OUTLINES OF ENTOMOLOGY

by

A. D. IMMS, D.Sc., F.R.S.
Reader in Entomology and Fellow of Downing College,
University of Cambridge

WITH 96 ILLUSTRATIONS

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PREFACE

THIS book is intended for anyone who is willing to take sufficient pains to acquire an elementary knowledge of entomology as a branch of general zoology. It is consequently written more especially for the student who embarks upon a university training in zoology or agriculture in preparation for a career. It will further serve as a preliminary manual for the would-be professional entomologist during his first year's course. The more progressive devotees to biology in public schools may also find this book of interest and assistance.

The author is not alone in the belief that there is considerable need for a book of this kind in the English language. It represents his ideas as to what constitutes the fundamentals of the subject and is based upon nearly forty years of experience at home and abroad.

It is recommended to omit, on first reading, those sections dealing with the muscular system, the smaller orders and the relationships of insects. Subsequently, when the general groundwork has been explored, the sections referred to will be more readily assimilated.

The reader will find a few discrepancies between statements made in this book and the author's *General Textbook of Entomology*. These, it may be added, will be rectified when circumstances allow of the publication of a revised edition of the last-named work.

While most of the illustrations are original a few have been borrowed, and chiefly from Wigglesworth's *Principles of Insect Physiology*.

The chief features of the second edition are the provision of an 'Appendix on Literature' and some minor alterations.

July 1944

A. D. IMMS

CONTENTS

I. INTRODUCTION

INSECTS are segmented animals, breathing by means of air-tubes or tracheae, and have the body divided into head, thorax and abdomen. The head is the sensory and feeding centre. It bears the mouth-parts together with a single pair of antennae homologous with the antennules of Crustacea: compound eyes are usually present and often simple eyes or ocelli. The thorax is the locomotory centre and carries three pairs of legs and usually two pairs of wings. The abdomen is the metabolic and reproductive centre: it is here that digestion and excretion take place together with those functions directly connected with the organs of sex. After emergence from the egg the growth of an insect is seldom direct and a metamorphosis is, therefore, usually undergone.

The number of known kinds, or species, of insects is difficult to compute but it certainly exceeds that of the whole of the rest of the animal kingdom. That approximately 700,000 different insects have been named and described is probably a conservative estimate. Usually several thousand new species are described in a single year, but notwithstanding this rate of discovery there is no doubt that the numbers yet to be brought to light exceed those of all the known kinds. The single order Coleoptera, or beetles, alone comprises over 250,000 named species according to the latest world catalogue. Even the one family Curculionidae, or weevils, includes nearly 40,000 known species, while the Carabidae, or ground beetles number about 25,000 kinds.

This remarkable capacity for differentiation shown by insects does not lend itself to exact analysis. It is, however, a matter of interest to consider what attributes have most likely helped the members of this class to attain their dominant position in the animal kingdom. The most significant of these attributes will be briefly referred to, but not necessarily in their order of importance, which will vary in different groups.

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

(*b*) *Adaptability.* No other single class of animals has so thoroughly invaded and colonized the globe as the Insecta. Their distribution ranges from the poles to the equator: every species of phanerogamic plant provides food for one or more kinds of insect, while decomposing organic materials attract and support many thousands of different species. A very large number live as parasites on or within the bodies of other insects and of some very different animals including vertebrates. The soil and fresh waters support their own populations of insect life. Great cold is not an impassable barrier since there are kinds that can withstand temperatures of about — 50° C. At the opposite temperature range there are those kinds that are denizens of hot springs that exceed 40° C. and of deserts whose mid-day surface temperature may be twenty degrees higher. Even the most unpromising substances provide sustenance and environment for some kinds of insects. Thus, the petroleum pools of California are inhabited by the larva of a fly of the family Ephydridae. Beetles are known to be capable of living and breeding in such media as argol (containing 80 per cent potassium bitartrate), opium, Cayenne pepper, sal ammoniac and strychnine.

(*c*) *Size*. The usually small size of insects confers on them many advantages not possessed by larger animals. The quantity of food required to nourish them individually is in itself very small: many are, therefore, able to live on such insignificant amounts of nourishment as would be useless for larger creatures. Huge populations of minute forms of insect life utilize media neglected by other animals. Their small size enables them to occupy niches in the environment that afford security from a whole range of enemies. Thus, one or more leaf-mining larvae will develop in the tissue between the upper and lower epidermal layers of a single small leaf: a weevil will undergo its complete development in one small seed of the gorse and a very moderate-sized fungus will support a whole population of small beetles and fly larvae. Thus, it will be noted that the food medium of many insects also provides, at the same time, lodging and concealment from enemies.

It has been said that some insects are smaller than the largest Protozoa and others are larger than the smallest Vertebrata. There are, indeed, minute hymenopterous parasites only 0·2 mm. long, while at the other extreme are such creatures as the bulky Goliath Beetle with a length up to 120 mm. They are exceptional types and there are certain disadvantages attendant upon the lives of both the minute and the gigantic forms of the insect world. That the vast majority of insects are of small or very moderate size is a matter of common observation and one of the reasons for their dominance is the factor of size. Very small insects soon become helpless should they come under the powerful influence of surface tension. In other words, if they become wetted the weight of the encompassing water will soon exhaust their efforts in freeing themselves. Thus almost all the minute forms of other animals avoid this complication by living permanently in water or other fluid media. Very large insects are, in general, specialized end-developments of the stocks to which they belong. As with elephants, whales and the great reptiles of the past, these monsters are members of declining groups. Here and there relatively gigantic forms occur, for example, among beetles, grasshoppers, water bugs, moths and fossil dragon-flies, but they constitute a relatively insignificant numerical population among their own groups. When an insect exceeds a diameter of about 2 cm. its method of respiration is liable to incommode it and make it sluggish—further increase in bulk would make it too inert to survive competition with other creatures. It needs to be borne in mind that in tracheal respiration the exchange of gases takes place in the ultimate capillaries or tracheoles. An appreciable increase in the diameter of an insect will tend to lengthen these tracheoles proportionately. The respiratory exchange is effected by the physical process of diffusion and, as J. B. S. Haldane has expressed it, gases ' diffuse easily through very small distances, not many times longer than the average length travelled by a gas molecule between collisions with other molecules '. Now when the relatively vast distance of nearly 1 cm. from the outer air becomes involved shortage of oxygen is liable to supervene. Hence it will be noted that very few insects assume a diameter greater than about half an inch. In many notably large insects this difficulty is avoided by a great extension of body-length with but little enlargement of diameter. Thus the giant stick insect *Pharnacia serratipes* measures up to 260 mm. long but retains a proportionately attenuated form. Some of the great fossil dragon-flies of Carboniferous times had wings exceeding 2 feet in expanse but with typically slender bodies. The giant Noctuid moth *Erebus agrippina* has a wing spread of 280 mm., but its slender body is no more than 55 mm. long, and the same applies to the giant Atlas moths and the Ornithoptera butterflies of the Orient.

(*d*) *The Skeleton.* The skeleton of insects, like that of other arthropods, is primarily an exoskeleton, and this feature has undoubtedly proved an invaluable aid to its possessors in the long course of their evolution. Its construction in the form of a series of jointed tubes that enclose the body and appendages is adapted to give a much greater power of resistance to bending than a comparable skeleton of a vertebrate. The two cases have been contrasted by the Russian writer S. S. Chetverikov. On referring to Fig. 1, A represents a cross-section of a limb with the diameter of its inner area *d*, say, $\frac{4}{5}$ that of the outer diameter. At B and C are comparable cross-sections of limbs with the skeleton axial instead of being peripheral as in A. On the theory of the resistance of materials the modulus of resistance to bending in a solid cylinder and in a hollow one is given by the two formulae

$$M = \frac{\pi D^3}{32} \text{ and } M_1 = \frac{\pi (D_1{}^4 - d^4)}{32 D_1}$$

where M and M_1 are the respective moduli : D is the diameter of the endoskeleton : D_1 is the outer diameter of the exoskeleton and *d* is the diameter of the area enclosed by the latter. It is assumed that the diameter of the limb is the same in A and B, the area of the cross-section of the skeleton and muscles being equal in both cases, then the limb with the solid axial skeleton will appear to be nearly three times weaker than that with the hollow peripheral skeleton. If it be calculated what diameter the cross-section of the solid axial skeleton would have to be in order that, with the same size of limb, its strength would be equal in the two cases, it will be revealed that the skeleton must be 84 per cent of the diameter of the whole of the cross-section (C). Under such conditions it will be evident that very little space is left for any musculature.

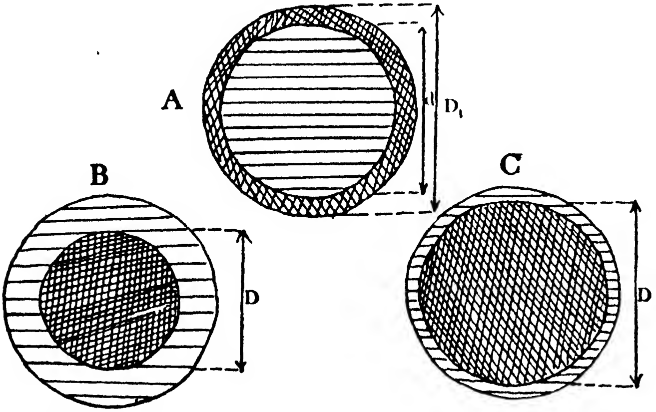

FIG. 1.—DIAGRAM OF CROSS-SECTIONS OF LIMBS ; FROM CHETVERIKOV
A, exoskeleton with diameter of the internal area $d = \frac{4}{5}$ of the external diameter D_1. B and C, endoskeletons. (Skeleton cross-hatched : musculature, &c., horizontal lines)

The insect skeleton, therefore, combines great strength with lightness. Composed as it is of an amazingly plastic material, it has lent itself to the most varied processes of modification under the influence of evolution. Increased deposition of cuticular substance has occurred in endless ways and in adaptation to manifold requirements. Especially to be noted are the immensely varied developments of form and size in the head and jaws : the growth of horns, spines and other processes : of bristles and of scales : of membranous wings and horny elytra : of stout fossorial legs : of needle-like ovipositors, and so forth. It is, furthermore, the exoskeleton that has afforded the scope for the development of the innumerable structural characters that form the basis of the enormous amount of species differentiation that prevails among insects. The protective value of the exoskeleton is also considerable. With the development of tracheal respiration the thinness of cuticle associated with cutaneous breathing is no longer necessary. The acquisition of a thickened impermeable cuticle, as a guard against undue water-loss, has played an important part in enabling insects to become the dominant class of terrestrial invertebrates.

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

II. ANATOMY AND PHYSIOLOGY

THE INTEGUMENT AND ITS DERIVATIVES

The Integument (Fig. 2). The cellular layer of the integument is the *epidermis* (or hypodermis): internally it is bounded by a very thin *basement membrane.* The epidermis secretes the *cuticle,* which is also present as a lining to the fore and hind intestine, to the tracheae and to the other parts that are similarly formed by ingrowth of the ectoderm. Typically, the cuticle is divisible into three layers.

(1) The *epicuticle,* less than 1μ in thickness, is formed of a substance termed *sclerotin* (or cuticulin): in many insects it renders the cuticle impermeable to water.

(2) The *exocuticle,* a much thicker layer composed of chitin and a protein. It is impregnated with amber-coloured *sclerotin,* often together with melanin.

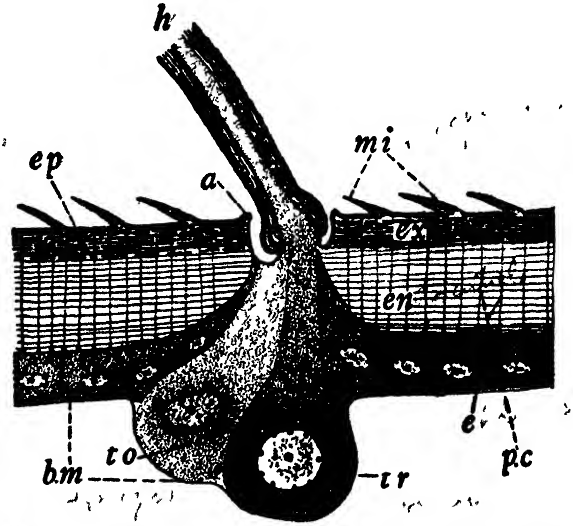

FIG. 2.—INTEGUMENT OF AN INSECT, SEMI-SCHEMATIC SECTION

a, alveolus; *b.m,* basement membrane; *e,* epidermis; *en,* endocuticle; *ep,* epicuticle; *ex,* exocuticle; *h,* hair; *mi,* microtrichia; *p.c.* pore canals; *to,* tormogen; *tr,* trichogen

(3) The *endocuticle* is similarly composed of chitin and a protein but is devoid of sclerotin and is very flexible. It is the thickest layer of the cuticle and shows a laminated structure. Vertical

pore-canals which seem to contain protoplasmic filaments from the epidermis are often visible.

The relative hardness of insect cuticle depends upon the extent to which the exocuticle is impregnated with sclerotin. At the intersegmental membranes of the body and its appendages flexibility is attained by the exocuticle being wanting from such areas or, if present, by its being divided into more or less separate blocks. In many of the smaller insects, and in numerous larvae, there is no exocuticle, the endocuticle being in contact with the epicuticle over the whole body.

Chitin is a nitrogenous polysaccharide with the empirical formula $(C_8H_{13}O_5N.)_x$. It rarely forms more than 50 per cent of the entire cuticle. It is resistant to concentrated alkalies and dilute acids: when heated in a saturated solution of potassium hydroxide at about 160° C. for twenty minutes it becomes converted into chitosan. After being well washed and immersed in a 0·2 per cent iodine in 1 per cent sulphuric acid, chitosan becomes rose-violet in colour. *Sclerotin* is insoluble in concentrated hydrochloric or sulphuric acids, but dissolves in caustic alkali. Little is known of its composition, but it is stated to be formed by the action of a phenol on a protein.

Integumentary Processes. These may be grouped into two categories as follows (Fig. 2).

1. Rigid, non-articulated outgrowths comprising microtrichia and spines.

Microtrichia are superficial, non-cellular, hair-like structures of minute size. They are formed entirely of cuticle and occur on the wings, for example, of many insects. *Spines* are heavily sclerotized thorn-like structures of multicellular origin. They are well seen on the legs of chafers and dor-beetles (*Geotrupes*). Spinous or non-articulated hairs are also sometimes present.

