meig. Nature, vol. 161, pp. 439-440.

## THOMSEN, M.

1943. Effect of corpus cardiacum and other insect organs on the color-change of the shrimp, *Leander adspersus*. K. Danske Vidensk. Selsk. Biol. Medd., vol. 19, No. 4, 38 pp., 4 pls.
1951. Weismann's ring and related organs in larvae of Diptera. K. Danske Vidensk. Selsk. Biol. Skr., vol. 6, No. 5, 32 pp., 14 pls.

## THORPE, W. H.

1931. The biology, post-embryonic development and economic importance of *Cryptochaetum iceryae* (Diptera, Agromyzidae) parasitic on *Icerya purchasi* (Coccidae, Monophlebinae). Proc. Zool. Soc. London for 1931, pp. 927-971.
1938. Further experiments on olfactory conditioning in a parasitic insect. The nature of the conditioning process. Proc. Roy. Soc. London, B, vol. 126, pp. 370-397.
1939. Further studies on pre-imaginal olfactory conditioning in insects. Proc. Roy. Soc. London, B, vol. 127, pp. 424-433.
1941. The biology of *Cryptochaetum* (Diptera) and *Eupelmus* (Hymenoptera) parasites of *Aspidoproctus* (Coccidae) in East Africa. Parasitology, vol. 33, pp. 149-168, 26 figs.

## TIEGS, O. W.

1922. Researches on the insect metamorphosis. Part I. On the structure and post-embryonic development of a chalcid wasp, *Nasonia*. Part II. On the physiology and interpretation of the insect metamorphosis. Trans. and Proc. Roy. Soc. South Australia, vol. 46, pp. 319-527, 16 pls.

## TILLYARD, R. J.

1917. The biology of dragonflies, 396 pp., 188 text figs., 4 pls. Cambridge.
1926. The insects of Australia and New Zealand, 560 pp., 42 pls. Sydney.

## TIMBERLAKE, P. H.

1912. Experimental parasitism: A study of the biology of *Linnerium validum* (Cresson). U. S. Bur. Ent., Techn. Ser., Bull. 19, pt. 5, pp. 71-92, 10 figs.

TOWER, W. L.

1903. The origin and development of the wings of Coleoptera. Zool. Jahrb., Anat., vol. 17, pp. 517-572, 8 text figs., 7 pls.

TOYAMA, K.

1902. Contributions to the study of silk-worms, I. On the embryology of the silk-worm. Bull. College Agr., Tokyo Imp. Univ., vol. 5, pp. 73-118.

VACHON, M.

1938. Recherches anatomiques et biologiques sur la reproduction et la développement des pseudoscorpions. Ann. Sci. Nat., ser. 11, Zool., vol. 1, pp. 1-207, 85 figs.
1950. Remarques préliminaires sur l'alimentation, les organes chélicériens, le biberon et la tétine de l'embryon du scorpion: *Ischnurus ochropus* C. L. Koch (Scorpionidae). Arch. Zool. Exp. Gén., vol. 86, pp. 137-156, 9 figs.
1953. The biology of scorpions. Endeavour, vol. 12, No. 46, pp. 80-89, 16 figs.

VAN DER KLOOT, W. G., AND WILLIAMS, C. M.

- 1953a. Cocoon construction by the *Cecropia* silkworm I. The role of the external environment. Behaviour (Leiden), vol. 2, pp. 141-156, 8 figs.
- 1953b. Cocoon construction by the *Cecropia* silkworm II. The role of the internal environment. Behaviour (Leiden), vol. 3, pp. 157-174, 12 figs.

VAN REES, J.

1889. Beiträge zur Kenntnis der inneren Metamorphose von *Musca vomitoria*. Zool. Jahrb., Anat., vol. 3, pp. 1-134, 14 text figs., 2 pls.

VAYSSIÈRE, A.

1882. Recherches sur l'organisation des larves des Ephémérines. Ann. Sci. Nat., ser. 6, Zool., vol. 13, pp. 1-137, 11 pls.
1890. Monographie zoologique et anatomique du genre *Prosoptestoma*. Ann. Sci. Nat., ser. 7, Zool., vol. 9, pp. 19-87, 4 pls.
1934. Étude anatomique des larves nymphales des *Bactisca obesa* et *carolina*. Ann. Sci. Nat., ser. 10, Zool., vol. 17, pp. 381-406, 2 pls.

VERSON, E.

1905. Zur Entwicklung des Verdauungskanal bei *Bombyx mori*. Zeitschr. wiss. Zool., vol. 82, pp. 523-600, 4 pls.

WADSWORTH, J. T.