2. Movable articulated outgrowths whose essential feature is that each is attached basally by means of a ring of articular membrane. The latter may be depressed in a cuticular socket or *alveolus* or elevated on a tubercle. Articulated outgrowths may be classified into macrotrichia and spurs.

Macrotrichia or *setae* are hollow extensions of the exocuticle covered by a layer of epicuticle. Each is formed around a protoplasmic outgrowth from a single enlarged epidermal cell or *trichogen*: the socket is the product of a special formative cell or *tormogen*. Setae are of various types and they, together with their derivatives, include the following: A. *Clothing hairs* which cover the general surface of the body and its appendages. These may be branched and form compound or *plumose hairs*, as in many bees: or when specially stiff and hardened they form *bristles* that are well shown in Tachinid flies. B. *Scales* that are, morphologically, modified hairs, characteristic of adult Lepidoptera: they are also found among Collembola and in some Diptera and Coleoptera. Transitional forms between ordinary setae and scales are frequent. C. *Glandular setae* which function as outlets for the secretions of dermal glands: setae of this kind occur among caterpillars having irritant properties such as those of the Brown-tail moth (*Euproctis chrysorrhóea*) and its allies. D. *Sensory setae* which, in their simplest form, do not differ from clothing setae except in that each has an associated nerve connection near its origin in the integument. Sensory setae and their derivatives are considered later (p. 30). *Spurs* are multicellular in origin and are thick-walled structures found, more especially, on the tibiae of the legs.

Dermal Glands. These are usually modified single epidermal cells of secretory function, but, in some cases, they are multicellular; among other kinds they include wax glands, lac glands and moulting glands, which are dealt with in later chapters.

Apodemes. These are integumentary ingrowths which collectively form the *endoskeleton.* They are hardened processes which serve for the attachment of muscles and the support of other organs. In some insects the mouths of these tubular inflexions remain, but more usually apodemes become solid by the deposition of cuticular material. The endoskeleton of the head forms the *tentorium* (Fig. 3),

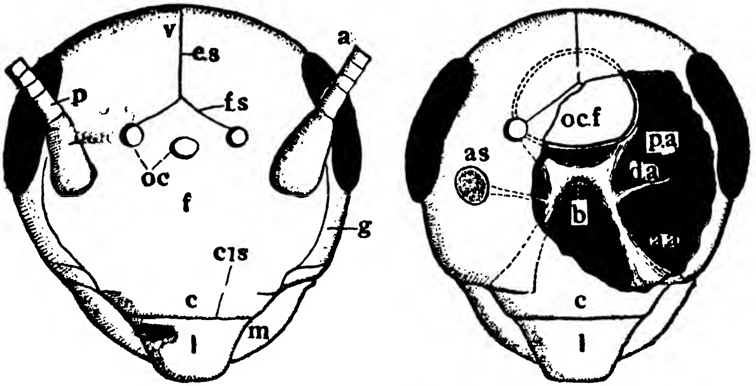

FIG. 3.—HEAD OF AN ORTHOPTEROUS INSECT: *right*, FIGURE WITH PART OF HEAD-WALL CUT AWAY

a, antenna; *a.a*, anterior, *d.a*, dorsal, and *p.a*, posterior arms of tentorium; *a.s*, antennal socket; *b*, body of tentorium; *c*, clypeus; *cl.s*, clypeo-labral suture; *e.s*, epicranial suture; *f*, frons; *f.s*, frontal suture; *g*, gena; *l*, labrum; *m*, mandible; *oc*, ocelli; *oc.f*, occipital foramen; *p*, pedicel; *s*, scape; *v*, vertex

which consists of *anterior* and *posterior arms* whose inner ends amalgamate to form the *body of the tentorium.* In addition, slender dorsal arms may be also present as in *Blatta.* The tentorium strengthens the head capsule, giv[illegible]tach[illegible] muscles, and supports the brain and oesophagus. In the thorax and abdomen (Fig. 21) there are dorsal apodemes or phragmas (*ph*), lateral apodemes (*pl. r.*) and sternal apodemes or apophyses (*a*).

SEGMENTATION AND THE BODY REGIONS

Segmentation. While the cuticle of an insect forms a continuous investment over the whole body, it remains flexible along certain definite and usually transverse lines. In these positions it is infolded and membranous in character. The body of an insect consequently has a jointed structure, which is termed segmentation owing to its being divided into successive rings known as *segments* or *somites*. The flexible infolded cuticle between adjacent segments is the *intersegmental membrane*, whose function is to allow of freedom of movement of the body.

Segmentation is not only manifested externally but it also involves certain of the inner organs. Thus, the segmental repetition of parts is shown, to a varying extent, in the nervous system, the heart, tracheal system and the body musculature.

The cuticle usually shows localized areas of hardening forming definite sclerotized plates or *sclerites*. Such plates are commonly separated by lines or narrow membranous areas termed *sutures*. Complete fusion of adjacent sclerites, resulting in the obliteration of the sutures, is common especially in the head among the higher orders of insects.

The Body Regions. The insect body is made up of twenty primitive segments which are grouped together to form three well-defined regions or *tagmata*—the head, the thorax, and the abdomen.

The Head is composed of six closely amalgamated segments forming a hard case or capsule. It exhibits but few indications of its segmental origin apart from the fact that it carries paired appendages. The head bears the organs of feeding and of special sense.

The Thorax is formed of three segments and bears the locomotory organs, e.g. legs and wings. It is connected with the head by an intersegmental region known as the *cervicum* or neck.

The Abdomen is composed of eleven original segments, but seldom more than ten are discernible. It is concerned with reproduction and the general metabolic processes.

The Divisions of a Segment. In many soft-bodied larvae, such as those of blow-flies and other Diptera, the cuticle is membranous and each segment is a simple ring without division into separate areas. In the majority of insects, however, a typical segment is divisible into four main regions, viz. a dorsal region or *tergum*, a ventral region or *sternum*, and, on either side, a lateral region or *pleuron*. The cuticle of each of these regions may be differentiated into separate sclerites. In this case, those composing the tergum are known as *tergites*, those of the sternum are termed *sternites* and those of the pleura are the *pleurites*.

The Appendages. In the embryo each segment may bear a pair of outgrowths or appendages which may be retained in post-embryonic life. An appendage is a jointed tube implanted in the pleuron of its side. Between each pair of joints or segments the cuticle is flexible and forms the articular membrane. On account of its jointed structure the whole or part of an appendage is movable by means of muscles. A typical insect appendage consists of a limb-base and a shaft. While the shaft is homologous with the telopodite of a Crustacean limb there is no certain evidence of a biramous condition in any pair of appendages of insects.

THE HEAD

The Head Capsule. The exterior of the head is formed of several sclerites which are amalgamated to form a hard compact case or *head capsule* (Fig. 8). The dorsal region is the *epicranium* which, in generalized insects, is divided by the median *epicranial suture*. Anteriorly this suture bifurcates into two arms or *frontal sutures*. The region below and in front of those sutures is the *frons* which bears the median ocellus: the distal limit of the frons is marked on either side by the origins of the anterior arms of the tentorium. Immediately anterior to the frons is the clypeus, to which the *labrum* or upper lip is hinged along the *clypeo-labral suture*. That part of the epicranium just above the frons, and between the compound eyes, is the *vertex*. Between the vertex and the neck is the *occiput*, while the side walls of the head, below and behind the eyes, are formed by the *genae*. Where each gena joins the clypeus it bears a facet for articulation with the ginglymus of the mandible and proximally the gena presents a cavity for the articulation of the mandibular condyle. Between the genae ventrally, and separating the labium from the occipital foramen, there is present in many beetles a median sclerite or *gula* (Fig. 82, c). The hind surface of the head is perforated by the *occipital foramen*, through which the nerve cord, oesophagus, &c., enter the thorax. Two types of head prevail among insects according to the inclination of the long axis and the position of the mouth-parts. In the *hypognathous type*, well seen in cockroaches, grasshoppers and flies, the long axis is vertical, or inclined backwards, with the mouth parts ventral. In the *prognathous type*, prevalent in many beetles, the long axis is more or less horizontal and the mouth-parts are placed anteriorly. These two types vary according to habits, especially feeding, and change from one type to another may occur in the same individual during metamorphosis.

The *antennae* are freely mobile appendages articulated with the head in front of or between the eyes. They often show marked differences in the two sexes, being deeply pectinated in the males of certain moths and plumose in male mosquitoes and midges. Functionally, antennae are sensory appendages bearing olfactory and tactile receptors. The antennae are movable by means of extrinsic muscles usually arising from the tentorium and inserted into the base of the enlarged first segment or *scape* (Fig. 3). Intrinsic muscles arising from the scape are inserted into the *pedicel* or second segment. The remaining divisions of the antennae are entirely without muscles, except in a few of the most primitive insects (e.g. *Campodea*, &c.).

The **Mouth-Parts** (Fig. 4) consist of a upper lip or *labrum*, the *labium* or lower lip, an anterior or upper pair of jaws termed *mandibles*, and a posterior or lower pair of jaws known as *maxillae.* Arising from the floor of the mouth is a median lobe or *hypopharynx*, and associated with the latter in the more primitive insects are small paired lobes, the *superlinguae.* The mouth parts vary in form to a greater extent than almost any other organs, the variation being correlated with the mode of feeding or other uses to which they may be subjected. While the majority of insects have biting or chewing mouth-parts, in the Hemiptera and certain Diptera they are greatly modified to form organs for piercing the tissues of animals and plants and sucking up the contained fluids. In mayflies and a considerable

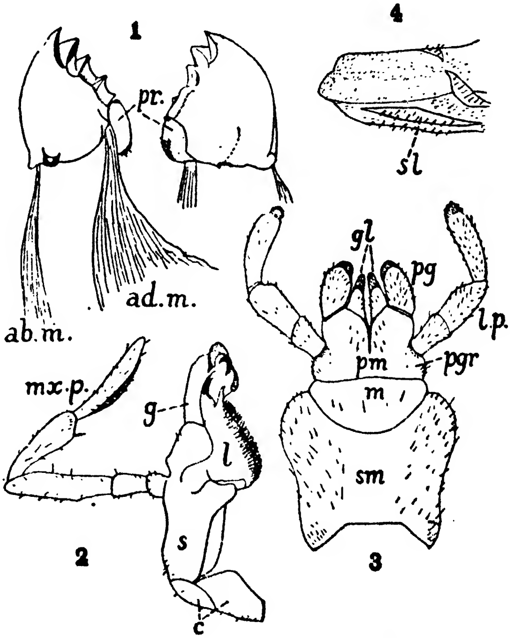

FIG. 4.—MOUTH-PARTS OF *BLATTA*

1, Mandibles: *ab.m*, *ad.m*, abductor and adductor muscles; *pr*, prostheca. 2, Maxilla: *c*, cardo; *g*, galea; *l*, lacinina; *mx.p*, maxillary palp; *s*, stipes. 3 Labium: *gl*, glossa; *l.p*, labial palp; *m*, mentum; *pg*, paraglossa; *pgr*, palpiger; *pm*, prementum; *sm*, submentum. 4, Hypopharynx: *sl*, rudiment of left superlingua number of moths the mouth-parts are atrophied and non-functional, no food being taken in the adult condition. The *labrum* has its ventral or pharyngeal surface provided with gustatory receptors which form the *epipharynx* or membranous roof of the mouth.

The *mandibles* are derivatives of the coxopodite of the typical arthropod limb. They are stout and tooth-like in chewing insects and are hinged by ball-and-socket joints to the genae, as already mentioned (p. 10). Each is moved by abductor and adductor muscles that arise from the head wall. In piercing insects the mandibles are drawn out into stylet-like processes, while among moths they are usually absent or vestigial. The *maxillae* are each composed of a proximal *cardo* or hinge which articulates with the head capsule just behind the mandibles. Distally it is jointed with the *stipes* which bears two lobes or endites, viz., an outer *galea* and an inner *lacinia*. Externally to the galea is the *maxillary palpus* which represents the telopodite of a walking leg. The part of the stipes bearing the palpus is often differentiated as a *palpifer*.

The labium (2nd maxillae) is formed by the union of a pair of appendages resembling maxillae. It is divisible into a free, distal *prementum* and a proximal *postmentum* which is largely attached to the head wall. The prementum in generalized insects shows evidence of its paired origin and is homologous with the stipites of the maxilla. Distally it bears the *labial palpi* and the *ligula*: the palpi often arise from side lobes of the prementum known as the *palpigers*. The ligula, when complete, consists of a pair of inner lobes or *glossae* and outer lobes or *paraglossae*: these two pairs of lobes are the counterparts of the laciniae and the galeae, respectively. The postmentum represents the fused cardines of the maxilla: as shown in Fig. 4 it is commonly secondarily divided into two plates—the *mentum* and the *submentum*. The *hypopharynx* receives the opening of the common salivary duct: in the Apterygota and in nymphs of may-flies well-developed side lobes or *superlinguae* are present. In other insects these lobes are usually reduced to vestiges or have disappeared.

The **Cervicum**, or neck, is the flexible intersegmental region between the head and thorax. Paired plates, the *cervical sclerites* (Fig. 21), are usually present in the membrane of the cervicum. The most important of these are the lateral cervical sclerites which act as a fulcrum between the head and the prothorax: distally they articulate with the occipital condyles of the head and proximally with episterna of the pro-thorax. Muscles arising from the head and pronotum are inserted on to the lateral sclerites to form a protractor mechanism of the head, the angle between the two lateral sclerites of each side being narrowed or widened, as the case may be.

THE THORAX

The three thoracic segments are termed respectively the *prothorax*, the *mesothorax* and *metathorax*. The thorax is seen in its simplest form in the Apterygota and in many larvae: in these examples the segments differ very little in size and proportions. With the acquisition of wings a correlated specialization results, the meso- and metathorax becoming more or less intimately fused. The prothorax is best developed in such cursorial insects as cockroaches and beetles, its tergum being developed as a large shield. The degree of development of the other segments is dependent upon the condition of the wings. The meso- and metathorax are about equally developed in termites and dragon-flies, where the two pairs of wings are very similar. In the Diptera, on the other hand, with but a single pair of wings, the mesothorax is the largest of the three components. In referring to the sclerites of the thorax the prefixes *pro*, *meso*, and *meta* are used with regard to those of a particular segment. Thus the protergum refers to the tergum of the prothorax and the mesepimeron to the epimeron of the mesothorax.

In many larvae and pupae, and in the adults of the more generalized insects, the tergum of each segment (Fig. 5, A) is a simple undivided plate or *notum*. In the wing-bearing segment of most insects a *postnotum* or *postscutellum* is developed as a sclerotization of the intersegmental membrane. The notum is typically divided into three sclerites, viz. the *prescutum*, the *scutum*, and the *scutellum*.

The *pleura* (Fig. 5) only acquire their full development of sclerites in winged insects. The pleural sclerites are formed from the subcoxae of the legs, which become incorporated into the thoracic wall and, in this way, provide the latter with rigidity and support. The subcoxa becomes divided into two chief pleurites, viz. an anterior *episternum* and a posterior *epimeron* which are demarcated and strengthened by an internal pleural ridge, indicated outwardly by the *pleural suture*. In a wing-bearing segment the pleuron develops dorsal and ventral articular processes for the wing and leg respectively. Both epimeron and episternum may undergo subdivision into upper and lower sclerites.

The *sternum* presents many modifications, often confusing to the elementary student. Thus, it may consist of a single sclerite (Fig. 5, C), as in many nymphs. Or this plate may be divided into a chief sclerite or *basisternum* and a *sternellum*. The latter bears a pair of apophyses (*a* in Figs. 5 and 21) that give attachment to important muscles; or the apophyses may be united by a common base forming a two-armed *furca*. A *poststernellum* is often present intersegmentally and gives origin to a median *spina* (*s* in Figs. 5 and 21).

The Legs. The legs present many adaptive modifications. Thus in mole crickets and dor beetles the fore legs are modified for burrowing and in the Mantidae they are used for seizing the prey. In many flies the legs are very slender and function as alighting rather than locomotory organs. In dragon-flies all the legs are used for grasping either when at rest, or for holding the prey, and are of little use for walking. In aquatic insects the hind legs are often specially adapted for swimming.

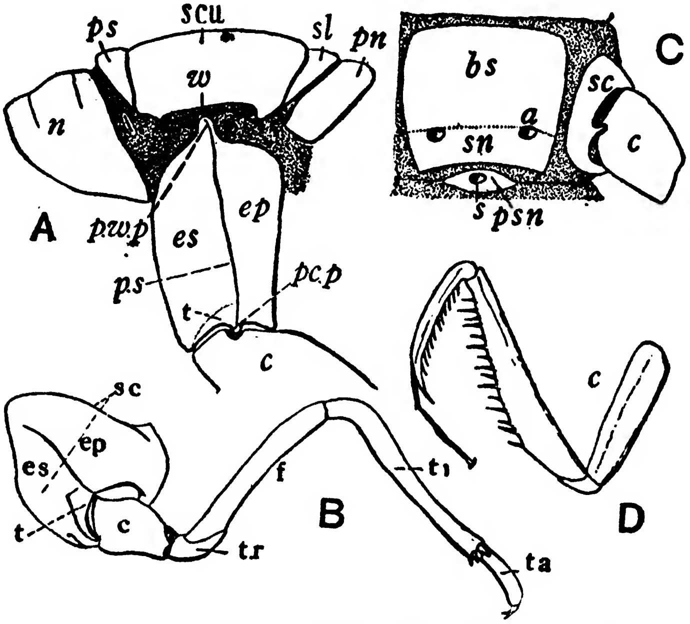

FIG. 5.—THORAX AND LEGS

A, Schematic figure showing pronotum *n*, mesonotum and mesopleuron. B, Hind leg and subcoxa of a nymphal Cicada (*adapted from* Snodgrass). C Schematic figure of a sternum of a wing-bearing segment. D, Fore leg of a Mantid. *a*, pit leading into sternal apophysis ; *bs*, basisternum ; *c*, coxa ; *ep*, epimeron ; *es*, episternum ; *f*, femur ; *p.c.p*, pleural coxal process ; *pn*, postnotum ; *ps*, prescutum ; *p.s*, pleural suture ; *psn*, poststernellum ; *p.w.p*, pleural wing process ; *s*, pit leading into spina ; *sc*, subcoxa ; *scu*, scutum ; *sl*, scutellum ; *sn*, sternellum ; *t*, trochantin ; *ta*, tarsus ; *ti*, tibia ; *w*, wing-base

The primitive *leg* (Fig. 5, B) consists of the following parts ; subcoxa, coxa, trochanter, femur, tibia, tarsus, and pretarsus. The *subcoxa* is retained among Apterygota and some immature Pterygota, but otherwise, as already noted, it gives rise to the pleurites. Small basal articular sclerites, and in particular the *trochantin*, are also derived from the subcoxa. The *coxa* is the functional limb-base and articulates with the *pleural coxal process* and sometimes also with the trochantin or with the sternum. In carnivorous insects with prehensile fore legs the fore coxae are greatly elongated. The *trochanter* articulates with the coxa, its femoral end being fixed. In dragon-flies each trochanter is divided, while among many parasitic Hymenoptera (Fig. 86, F) the apparent second trochanter is formed by the constricted proximal end of the femur. The *femur* is usually the largest component of the leg: it attains a great size in grasshoppers in order to accommodate the enlarged tibial muscles used in leaping. The *tibia* is generally slender and shaft-like, while the *tarsus* is commonly divided into two to five subsegments or *tarsomeres*, but retains its primitive undivided condition in some of the Apterygota and in many larvae. The end segment of the leg is the *pretarsus*, which is the counterpart of the dactylus of a crustacean limb. It is shown in its simple claw-like form in Protura, in some Collembola and in many larvae. In most insects paired claws are present, the original median claw usually having atrophied. Between the claws is a median pad or *arolium*: in many Diptera a lateral lobe or *pulvillus* is present beneath each claw. The pulvilli may co-exist with an arolium or with a median bristle termed the *empodium*.

The empodium (Fig. 22, B) arises from a median *flexor plate* (or *unguitractor*) which lies on the under side of the pretarsus and is partly inserted into the tarsus. The flexor plate gives attachment to the flexor (retractor) muscle of the claws. On the under side of the tarsal subsegments there are frequently pad-like organs, the *plantulae*, well seen in *Blatta*. The arolium and pulvilli are finely hairy below and are applied to smooth or steep surfaces, enabling their possessors to climb: the plantulae perform a similar function. The mechanism involved has been much discussed. In some cases the organs in question act as suckers and are kept applied to the surface by atmospheric pressure, the small amount of secretion present enabling an airtight union to be maintained. In others a sticky secretion is stated to enable cohesion between the organ and the surface to operate. In the bee and the blood-sucking bug *Rhodnius* the extremities of glandular hairs are applied so closely to the surface that in the presence of a small amount of secretion adhesion takes place or, in other words, the insect adheres by surface molecular forces.

Walking. During walking an insect moves its legs in two series so that the fore and hind legs of one side and the middle leg of the opposite side are carried forward. By this means the body is momentarily supported on a tripod formed by the remaining three legs. The fore leg acts as a tractor; having fixed its claws, it pulls the body forward; the middle leg supports and lifts the body on its own side, while the hind leg pushes the body forward and turns it. As a result of these movements the insect turns forward and outward, but when its centre of gravity falls outside the base of the triangle formed by the three supporting limbs the support is taken over by the other three legs and the long axis of the insect is turned to the opposite side. The result is that the insect, in reality, follows a zigzag course as it progresses.

Wings. Wings are thin two-layered expansions of the integument that originate as lateral folds of the margins of the terga of the meso- and metathorax. Early in development they are seen to be composed of the same layers as the integument, i.e. cuticle, epidermis, and basement membrane. The completed organs, however, are largely cuticular formations with the original epidermal layer greatly attenuated and often hard to detect. Wings are supported by a framework of narrow sclerotized tubes known as *veins*. During development the upper and lower epidermal layers meet and fuse, except along certain linear channels which determine the courses of the future veins and contain wing-nerves, tracheae, and blood. In the adult wing, circulation of the blood occurs along the main veins: many of the tracheae persist and sensilla are often abundant on the wing surfaces. While the Apterygota are primitively wingless creatures, many other insects have lost their original wings and become secondarily apterous. This condition is prevalent among certain types of individuals, as in aphides, soldier and worker ants and termites, and among ectoparasites such as lice and fleas. Among Diptera the mesothoracic wings alone persist, the hind pair being modified into sensory appendages termed *halteres*. Frequently the fore wings are modified for protecting the hind wings that are folded beneath. Thus, in cockroaches and other Orthoptera the fore wings have acquired a leathery texture and are known as *tegmina*; in many Hemiptera the basal half of the wing only is hardened, the remainder being membranous, such a wing being known as an *hemelytron*. In the Coleoptera the whole of each fore wing is horny, or otherwise sclerotized, forming an *elytron*.

In the more generalized insects the posterior flexible part of the hind wing becomes enlarged to form a fan-like expansion—the *anal lobe* or *vannus*, which is demarcated from the rest of the wing by the *anal* or *vannal furrow*. Among Diptera that part of the wing nearest to the body is marked off as a lobe or *alula*: in the blow-fly and many related forms the alula is especially large and forms the *calypter* which covers the haltere of its side. A small scale-like sclerite or *tegula* (Fig. 86, D, E) overlaps the base of the fore wing in Lepidoptera and some Hemiptera and in Hymenoptera. In many insects the wings of a side operate in unison owing to their being held together by a *wing-coupling apparatus*. This, in many moths, consists of a stout bristle or group of bristles, known as the *frenulum*, arising from the base of the hind wing and interlocking with a hook-like *retinaculum* on the underside of the fore wing (Fig. 81, B). In Hymenoptera a series of hooks or *hamuli* on the front margin of the hind wing engage with the reflexed hind border of the fore wing and, in this way, unite the two wings of a side (Fig. 86, B).

The wing surface may be smooth or clothed with microtrichia (Fig. 2) or macrotrichia ; or they may be partially scaled (mosquitoes) or wholly scaled as in Lepidoptera.

In the more primitive insects the wings show a tendency to be longitudinally ridged or plicated with intervening furrows—a condition well shown in Ephemeroptera. Veins disposed on the ridges are termed *convex veins* (indicated +) and those in the furrows are *concave veins* (—). The convex or concave nature of the veins is a character stressed by Lameere as affording evidence in determining their identity, especially in fossil forms where recourse to the tracheation is not possible.

Venation. The complete system of veins of a wing is termed the *venation.* By means of a study of the tracheae which precede and, in a general way, determine the positions and homologies of the veins in the lower orders, it is possible to formulate a generalized type of venation from which all others have presumably been derived (Fig. 6). The results from this method of approach have been amplified by evidence afforded by the study of the venation of early fossil insects. The main longitudinal veins are named after preexistent tracheae displayed in the nymphs or pupae, as the case may be. Beginning from the anterior or *costal margin* of the wing, the first vein is the *costa* (C), which is unbranched and forms the wing margin. The *subcosta* (Sc) lies closely behind the costa and is usually undivided. The *radius* (R) or third vein forks into an anterior branch R_1 and a posterior branch or *radial sector* (Rs), which divides into four branches, R_2 to R_5. The fourth vein or *media* (M) forks into an *anterior media* (MA) which is typically 2-branched, and a *posterior media* (MP) which is 4-branched. The fifth vein or *cubitus* (Cu) likewise divides into anterior and posterior branches. The *anterior cubitus* (Cu_1) is typically 2-branched and the *posterior cubitus* (Cu_2) is undivided. Finally, a variable number of *anal veins* (1A, 2A, &c.) are present.

The hypothetical venational type is most nearly approached in some of the Palaeozoic fossil insects. Among living forms the least departure from this type is seen in Ephemeróptera and Trichoptera. In the last-named order, as in most recent insects, the media is represented by the posterior media only and is usually indicated by the symbol M. In the Ephemeroptera, however, the media is more or less complete. In some orders, like the Neuroptera, specialization of the venation takes place by the addition of subsidiary branches to the main veins. More often specialization occurs by reduction of the branching of the veins, and in some parasitic Hymenoptera the venation has even entirely atrophied.

Additional rigidity of the wing membrane is obtained by the development of a network of *cross-veins* between the veins. While these are numerous and variable in the Ephemeroptera and Odonata, in the higher orders they tend to become few and located at fixed positions of mechanical advantage. The main cross-veins and their symbols are the *radial* (*r*) from R_1 to Rs : the *radio-medial* (*r-m*) from R to M : the *medial* (*m*) from MP_2 to MP_3, and the *medio-cubital* (*m-cu*) from MP to Cu.

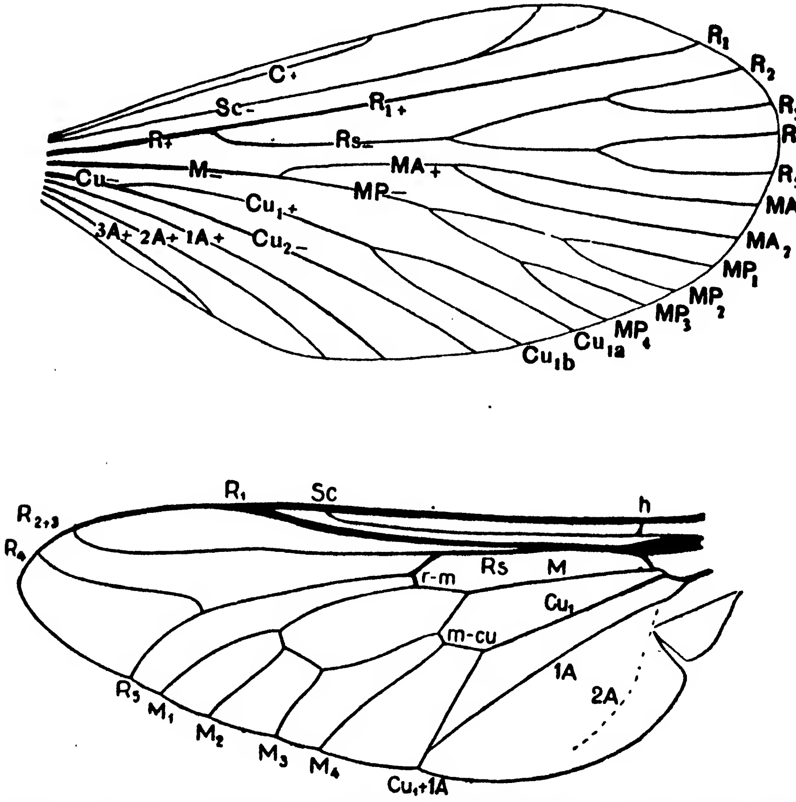

FIG. 6.—*Above.* HYPOTHETICAL PRIMITIVE TYPE OF VENATION (CONVEX VEINS + AND CONCAVE VEINS −). *Below.* WING OF HORSE-FLY (*TABANUS*)
For reference lettering, see p. 17

The veins divide up the wing area into *cells* and the name of each cell is taken from that of the vein which forms its anterior border.