1915. On the life-history of *Aleochara bilineata* Gryll., a staphylinid parasite of *Chortophila brassicae* Bouché. Journ. Econ. Biol., vol. 10, pp. 1-27, 2 pls.

WAHL, B.

1901. Über die Entwicklung der hypodermalen Imaginalscheiben im Thorax und Abdomen der Larve von *Eristalis* Latr. Zeitschr. wiss. Zool., vol. 70, pp. 171-191, 4 text figs., 1 pl.

WEBER, H.

1930. Biologie der Hemipteren, 543 pp., 329 figs. Berlin.
1931. Lebensweise und Umweltbeziehungen von *Trialeurodes vaporariorum* (Westwood) (Homoptera-Aleurodina). Zeitschr. Morph. Ökol. Tiere, vol. 23, pp. 575-753, 59 figs.

1934. Die postembryonale Entwicklung der Aleurodinen (Hemiptera-Homoptera). Zeitschr. Morph. Ökol. Tierre, vol. 29, pp. 268-305, 14 figs.
- WEISMANN, A.  
1864. Die nachembryonale Entwicklung der Musciden nach Beobachtungen an *Murca vomitoria* und *Sarcophaga carnaria*. Zeitschr. wiss. Zool., vol. 14, pp. 187-336, 7 pls.
- WELCH, P. S.  
1916. Contribution to the biology of certain aquatic Lepidoptera. Ann. Ent. Soc. Amer., vol. 9, pp. 159-190, 3 pls.
- WHEDON, A. D.  
1927. The structure and transformation of the labium of *Anax junius*. Biol. Bull., vol. 53, pp. 286-301, 2 pls.
- WIGGLESWORTH, V. B.  
1933. The physiology of the cuticle and of ecdysis in *Rhodnius prolixus* (Triatomidae Hemiptera); with special reference to the function of the oenocytes and the dermal glands. Quart. Journ. Micr. Sci., vol. 76, pp. 269-318, 15 figs.  
1936. The function of the corpus allatum in the growth and reproduction of *Rhodnius prolixus* (Hemiptera). Quart. Journ. Micr. Sci., vol. 79, pp. 91-121.  
1940. The determination of characters at metamorphosis in *Rhodnius prolixus* (Hemiptera). Journ. Exp. Biol., vol. 17, pp. 201-222, 12 text figs., 1 pl.  
1942. The significance of "chromatic droplets" in the growth of insects. Quart. Journ. Micr. Sci., vol. 83, pp. 141-152, 3 figs.  
1948. The functions of the corpus allatum in *Rhodnius prolixus* (Hemiptera). Journ. Exp. Biol., vol. 25, pp. 1-14.  
1951a. Hormones and the metamorphosis of insects. Endeavour, vol. 10, No. 37, 5 pp., 14 figs. (Reprinted in Ann. Rep. Smithsonian Inst. for 1951, pp. 313-318, 4 pls., 1952.)  
1951b. Source of moulting hormone in *Rhodnius*. Nature, vol. 168, pp. 558-559.  
1952a. The thoracic gland in *Rhodnius prolixus* (Hemiptera) and its role in moulting. Journ. Exp. Biol., vol. 29, pp. 561-570.  
1952b. Hormone balance and the control of metamorphosis in *Rhodnius prolixus* (Hemiptera). Journ. Exp. Biol., vol. 29, pp. 620-631.  
1953a. Hormones and metamorphosis, with special reference to hemimetabolic insects. Trans. IX Internat. Congr. Ent., Amsterdam, vol. 2, pp. 51-57.  
1953b. The origin of sensory neurones in an insect, *Rhodnius prolixus* (Hemiptera). Quart. Journ. Micr. Sci., vol. 94, pp. 93-112, 16 figs.
- WILLIAMS, C. M.  
1947. Physiology of insect diapause. II. Interaction between the pupal brain and prothoracic glands in the metamorphosis of the giant silkworm, *Platysamia cecropia*. Biol. Bull., vol. 93, pp. 89-98, 2 pls.  
1948. Physiology of insect diapause. III. The prothoracic glands in the *Cecropia* silkworm, with special reference to their significance in embryonic and post-embryonic development. Biol. Bull., vol. 94, pp. 60-65, 2 figs.

1952. Physiology of insect diapause. IV. The brain and prothoracic glands as an endocrine system in the *Cecropia* silkworm. Biol. Bull., vol. 103, pp. 120-138, 11 figs.

Wu, C. F.

1923. Morphology, anatomy, and ethology of *Nemoura*. Bull. Lloyd Library, No. 23, Ent. Ser. No. 3, 81 pp. 16 pls.