Thus, the cell lying behind the main stem of the media is cell M, while a cell lying behind R_1 is cell R_1. Where two veins have fused the cell immediately behind is named from the posterior component: thus, when veins R_4 and R_5 coalesce the area behind is cell R_5.

A small, thickened, darkly pigmented area near the costal margin of the fore wing in many Hymenoptera and on both pairs of wings in Odonata is known as the *stigma* or *pterostigma* (Fig. 71).

Origin of Wings The *tracheal gill* theory claims that wings were derived from thoracic gills of the plate-like kind, well shown in may-fly nymphs. Being basally articulated with the body and already supplied with muscles and tracheae, it is claimed that they only required to become enlarged and adapted for flight. Wings, however, differ in their mode of development and are not serially homologous with tracheal gills. The theory also involves the assumption that the ancestors of winged insects were aquatic, which is contrary to evidence. The *paranotal theory* postulates that wings arose from lateral tergal expansions, or *paranota*, of the thorax. It is maintained that the prothoracic lobes of some of the most ancient fossil insects are organs of this kind which had persisted long after the paranota of the other thoracic segments had developed into wings. Paranotal expansions occur in positions characteristic of wings, not only on the thorax but also on the abdomen in various arthropods: among insects they are seen in *Lepisma* and in many larvae. It is suggested that they became sufficiently large to function after the manner of gliding planes, in leaping insects. Later they acquired basal articulations which, along with the development of muscles, enabled them to become organs of independent movement. The paranotal theory is the more generally accepted explanation and is furthermore consistent with the facts of wing-development.

Mechanism of Flight. The movements of each wing during flight are effected by two sets of muscles:—the indirect muscles and the direct muscles. The *indirect wing muscles* (Fig. 7) are the largest in the body and are attached to the thoracic wall and not to the wing bases. The vertical muscles depress the tergum, with the result that the wings are forced upwards owing to the nature of their articulation with the thorax. The longitudinal muscles effect an arching of the tergum, thus forcing the wings downwards. The *direct wing muscles* are sterno-pleural in origin and are inserted either directly on to the wing base or to small basal wing sclerites (Fig. 21). The most important are anterior and posterior extensors. During flight, while the indirect muscles are alternately elevating and depressing the wings, the forward and backward movements are effected by the extensor muscles. The complete mechanics of the wing during flight is a complex process. During the downstroke the wing is pulled downward and forward, its anterior margin being deflected and its posterior area elevated. In the upstroke the wing is pulled upward and backward, the posterior area being deflected (Fig. 7). Thus, in each complete stroke there is a turning of the wing on its long axis which has a mechanical effect like that of the revolution of a propellor blade. In the flying insect there is a flow of air across its wings such that a difference in pressure between the upper and lower surfaces results in an aerodynamic force which acts upward on the wings and supports the body during flight. The trajectory or path described by the wing-tip, relative to the long axis of the insect, has been observed with the aid of various mechanical devices. If a blow-fly or allied insect be held stationary the wing tip describes a trajectory of the form of a figure of eight, obliquely to the long axis, while during normal forward flight the wing-tip traverses a series of open loops. In general, flies and bees have the greatest rate of wing movement and the number of strokes per second is stated to range from 180 to 197 in the house-fly, from 180 to 203 in the hive bee, and from 278 to 307 in a mosquito. In a dragon-fly the wing-beats may be only 28 per second and no more than 9 per second in a cabbage butterfly. Among the swifter flying insects are Sphingidae, or hawk moths, and certain dragon-flies. A species of the latter has been recorded as attaining a speed of 90 miles per hour (40 metres per second).

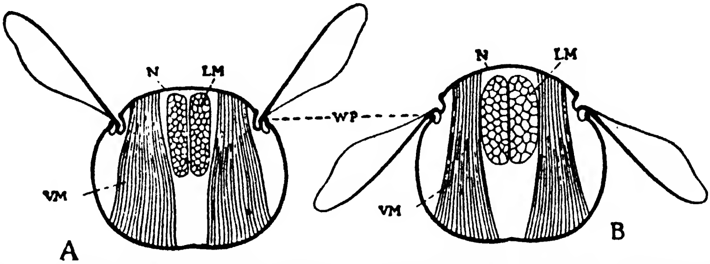

FIG. 7.—CROSS-SECTION OF THORAX OF AN INSECT SHOWING ACTION OF INDIRECT FLIGHT MUSCLES

A, wings forced upwards on pleural wing-process, WP, by depression of tergum, N, caused by contraction of tergo-sternal muscles, VM. B, wings forced downwards by elevation of tergum caused by contraction of dorsal longitudinal muscles, LM. (*After* Snodgrass)

THE ABDOMEN

The maximum number of abdominal segments is twelve. The 12th segment or *telson* is rarely evident and never bears appendages. It is present in the embryos of certain insects but seldom persists after eclosion from the egg : it is retained, however, in adult Protura. In Thysanura and the lower Pterygota the abdomen ends in the

11th segment which is reduced, or merged into the 10th segment. Its tergum or *epiproct* is a small plate above the anus and its sternum is divided into two lobes or *paraprocts.* A pair of appendages or *cerci* may be implanted in the membrane between the epiproct and paraprocts (Fig. 9, A). In the Endopterygota not more than 10 segments are usually present and often only nine segments are distinct. With the atrophy of the 11th segment the cerci become attached to the 10th segment. In Thysanura and many Ephemeroptera the epiproct is elongated into a median caudal filament (Fig. 8), and in dragon-fly nymphs of the suborder Zygoptera both this filament and the cerci are modified into gill lamellae (Fig. 72, C). In the embryo of most insects evident appendages occur as outgrowths from each of the eleven abdominal segments. While rudiments of these appendages are retained on almost all these segments among Diplura and Thysanura, in the Pterygota they are represented only by cerci and parts of the genitalia, the remainder being resorbed. In larvae of the Pterygota, on the other hand, abdominal limbs are often present, as for example in caterpillars, &c.

An acquaintance with the morphology of the abdominal sterna is necessary for an understanding of the homologies of the external genitalia. In the Machilidae (Thysanura) the 2nd to 9th sterna support a pair of *limb bases* (the so-called coxites) bearing *styli* very like those on the coxae of the 2nd and 3rd thoracic legs (Fig. 63, A and B). In *Campodea* and other Diplura similar styli are present in relation to most of the abdominal segments, but the limb bases and the primitive sterna are fused into simple plates (Fig. 60, C). Among the Pterygota this composite sternum prevails, but is devoid of styli. It is only in relation to the genital segments that a modification of the primitive arrangement obtains in many orders and is discussed below.

The External Genitalia. In the male the *genital segment* is the 9th and the *gonopore* is located on, or immediately behind, the sternum of that segment. The complete *external genitalia* comprise the *penis*, a pair of inner processes or *parameres* and a pair of *claspers* that serve to grasp the female when mating. The *penis*, or intromittent organ, is formed by the fusion of paired outgrowths and it bears the male gonopore. It is only among may-flies and in certain primitive earwigs that the original paired condition remains (Fig. 8, A). *Parameres* are present in many orders, but it is uncertain whether they are strictly homologous in all cases. The *claspers* are derived from the appendages of the 9th segment and are often termed *gonopods.* In the Machilidae they are unmodified limb-bases, bearing long styli, but perform no genital functions. In many of the lower Pterygota they are often undeveloped, and the 9th sternum is a subgenital plate or *hypandrium* bearing unmodified styli as in

Blatta (Fig. 8, B). In other orders, such as Ephemeroptera, Mecoptera, and Trichoptera, the styli along with their limb bases form the functional clasping organs. In many Lepidoptera and Diptera the claspers are derived from the styli, the limb-bases being fused with the 9th sternum (Fig. 8, C). In Coleoptera claspers are wanting.

In the female the *genital segments* are the 8th and 9th, and these carry the *external genitalia.* The latter form, collectively, the *ovipositor* or egg-laying organ. The primitive position of the *gonopore* is just behind the 7th sternum, but in most orders a backward shifting occurs during growth and the gonopore comes to lie behind the 8th or 9th sternum, as the case may be. The ovipositor (Fig. 9, A) is composed of three pairs of components whose shafts are termed *valves* and each valve is associated with a basal plate or *valvifer.* The valvifers are derived from the limb-bases of the 8th and 9th segments. The muscles operating the ovipositor arise from the terga of those segments and are inserted into the valvifers. The *anterior* or *ventral valves* are, in most cases, median outgrowths of the limb-bases of the 8th segment. The *posterior* or *inner valves* are median outgrowths of the limb-bases of the 9th segment. The *lateral* or *dorsal valves* are the drawn-out or modified limb-bases of the 9th segment. In many Orthoptera all three pairs of valves are interlocked and form parts of the functional ovipositor (Fig. 9, B):

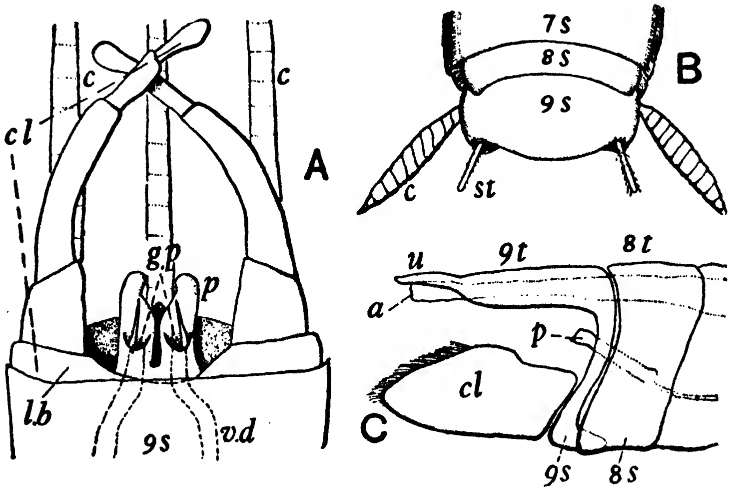

FIG. 8.—MALE GENITALIA

A, *Ephemera.* B, *Blatta* (ventral view). C, *Pieris* (lateral view). *a*, anus; *c*, cercus; *cl*, clasper; *g.p*, gonopores; *lb*, limb-base or coxite; *p*, penis; *s*, sternum; *t*, tergum; *u*, uncus or process of 9th tergum; *v.d*, vas deferens in locusts and crickets, however, the posterior valves are rudimentary or wanting.

In Hemiptera and Hymenoptera the lateral valves are quite

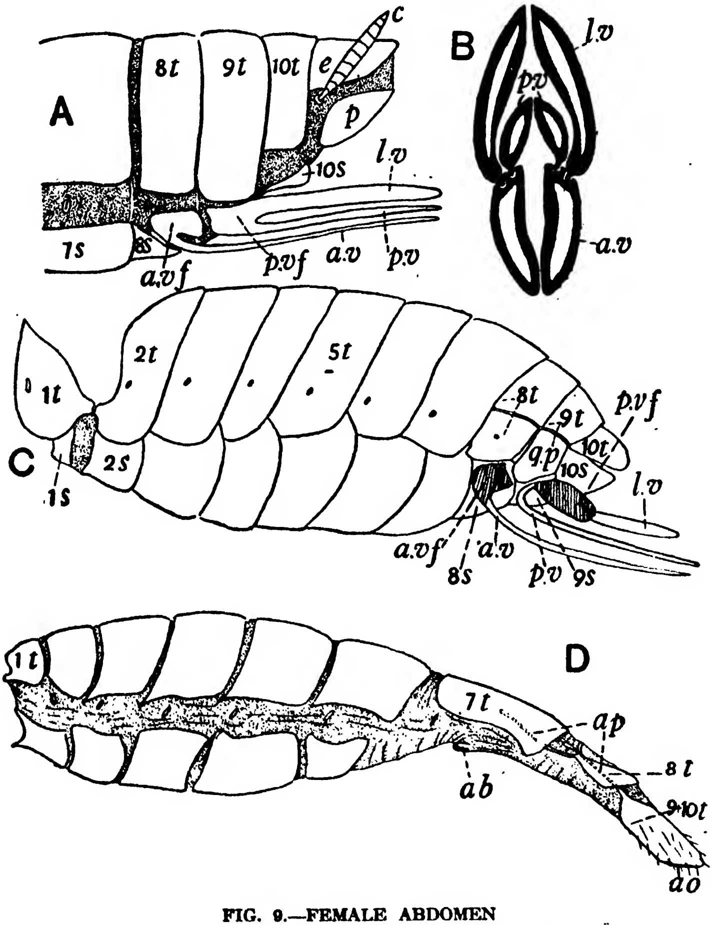

FIG. 9.—FEMALE ABDOMEN

A, schematic. B, transverse section of ovipositor of long-horned grasshopper. C, hive bee. D, a moth (*Lymantria*; *from* Eidmann), showing telescopic end-segments that function as an ovipositor. *ab*, aperture of bursa copulatrix; *a.o*, aperture of oviduct; *ap*, apodemes; *a.v*, anterior valve; *a.vf*, anterior valvifer; *c*, cercus; *e*, epiproct; *l.v*, lateral valve; *p*, paraproct; *p.v*, posterior valve; *p.vf*, posterior valvifer; *qp*, quadrate plate; *s*, sternum; *t*, tergum

separate and serve to ensheath the functional ovipositor or *terebra* when not in use. In these orders the posterior valves are united to form a guide or median stylet with which the anterior valves or lancets articulate by a ridge-and-groove device (Fig. 10, B). The gonopore is so situated that the eggs pass down the channel formed by the anterior and posterior valves. In the parasitic Hymenoptera the eggs are often greatly compressed to allow of their passage down the bristle-like terebra. In locusts and crickets the egg-channel is formed by the anterior and lateral valves.

The ovipositor in stinging Hymenoptera (Fig. 9, C) loses its original function and becomes a poison-injecting instrument which reposes in a pocket within the 7th abdominal segment (Fig. 10, C). In order to be brought into operation it is protracted from its pocket and, at the same time, deflected. These movements largely result from muscular action exerted on the quadrate plates, or side-pieces of the 9th tergum, which serve as levers. Thus, contraction of muscle *am* in Fig. 10, A pulls the quadrate plate forward and rotates the anterior valvifer downward, thus protruding the lancet. Contraction of muscle *pm* pulls the quadrate plate backward and, by rotating the anterior valvifer upward, it retracts the lancet. It will be observed, therefore, that the principal muscles have no direct connection with the lancets. The latter, it may be noted (Fig. 10, B), are grooved throughout their length so as to fit into and slide along two ventral 'guide rails' on the combined stylets.

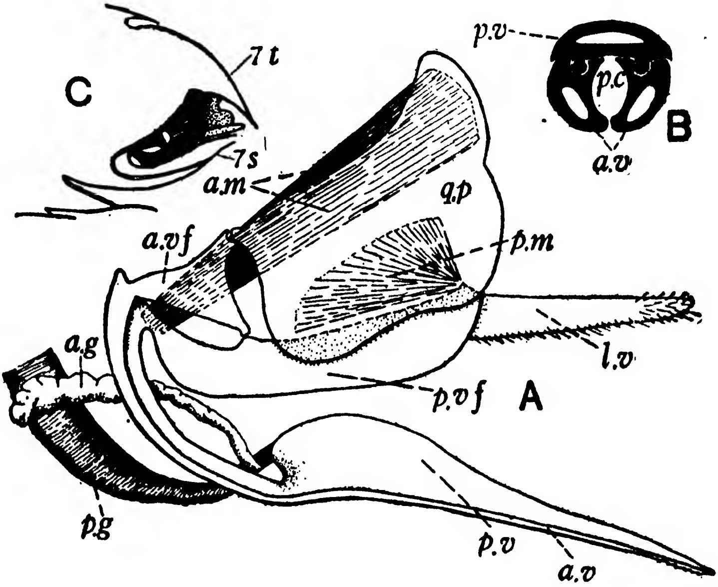

FIG. 10.—STING OF BEE

A, sting of bee, left side : *a.g*, alkaline gland ; *a.m*, *p.m*, anterior and posterior muscles ; *p.g*, poison gland. B, transverse section of terebra : *p.c*, poison canal. C, position of sting in repose (*after* Snodgrass). Other lettering as in Fig. 9

The poison gland is the right accessory gland which discharges into the poison sac whose opening is into the bulb-like base of the median stylet. The left accessory gland or alkaline gland opens separately and its secretion apparently does not mix with that of the poison gland as is often stated. The apices of the stylet and the lancets are provided with fine forwardly directed barbs. These hold the terebra in the puncture while alternating stabs by the lancets buries the organ deeper into the flesh.

Among many orders, including Coleoptera, Lepidoptera, Diptera, &c., there is no special organ for the deposition of the eggs. Many members of these orders, however, have the posterior segments of the abdomen modified into a slender telescopic tube bearing the opening of the egg-passage distally. In such cases the eggs are commonly laid in crevices or other concealed situations (Fig. 9, D).

THE NERVOUS SYSTEM

The nervous system comprises the central nervous system, the visceral nervous system, and the peripheral sensory nervous system.

The Central Nervous System

This is composed of a double series of nervous centres or ganglia joined together by means of longitudinal and transverse tracts of nerve fibres. The longitudinal tracts of fibres are the *connectives* (*c* in Fig. 18) and they serve to unite a pair of ganglia with those in front and behind. The transverse fibres or *commissures* unite the two ganglia of a pair. While there is usually a pair of ganglia in almost every segment in the lower insects (Fig. 11, A), a varying degree of fusion occurs in the higher groups (C, D). Also, the members of a pair are so closely amalgamated that they seem to form a single ganglion. The connectives are separate and distinct in the more primitive insects, but often they are so closely approximated as to appear as a single longitudinal cord (Fig. 11, D). The central nervous system is divisible into the brain and the ventral nerve cord.

The *neurones* or components of the nervous system are extremely attenuated cells of ectodermal origin. Each neurone (Fig. 12) consists of a nerve-cell with its nucleus and a nerve-fibre or *axon*. The axon often has a side branch or *collateral*, and both end in delicate branching fibrils forming *terminal arborizations*. Each axon is covered by a nucleated coat or *neurilemma*: there is no myelin sheath as in vertebrates. The neurones are of three kinds. The *sensory neurones* are located peripherally in association with the integument, whereas in vertebrates such neurones lie internally close to the central nervous system. A sensory nerve-cell is generally bipolar with a distal process adapted to receive a particular kind of stimulus. The axon is believed to be formed by inward growth from the sensory cell and ultimately ends as an arborization within a central ganglion. Fibres from neighbouring sensory cells form, collectively, an *afferent* or *sensory nerve.* Other neurones, the *motor neurones,* lie within the ganglia: they are mostly unipolar and their axons form an *efferent* or *motor nerve.* The latter passes to the muscles where its axons end in minute conical projections (Doyère's hillocks) or in fine branches. As a rule a nerve contains both motor and sensory fibres. *Association neurones* form a two-way system between sensory and motor neurones by means of their axons and collaterals. The terminal arborization of a sensory neurone and that of a collateral or of a motor neurone come into close association with the arborizations of an association axon. In this way a *synapse* as it is termed, is formed. In the simplest cases the synapse is effected without the intervention of an association neurone. It should be noted that the fibrillae that form a synapse are not in actual contact with one another. It would seem that an impulse does not itself cross a synapse but induces the secretion of a substance (acetylcholine or adrenaline?) which behaves as a 'facilitator' and activates another neurone. While there is good evidence of this process happening in other animals, it has not so far actually been shown to prevail in insects.

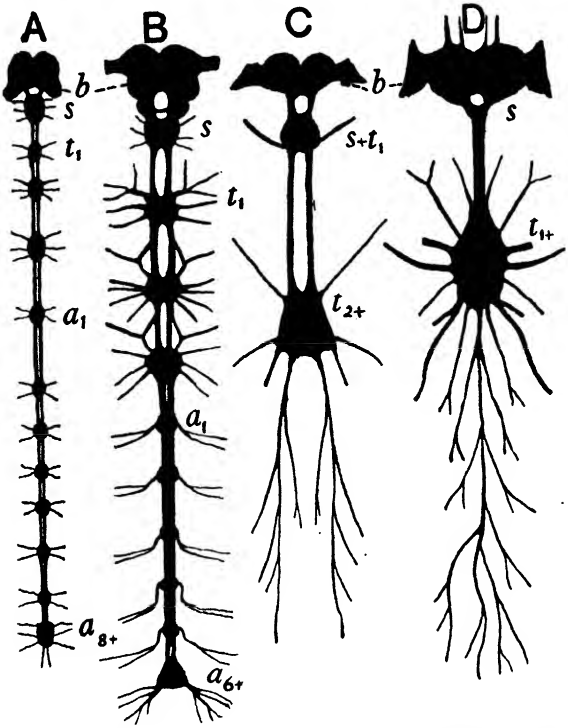

FIG. 11.—TYPES OF NERVOUS SYSTEM (ADAPTED FROM VARIOUS AUTHORS)

A, *Japyx*. B, *Blatta*. C, Water bug (*Belostoma*). D, House-fly (*Musca*). *a*, abdominal ganglia; *b*, brain; *s*, suboesophageal ganglion; *t*, thoracic ganglia

The ganglia of the central nervous system are mainly formed of peripheral aggregations of nerve-cells enclosing a central mass of nerve-fibres (the so-called neuropile). In addition there are irregular, branched interstitial cells forming the *neuroglia.* Each lateral nerve has two roots. The fibres of the dorsal root arise from motor-cells situated dorso-laterally in a ganglion and the sensory fibres, composing the ventral root, end in terminal arborizations on the ventrolateral aspect of the ganglion. The association neurones lie for the most part between the dorsal and ventral roots. Externally the ganglia and nerves are invested with a sheath or *perineurium.*

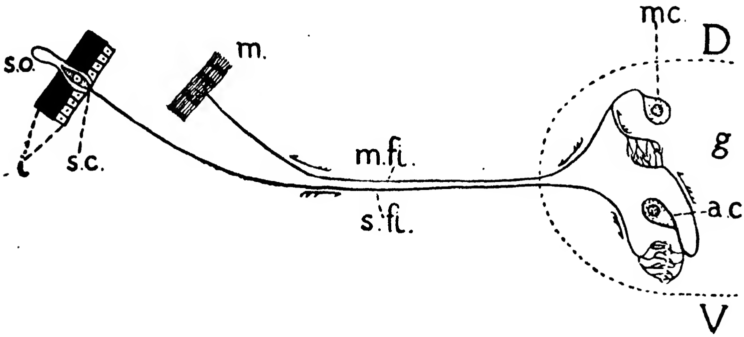

FIG. 12.—DIAGRAM OF THE REFLEX MECHANISM OF AN INSECT

One-half of a ganglion, *g*, of the ventral nerve-cord is shown. D, dorsal. V, ventral. A motor fibre, *m.fi*, and a sensory fibre, *s.fi*, of a lateral nerve are shown. *i*, integument; *s.o*, sensillum; *s.c*, sensory cyton or cell; *m*, muscle; *a.c*, association cyton; *m.c*, motor cyton. (The course traversed by a stimulus, received by the sensillum, is shown by arrows)

The Brain (or *supra-oesophageal ganglia*). The brain (Figs. 11 and 13) lies just above the oesophagus and is formed by the amalgamation of the first three embryonic neuromeres. These latter develop very unequally and give rise respectively to the *protocerebrum* (P), the *deutocerebrum* (D), and the *tritocerebrum* (T). The *protocerebrum* forms the greater part of the brain and represents the fused ganglia of the optic segment: it innervates the compound eyes (*e*) and ocelli (*oc*). Laterally this region is expanded to form the *optic lobes* (*o.l.*) which are the seat of the visual cells. These lobes contain the most intricate mechanisms in the insect nervous system and their degree of development is in correlation with that of the eyes. Within the protocerebrum are the so-called *mushroom-bodies* that are composed of vast numbers of small association cells whose axons are grouped together into stalk-like bundles. The size and complexity of these bodies corresponds in a general way with complexity and specialization of behaviour. The *deutocerebrum* is formed by the ganglia of the antennary segment: it is chiefly composed of the antennary lobes and innervates the antennae (*an*) and their muscles. The *tritocerebrum* is formed by the third pair of cephalic ganglia and lies beneath the antennary lobes. It is poorly developed owing to the absence of the 2nd antennae in insects and its function is to innervate the labrum (*l.n.*) and the fore intestine. Its component ganglia are widely apart and are joined by the *post-oesophageal commissure* (*po.c.*)

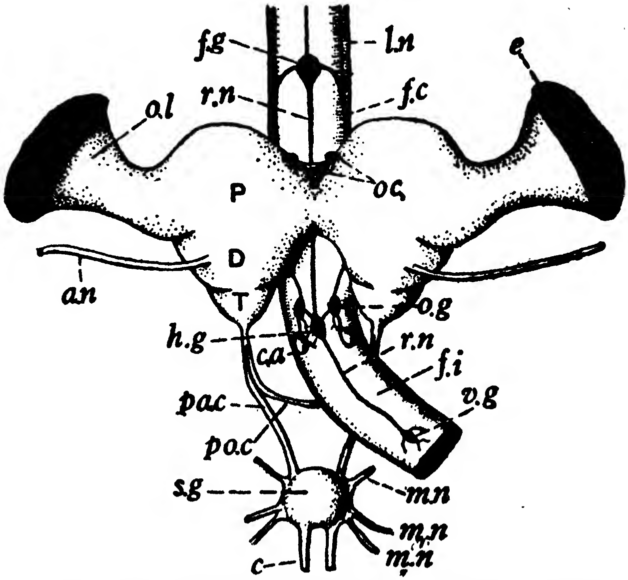

FIG. 13.—BRAIN OF AN INSECT WITH SUBOESOPHAGEAL GANGLION AND STOMATO GASTRIC SYSTEM

The fore intestine has been turned to one side. Explanation of lettering on pp. 27–29.

The brain is the chief seat of sensation and co-ordination but is of very minor importance as a locomotory centre. Removal of the brain renders an insect inert and it is no longer able to initiate instinctive acts. Brainless insects, when suitably stimulated, can walk or fly but are unable to seek out their food. When food is placed in contact with the mouth-parts they are, however, able to eat if the suboesophageal ganglion which controls the mouth organs be intact. The general tonus of the muscles on the two sides of the body is influenced by the brain. Removal of one side of this centre reduces the tonus on that side and movements are in a circle towards the uninjured side.

The Ventral Nerve-Cord. The ventral nerve-cord (Fig. 11) is a median chain of segmental ganglia lying beneath the alimentary canal. It is joined to the tritocerebrum by the *para-oesophageal* *connectives* (*pa.c.*). The first ventral nerve centre is the *suboesophageal ganglion* (*s.g.*) formed by the fusion of the 4th to 6th neuromeres or ganglia of the mandibular, maxillary, and labial segments. It gives off paired nerves (*m.n*, *m.,n*, *m.,,n*, Fig. 13) supplying their respective appendages. There follows three thoracic ganglia and, at most, eight ganglia in the abdomen. The first abdominal ganglion often fuses with that of the metathorax, and the end ganglion of the chain is always a composite centre formed by the fusion of at least three neuromeres. Among the higher Diptera the thoracic and abdominal ganglia are all fused into a single centre. Specialization of this kind is, however, by no means confined to the most highly evolved insects, and may be correlated with a reduction in the length and segmentation of the hind body as in sucking lice and in some Collembola.

The thoracic ganglia innervate the legs and wings, while each abdominal ganglion shows considerable autonomy and functions to some extent as a local centre for its segment. A complicated reflex act such as oviposition can be carried out with a living isolated abdomen when suitably stimulated provided the last ganglion and its nerves are intact.

The Visceral Nervous System. The principal component of the visceral or sympathetic nervous system is that known as the *stomatogastric* or *oesophageal system* (Fig. 13), which is formed by ingrowth of the dorsal part of the stomodaeum. It includes, firstly, a median *frontal ganglion* (*f.g.*) lying just anterior to the brain. This ganglion is joined by bilateral connectives (*f.c.*) to the tritocerebrum and gives off a *recurrent nerve* (*r.n.*) that ends in a *ventricular ganglion* (*v.g.*) on the hind part of the oesophagus. Behind the brain there are also paired *oesophageal ganglia* (*o.g.*) that are joined to its hind border and also connected to a median *hypocerebral ganglion* (*h.g.*). Closely associated with the oesophageal ganglia are the *corpora allata* (*c.a* : p. 86). The stomatogastric system contains both motor and sensory fibres and innervates the heart and fore intestine (*f.i.*).

The *ventral sympathetic system* consists of transverse nerves associated with each ganglion of the ventral cord : they supply the spiracles of their segment. Arising from the last abdominal ganglion are *splanchnic nerves* that innervate the reproductive organs and the hind intestine.

The Peripheral Sensory Nervous System. This is composed of a fine network of axons and sensory cells lying beneath the integument. The nerve-cells have branched distal processes that end in the epidermis itself. The axons combine and enter the paired segmental nerves of the ventral cord. This system is perhaps homologous with the nerve net of the lower invertebrates. Among insects it is best developed in soft-skinned larvae.

THE SENSE ORGANS

Sensory perception is achieved by means of structures termed *receptors* or *sensilla.* These take various forms and are situated at the peripheral endings of the sensory nerves. In many cases, the tactile receptors, for example, they are scattered in distribution, whereas in the eyes and tympanal organs they are aggregated often in large numbers. In their least modified form receptors closely resemble ordinary body hairs and only differ in having connection with the nervous system. The components of a simple type of receptor are the cuticular or external part with its trichogen or formative cell together with a bipolar sense cell. The latter lies in or just beneath the epidermis and its distal process penetrates the trichogen to enter the cavity of the cuticular part of the receptor. In many cases a tormogen or membrane cell is also present. Various types of receptors are evidently modified sense hairs derived from the simple trichoid structure shown in Fig. 14, A. They are characterized by the form of the cuticular parts and may be *bascionic, placoid, campaniform, coeloconic,* &c., or, in other words, peg-like, plate-like, dome-like or in pits. Receptors of a different kind are the ommatidia or components of the eyes, and the chordotonal receptors of the tympanal organs.

It is not possible at present to classify some of the prevailing kinds of receptors, with certainty, on a functional basis. We are consequently forced to argue what their rôle may be from their structure and the positions they occupy on the body. Experiments on the living insect enable general ideas to be gained with respect to its behaviour in relation to different stimuli. Amputation of appendages or of particular regions of the body, or the coating of parts with impermeable substances may enable the positions of specific receptors to be located. The minute size of receptors and the fact that they are often mingled with those of a different kind often makes their investigation a matter of great difficulty. In recent years, however, the development of a technique for the isolation of particular receptors from the rest of the nervous system and the determination of the nature of their sensitivity by the electrical detection of impulses in the ends of the cut sensory fibres, is advancing knowledge of sense physiology on a more exact basis than has been possible hitherto.

The following classification of receptors is convenient:

A. *Mechanoreceptors*: e.g. touch, tension, sound, balance.
B. *Chemoreceptors*: e.g. smell, taste.
C. *Photoreceptors*: e.g. sight.

The majority of these organs are *exteroreceptors* or those that

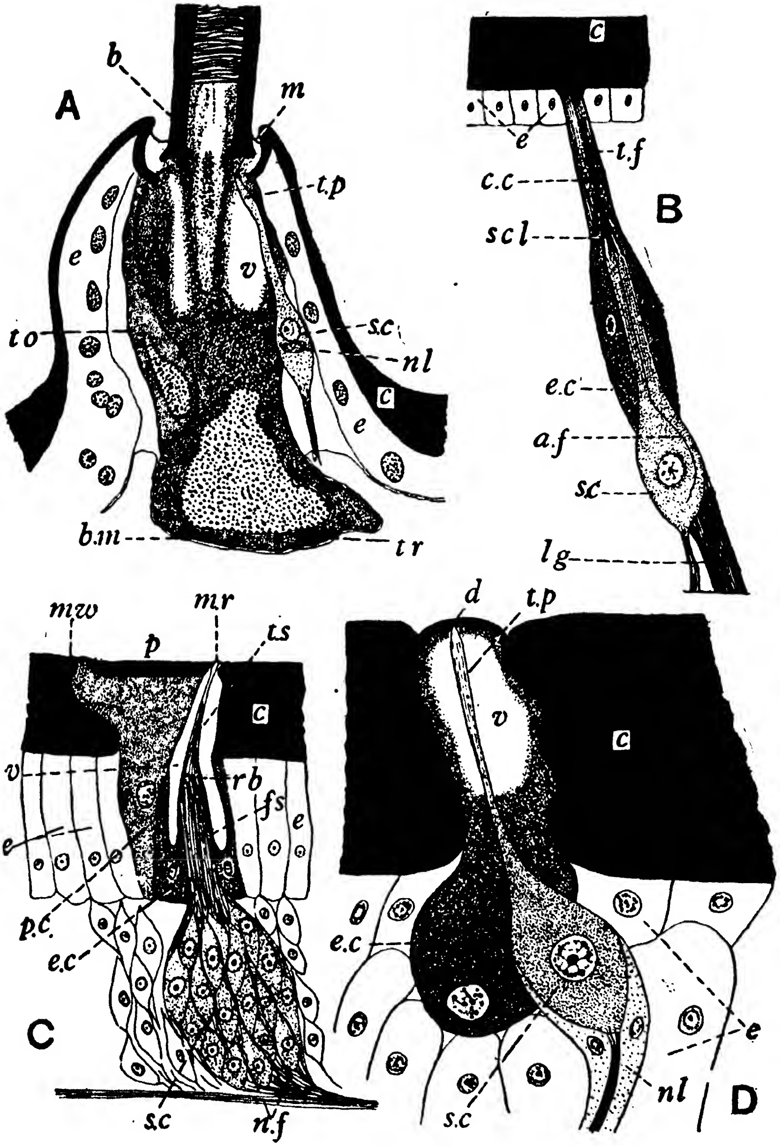

FIG. 14.—SENSORY RECEPTORS

A, base of trichoid receptor of larva of *Vanessa urticae* (*from* Hsu). **B**, chordotonal receptor. **C**, placoid receptor from antenna of hive bee (*from* Vogel). **D**, campaniform receptor from cercus of *Blatta* (*from* Sihler). *a.f*, axial filament; *b*, base of hair; *b.m*, basement membrane; *c*, cuticle; *c.c*, cap-cell; *d*, dome or cuticular cap; *e*, epidermis; *e.c*, envelope cell; *f.s*, fascicle of nerve endings; *lg*, ligament; *m*, alveolar membrane; *m.r*, membranous ring; *m.w*, marginal wall; *n.f*, nerve-fibres; *nl*, neurilemma cell; *p*, plate of receptor; *p.c*, plate cell; *r.b*, refringent bodies; *sc*, sense cell (or cells); *scl*, scolopale; *t.f*, terminal filament; *to*, tormögen; *tp*, terminal process; *tr*, trichogen; *t.s*, terminal strand; *v*, vacuole detect stimuli from the outside world. Some mechanoreceptors, however, serve as *proprioceptors* which register internal stimuli resulting from the position or movements of the insect's body.

A. MECHANORECEPTORS

These are of varied form and many are of the simple trichoid type, scattered over the body and its appendages (Fig. 14, A). It appears that an impulse is set up by the bending or movement of such a hair in its socket. Structures of this kind are numerous on the antennae and are *tactile receptors*. In many cases they occur over the body and cerci and are also known to perceive sound vibrations of low frequency. Caterpillars, for example, respond to sound so long as their body hairs are intact and free. Singeing, dusting such hairs with powders, spraying with water through an atomizer, smearing with vaseline, &c., tend to destroy this response. Sensitivity to pressure caused by air currents appears to lie in these same hairs. The longer trichoid receptors on the cerci of crickets and cockroaches are sensitive to sound vibrations of very low frequency, including those inaudible to man. It needs to be borne in mind that such stimuli as touch and sound vibrations appear to intergrade in insects as phases of a simple type of sensation perceived by the same kind of receptors.

Tension receptors are probably to be found in the *campaniform sensilla* (Fig. 14, D) that occur over the insect body where there are joints or articulating sclerites. Thus, they are found in relation to joints of the palpi, on the legs, sting, cerci, gills, halteres, wing-bases, &c. Recent research dealing with these receptors on the joints of the maxillary palpi and on the legs of cockroaches (*Periplaneta*) indicate that they respond to strains in the cuticle. In cases where they are circular they will react to flexion in any direction : where they are elliptical they will be affected by bending along the long axis (Fig. 15, F). This belief is supported by the fact that different groups of these receptors are orientated almost at right angles to each other. They appear to be proprioceptors that 'register' the force exerted on different parts through the compression of the neighbouring cuticle.

Chordotonal receptors occur singly or, more often, in small groups in many parts of the body and appendages of diverse insects including larvae. In the grasshopper *Melanoplus*, for example, E. H. Slifer has found 76 pairs of chordotonal organs, each composed of one or more of these receptors. On referring to Fig. 14, B it will be seen that a chordotonal receptor consists of a long cap-cell, attached to the integument, an envelope-cell and a sense-cell. The envelope-cell surrounds the distal process of the sense-cell, whose apex is prolonged into a terminal fibre that is fastened to the cuticle. At the apex of the sensory process is a sense-rod or scolopale of complex structure. A delicate axial fibre arises in the sense-cell and traverses the scolopale to terminate in its deeply staining cap or apical body. Any displacement of the scolopale, it would appear, sets up an impulse affecting the sense-cell through the axial fibre. Very often chordotonal receptors are attached at both their ends to the integument, and it is probable that they are proprioceptors sensitive to changes of tension in the muscles. Without some such organs there does not seem to be any means by which an insect is enabled to orientate itself in relation to the force of gravity—especially when in flight. So far no sensory nerve-endings have been detected in insect muscle, and it is probable that perception of afferent impulses. resulting from changes in muscle tension is by chordotonal receptors.

Both chordotonal and campaniform receptors may occur on the same appendage or part, and it seems probable that they are sensitive to changes of tension of different qualities—the former in regard to the muscles and the latter with respect to the cuticle. .The fullest proprioceptive capacity, on this theory, would be attained by the combined operation of the two kinds of receptors. This happens in the *halteres* of Diptera (p. 155) which are largely concerned with the maintenance of equilibrium during flight. Some flies, such as *Calliphora*, show complete loss of equilibrium in the air after the removal of the halteres.

The organ known as *Johnston's organ* lies in the pedicel or 2nd antennary segment of almost all insects. It is formed of chordotonal receptors whose distal attachments are to the articular membrane at the base of the flagellum (Fig. 15, J). Where it is highly developed and formed of very numerous receptors, as in midges and mosquitoes, the pedicel is specially enlarged. The function of Johnston's organ is probably for the perception of movements of the antennal flagellum through tension exerted on the articular membrane at its base.

Structures that are auditory in function are known as *tympanal organs* (Fig. 15, C, D, E). They are easily seen on either side of the base of the abdomen in Acrididae (short-horned grasshoppers) and at the proximal ends of the fore tibiae in Tettigoniidae (long-horned grasshoppers) and Gryllidae (crickets). In an Acridian each organ consists of an external membrane or tympanum and opposed to its inner side is a group of chordotonal receptors. Associated with the typanum are tracheal air-sacs which act as resonators. Sound waves impinging on the tympanum set up vibration which in turn is transmitted as impulses to the chordotonal receptors. Tympanal organs, in all cases, have a common structural plan and, it may be added, are also found in cicadas and in certain groups of moths. They respond to sounds of relatively high frequency (up to about 45,000 cycles per second) and are well adapted to enable an insect to locate the source of a particular sound. It is well known that sound-producing organs are present in the males among grasshoppers, crickets and cicadas and it appears that the sounds emitted are recognition signals of special significance in connection with mating. The sound of a stridulating male cricket transmitted by telephone will entice a female to the receiver in another room. The response is only obtained from adult *unmated* females, and ceases if both the

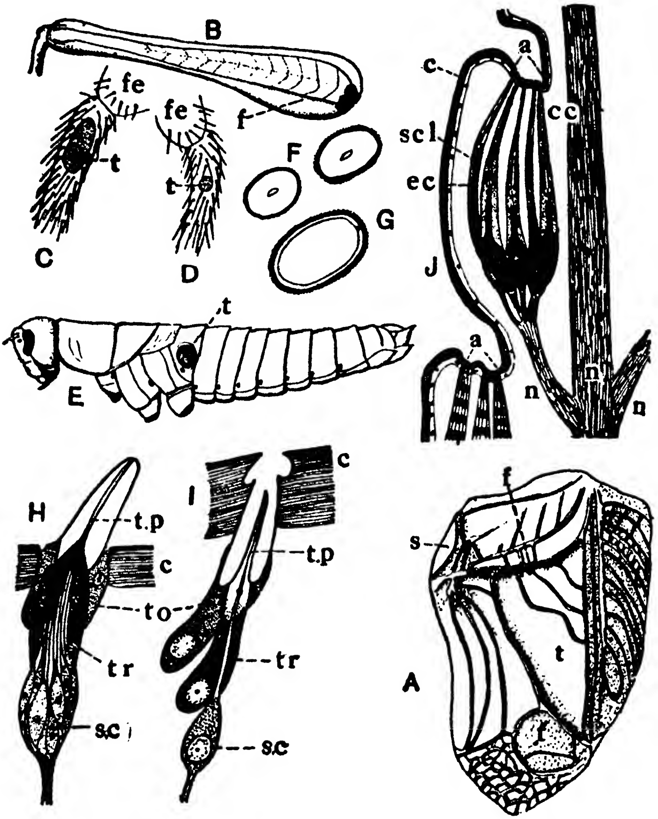

FIG. 15.—STRIDULATION AND HEARING, ETC.

A, right tegmen of male cricket (*Gryllus*) showing file, *f*, scraper, *s*, and resonating areas, *t*, *t'*. B, hind femur of grasshopper (Acrididae); *f*, file. C, outer and, D, inner surfaces of fore tibia of cricket (*Gryllus*), showing tympana, *t*. E, side view of an Acridian grasshopper (wings and legs removed), showing tympanum, *t*, F, campaniform and, G, placoid receptors in surface view. H, basiconic and, I, coeloconic receptors (*adapted from* Vogel). J, section of pedicel of antenna of a moth, showing Johnston's organ (one side only). *a*, articular membrane; *n*, antennary nerve; and nerve to Johnston's organ; *fe*, femur. Other lettering as in Fig. 14

attachment of muscles to the cuticle (Fig. 19) may either be directly to the under surface of the latter or by means of *tonofibrillae* which are cuticular fibres continuous with the sarcostyles. Where especially firm bases of origin and attachment are needed *apodemes*, or integumentary infoldings, are developed.

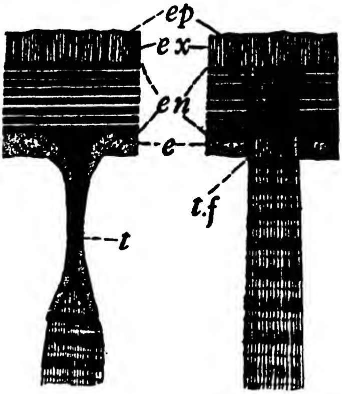

FIG. 19.—ATTACHMENT OF MUSCLES TO THE INTEGUMENT
Right, showing tonofibrillae, *tf*. *Left*, attachment to tendon, *t*, formed of endocuticle, *en*. Other lettering: *e*, epidermis; *ep*, epicuticle; *ex*, exocuticle. (*Adapted from* Weber)

The fact that insects are able to raise weights of much greater mass than their own bodies and can leap relatively long distances has given rise to the popular idea that their muscles possess unique powers. Such powers, however, are to be explained in terms of body size and are relative, not absolute. The power of a muscle varies as the square of a linear dimension, i.e. with its cross-section. The volume or mass of the body, on the other hand, varies as the cube of the linear dimensions. Consequently for muscles with the same physical properties the *relative* muscular power increases as the size of the animal diminishes. The *absolute* muscular power is the maximum load it can raise per square centimetre of its diameter. When considered in this light there is no very great difference between insect and vertebrate muscle but, on the whole, the absolute muscular power is greater in the latter. The chemical changes that occur in insect muscle during contraction appear to show no special peculiarities. Lactic acid is set free after stimulation of muscle in about the same proportion as in vertebrates.

Myology

The following account enumerates the principal muscles of a generalized insect. In so far as the appendages are concerned, the muscles are divided into two series, *extrinsic* and *intrinsic*. *Extrinsic muscles* have their origins outside the limb and are mainly concerned with its movements as a whole: *intrinsic muscles* have their origins within a limb and effect movements of individual segments or parts. The various muscles may be named according to their functions, but it needs to be pointed out that lack of a uniform nomenclature is shown among different writers. Muscles effecting forward and backward movements of a limb, in relation to the antero-posterior axis of the body, may be conveniently referred to as *protractors* and *retractors* respectively. Thus, the protractor of the coxa swings the whole leg forward. *Levators* and *depressors* are concerned, respectively, with the raising and lowering of an appendage in the vertical plane: these terms are less often applicable to individual parts or segments. For example, the extrinsic muscles of the antenna—the levator and depressor—raise and lower that appendage in relation to the body. *Flexors* draw one part towards another part and *extensors* are antagonistic in extending or drawing that same part away. As an example the flexor of the tibia draws that segment towards the femur. Many writers regard flexor and extensor as being synonymous with depressor and levator. *Adductors* draw an appendage towards its fellow, whereas *abductors* extend or draw away that appendage. Thus, during mastication the mandibles are drawn together and diverged, respectively, by their adductor and abductor muscles. Finally, *rotators* bring about turning movements of a limb or part.

1. **The Head Muscles.** The chief muscles of the head are the following (Fig. 20):

(*a*) *Labrum.* A pair of *levators* arise from the frons and are inserted on to the base of labrum on the dorsal side. A pair of *depressors* arise external to the origin of the levators and are attached ventrally to the base of the labrum and externally to the first-named muscles.

(*b*) *Antenna.* Inserted into the base of the scape are a *levator* and *depressor* whose origins are on the tentorium. The only other antennal muscles are the *protractor* and *retractor* of the *flagellum,* whose origins lie within the base of the scape and whose insertions are on the base of the pedical. The remainder of the antenna, often termed the flagellum, is devoid of muscles. It is only in Diplura and Collembola that intrinsic muscles are present and effect movements of individual segments of the antenna (see also p. 102).

(*c*) *Mandible.* A powerful *adductor* arises dorso-laterally on the head capsule and is inserted by means of a strong tendon on to the inner angle of the base of the mandible. A smaller *abductor* arises externally to the abductor and its tendonous insertion is on the outer basal angle of the jaw.

(*d*) *Maxilla.* An *abductor* arises from the postero-lateral region of the epicranium and is inserted on to the cardo. A pair of broad, flat *adductors* arise on the tentorium and have their insertions on the cardo and stipes. The *cranial flexor of the lacinia* is a long slender muscle originating on the occiput, while the *stipital flexor of the lacinia* and the *flexor of the galea* both have origins within the stipes. A *flexor* and an *extensor of the palp* also originate on the stipes and associated with the palpal segments are intrinsic muscles.

(*e*) *Labium.* The extrinsic muscles of the labium are the *dorsal* and *ventral premental muscles* whose origins are on the tentorium and their insertions are distal and proximal, respectively, in relation to the prementum. A pair of *median premental muscles* arises on the postmentum or submentum, as the case may be, and is inserted on the basal margin of the prementum. These three pairs of muscles impart a considerable range of movement to the prementum during feeding. The muscles of the ligula and palpi correspond to those of the galeae, laciniae and palpi of the maxillae, except that the cranial flexors of the laciniae have no counterparts in the labium.

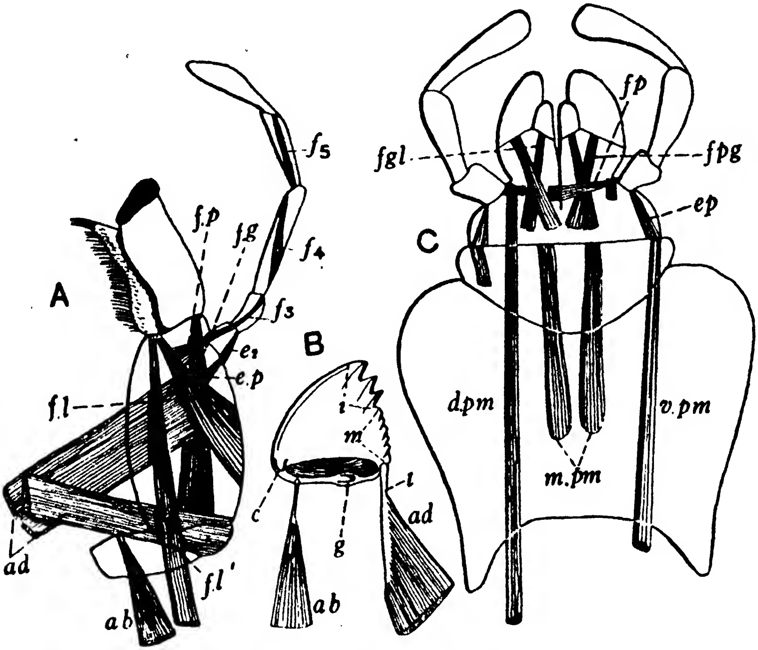

FIG. 20.—MUSCLES OF HEAD APPENDAGES OF AN ORTHOPTEROUS INSECT

A, maxilla, right : dorsal (anterior) view. B, Mandible, left. C, labium : dorsal (anterior) view. *ab*, abductor ; *ad*, adductor ; *c*, condyle ; *d.pm*, dorsal premental muscle ; t_2, extensor of 2nd palpal segment ; *ep*, extensor of palp ; $f_3 f_4 f_5$, flexors of 3rd, 4th, and 5th palpal segments ; *f.l.*, stipital flexor of lacinia ; *f.l.'*, cranial flexor of lacinia ; *f.g*, flexor of galea ; *f.gl*, flexor of glossa ; *f.p*, flexor of palp ; *f.pg*, flexor of paraglossa ; *g*, ginglymus ; *i*, incisor area ; *m*, molar area ; *m.pm*, median premental muscles ; *t*, tendon ; *v.pm.*, ventral premental muscle

2. The Thoracic Muscles. These muscles (Figs. 21 and 22) include :

(*a*) *Dorsal longitudinal*, attached to successive phragmata : they are best developed in the wing-bearing segments, where they form the main depressors of the wings. In apterous insects and in those with weak flight these muscles are more or less reduced or wanting.

In the prothorax they are of smaller calibre and are attached to the occipital region of the head.

(*b*) *Ventral longitudinal*: these extend from one sternal apophyses to another. In the prothorax they pass to the head, where they are inserted on to the occiput or the tentorium.

(*c*) *Ventral oblique*, consisting of anterior and posterior series that arise from the sternal apophysis and are attached to the spina of the segment in front and behind, respectively.

(*d*) *Dorso-ventral*, or tergo sternal, muscles which act as the main levators of the wings and are therefore antagonistic to (*a*). They are wanting in the prothorax and reduced in flightless insects. The two series *a* and *d* are known as the *indirect wing muscles* because their insertions are not upon the wing bases. The next group (*e*) constitutes what is commonly termed the *direct wing muscles* (see p. 20) on account of their attachments being very near to or on the wing-bases.

(*e*) *Pleural muscles* which include (1) the *anterior extensors of the wing* arising from the pleuron and the coxal margin and inserted on the anterior pleural (basalar) wing sclerite, beneath the wing base: (2) the *posterior extensor of the wing*, whose origin is on the margin of the coxa of its segment and the insertion on the posterior pleural (subalar) wing sclerite, beneath the wing base: (3) the *flexor of the wing*, which arise from the pleural ridge and is inserted on the wing base.

(*f*) *Leg muscles*, which comprise extrinsic (Fig. 21) and intrinsic (Fig. 22) series. The *extrinsic series* are concerned with movements of the leg as a whole. Arising from the tergum and inserted on to the trochantin and coxa, respectively, are the *protractor* and *retractor of the coxa*: these muscles effect forward and backward movements in the horizontal plane. A *levator* and a *depressor of the coxa* bring about up-and-down movements of the leg and arise from the sternum and the pleuron, respectively. *Anterior* and *posterior rotators* of the coxa, of sternal origin, effect partial rotation of the limb. Finally, the *depressor of the trochanter* (Fig. 22) represents a group of muscles with origins on the tergum and ventral margin of the coxa. When the articulation between the femur and trochanter is fixed, this muscle acts as a depressor of the leg.

The intrinsic series comprise (1) the *levator of the trochanter* which arises from the base of the coxa and is inserted into the base of the trochanter. As in the case of the depressor, this muscle moves the leg as a whole where the femoro-trochanteral joint is fixed. The only muscle moving the femur is the *flexor of the femur* which arises ventrally on the trochanter and is attached to the dorsal tip of the base of the femur: it is wanting in the hind legs of locusts and crickets. The cavity of the femur is largely occupied by the *flexor*

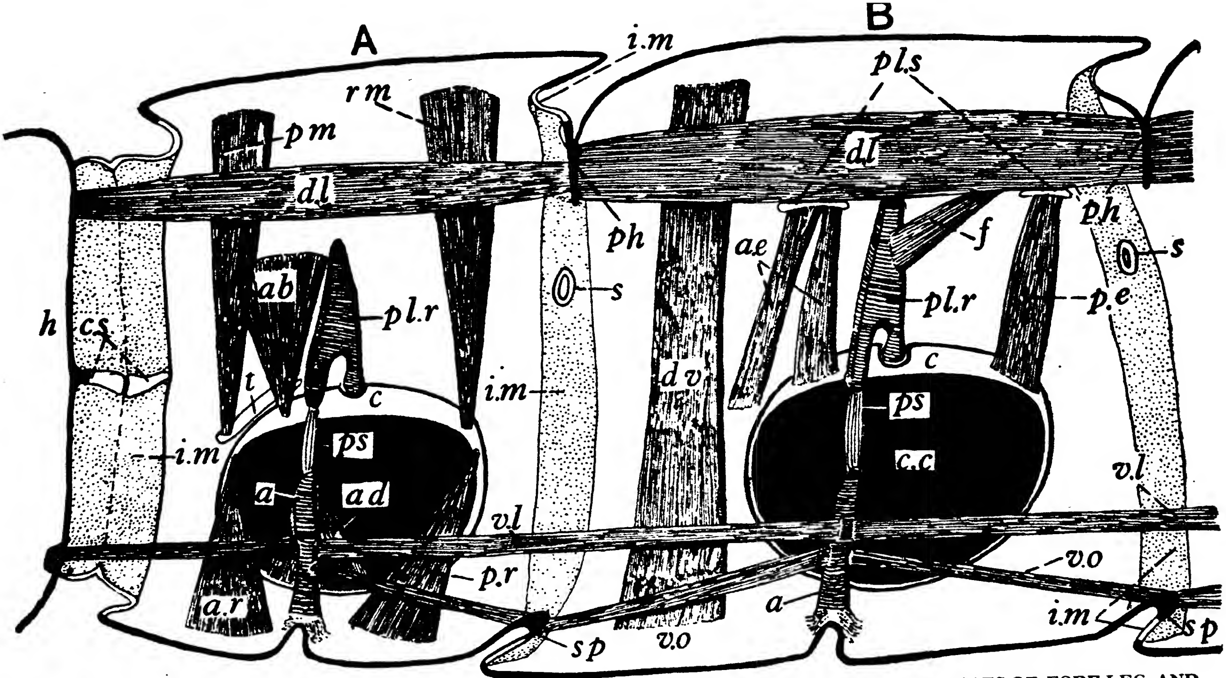

FIG. 21.—CHIEF MUSCLES OF PROTHORAX (A) AND MESOTHORAX (B) WITH EXTRINSIC MUSCLES OF FORE LEG AND WING MUSCLES OF RIGHT SIDE: DIAGRAMMATIC

a, sternal apophysis; *ab*, depressor of coxa; *ad*, levator of coxa; *a.e*, anterior extensors of wing; *a.r*, anterior rotator of coxa; *c*, margin of coxa; *c.c*, coxal cavity; *c.s*, cervical sclerites; *d.l*, dorsal longitudinal muscle; *d.v*, dorso-ventral muscle; *f*, flexor of wing; *h*, occiput; *i.m*, intersegmental membrane; *p.e*, posterior extensor of wing; *ph*, phragma; *pl.r*, pleural ridge; *pl.s*, pleural wing sclerites; *pm*, protractor of coxa; *p.r*, posterior rotator of coxa; *ps*, pleuro-sternal muscle; *rm*, retractor of coxa; *s*, spiracle; *sp*, spina; *t*, trochantin; *v.l*, ventral longitudinal muscle; *v.o*, ventral oblique muscle

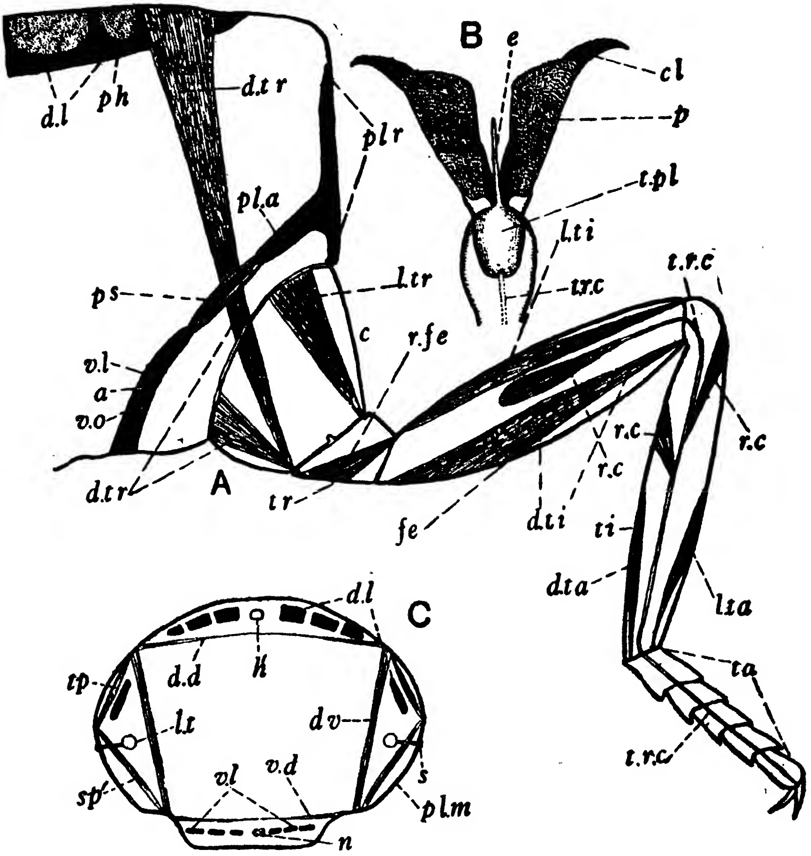

FIG. 22.—LEG MUSCLES, ETC.

A, leg of an insect showing intrinsic muscles. B, pretarsus with two pulvilli and an empodium. C, transverse section showing main abdominal muscles. *cl*, claw; *d.d*, dorsal diaphragm; *d.ta*, flexor of tarsus; *d.ti*, do. of tibia; *d.tr*, do. of trochanter; *e*, empodium; *fe*, femur; *h'*, heart; *l.t*, longitudinal tracheal trunk; *l.ta*, extensor of tarsus; *l.ti*, do. of tibia; *l.tr*, do. of trochanter; *n*, nerve-cord; *p*, pulvillus; *pl.a*, pleural arm; *pl.m*, pleural membrane; *r.c*, retractor of claws; *r.fe*, flexor of femur; *s*, spiracle; *sp'*, sterno-pleural muscle; *ta*, tarsus; *ti*, tibia; *tp*, tergo-pleural muscle; *t.pl*, tractor plate; *tr*, trochanter; *t.r.c*, tendon of retractor of claws; *vd*, ventral diaphragm. Other lettering as in Fig. 21.

and *extensor of the tibia.* A single muscle, the *retractor of the claws*, has points of attachment on the femur and tibia and its long tendon is inserted on to the tractor plate of the pretarsus. Its action is to pull the claws downward and towards the tarsus, the extension of the claws being effected by the elasticity of their basal supporting parts. Originating in the distal half of the tibia are the *flexor* and *extensor of the tarsus*, while their insertion is on the dorsal and ventral borders, respectively, of the base of the first tarsomere.

8. **The Abdominal Muscles.** The absence of legs and wings greatly simplifies the myology of the abdomen but, on the other hand, there are special muscles associated with the ovipositor and male genitalia. The principal abdominal muscles include the following (Fig. 22, c):

(*a*) *Dorsal longitudinal*, whose origins and insertions are on the intersegmental folds. They form a series along either side of the heart.

(*b*) *Ventral longitudinal*, that are the counterparts of (*a*) and lie on either side of the ventral nerve-cord.

(*c*) *Dorso-ventral*, that are mostly tergo-sternal in their attachments. They either lie within their segments of origin or cross from one segment to the next. They function as compressors of the abdomen and are of importance in respiration (p. 52).

(*d*) *Pleural*, including tergo-pleural and sterno-pleural series: in some insects they function as dilator and occlusor muscles of the spiracles.

THE RESPIRATORY SYSTEM

In the great majority of insects respiration takes place by means of internal tubes known as *tracheae*, which conduct air directly to the tissues. These tubes ramify over and among the various organs and open to the exterior by means of *spiracles*. In a relatively small number of insects respiration is cutaneous, while in the immature stages of many aquatic species special respiratory organs termed

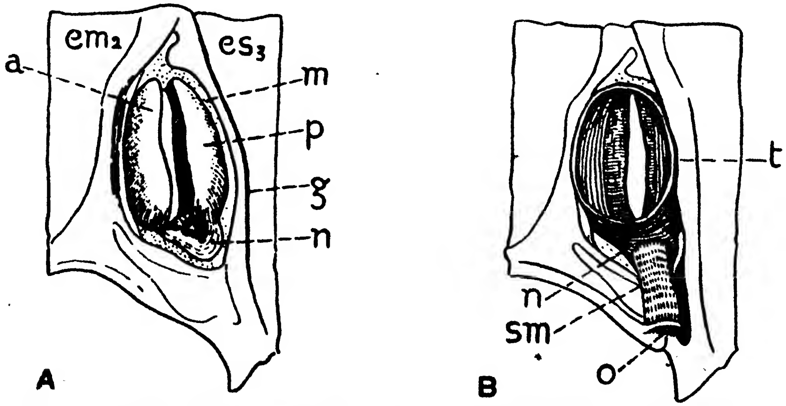

FIG. 23.—METATHORACIC SPIRACLE OF A GRASSHOPPER (*DISSOSTEIRA*)
A, outer view. B, inner view. *em*$_2$, mesepimeron; *es*$_3$, metepisternum; *g*, intersegmental fold; *m*, membrane; *t*, trachea. Further explanation in the text. (*Adapted from* Snodgrass, 1929)

gills (or *branchiae*) prevail. In all cases the respiratory organs are derived from the ectoderm : the tracheae are developed as tubular invaginations and the gills arise as outgrowths. Histologically, both types of organ consist of a thin layer of cuticle, an epidermal layer and usually a basement membrane, all of which are continuous with similar layers of the general integument.

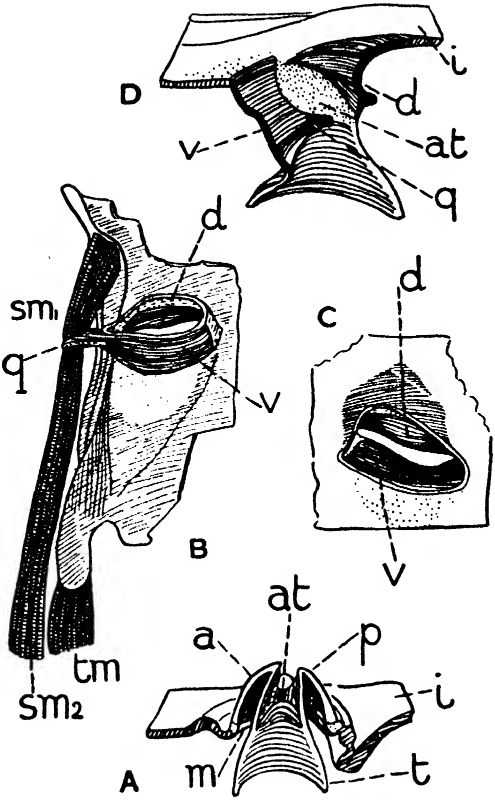

FIG. 24.—SPIRACLES OF A GRASSHOPPER (*DISSOSTEIRA*)

A, D, sections through metathoracic and 1st abdominal spiracles respectively. B, inner view and, C, outer view of 1st abdominal spiracle. *at*, atrium ; *i*, integument ; *tm*, tympanal muscles. Further explanation in the text.

(*Adapted from* Snodgrass, 1929)

The Spiracles. The spiracles are paired openings usually situated on the pleura of the meso- and metathorax and along the sides of the abdomen. In generalized insects such as Orthoptera and in many larvae there are ten pairs of spiracles, two pairs being thoracic and eight pairs abdominal in position (Fig. 15). Reductions in this number, however, are very frequent. Prothoracic spiracles may be present in the embryo, but become suppressed before hatching. In those cases where apparent prothoracic spiracles are retained their presence on this segment is apparently due to migration from the segment behind. Although spiracles are wanting in most Collembola, a single pair is present on the neck in certain of the Sminthuridae. In the Diplura some of the Japygidae carry four pairs of thoracic spiracles, i.e. the usual meso- and metathoracic pairs, together with two posterior pairs not represented in other insects.

Many structural types of spiracles occur, and the simplest is found in some Apterygota, where they are merely openings into the tracheal system and devoid of means of regulating their size. More usually the external opening is located into a depression of the integument termed the *atrium*, and a secondary spiracular opening is developed in consequence, the primary opening thus becoming the tracheal orifice. The spiracular orifice often lies in a small sclerotized plate or margin known as the *peritreme*. The passage of air in and out of the tracheae is regulated by a *closing apparatus* of which there are two main types (Figs. 23 and 24). In thoracic spiracles, in particular, the orifice is bounded by two movable valve-like plates or lips. The second type is found on the abdomen where the spiracles are without lips and an internal closing mechanism is present. The two types are well shown in cockroaches and in grasshoppers where, in the latter, the metathoracic spiracles have the lips (*a*, *p*) united by a ventral lobe (*n*). They open by means of their own elasticity, but are closed by an occlusor muscle (*sm*) arising from a process (*o*) on the mesocoxal cavity. The abdominal spiracles are without external lips and the integument is inflected to form two sclerotized walls of the atrium—one wall (*v*) being movable and the other (*d*) is fixed. The movable wall is prolonged into a process (*q*) to which *occlusor* (sm_1) and *dilator muscles* (sm_2) are attached. Spiracles of the second type often have the atrial wall produced into interlacing branched hair-like processes or *trabeculae* forming a filtering apparatus. This device allows of free passage of air, while the entry into the atrium of foreign particles or water is prevented. Provision of this kind is common in Lepidopterous larvae. In larvae of the blow-fly (*Calliphora*) and other Diptera there is no closing apparatus. The anterior spiracles consist of short lobes perforated at their apices and the posterior spiracles have three openings guarded by trabeculae (Fig. 91, D and E).

The Tracheae. The tracheae when filled with air present a silvery appearance. They are lined by cuticle continuous with that of the body-wall. This lining has a characteristic striated appearance that is due to thread-like ridges which run spirally around the inner circumference and form the so-called spiral thread. Continuity of the spiral is often interrupted and a new spiral then begins (Fig. 25). The functions of this spiral thickening is to keep the tracheae distended. and thereby allow of the free passage of air. Externally there is a layer of polygonal cells that secrete the cuticular lining. When a trachea is followed in its branching it finally enters a stellate *end-cell* (Fig. 26) and there

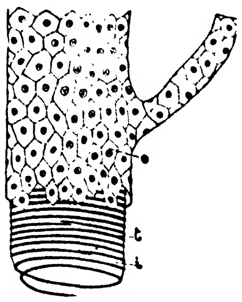

FIG. 25.—PORTION OF A TRACHEA STAINED WITH IRON-ALUM HAEMATOXYLIN (Highly Magnified)

e, epithelial layer (ectotrachea); *i*, chitinous intima (endotrachea) with taenidium, *t*

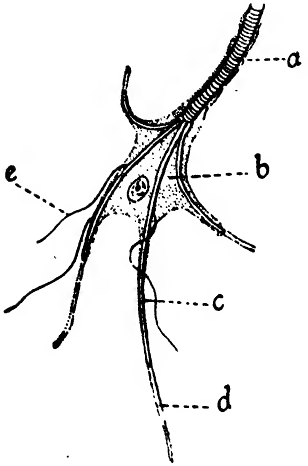

FIG. 26.—TRACHEAL END CELL IN HEAD OF MOSQUITO LARVA *AËDES AEGYPTI* (*After* Wigglesworth)

a, trachea ; *b*, tracheal end cell ; *c*, tracheole containing air ; *d*, terminal part of tracheole containing fluid ; *e*, fine branch of tracheole

divides into tracheal capillaries or tracheoles, which are less than 1μ in diameter and devoid of the spiral thickening. The mode of ending of tracheoles in the tissue is varied. Thus they may ramify and pass between the cells of the gut and salivary glands without penetrating their cytoplasm. In the fat-body and rectal papillae they may enter the cells, while in the flight muscles there is a network of intracellular tracheoles.

It is probable that originally most segments of the body had their own tracheal supply in connection with the respective pairs of spiracles. This condition is maintained in *Campodea* and in various Thysanura. The union of each segmental tracheal system by longitudinal trunks is a secondary development that provides more efficient aeration. As a rule there are present on each side of a typical segment three principal tracheae (Fig. 27) : these arise from the longitudinal trunk (*l*) near to where the *spiracular trachea* (*s*) joins it. A *dorsal trachea* (*d*) supplies the dorsal musculature and the dorsal vessel : a *visceral trachea* (*vs*) passes to the digestive canal, fat-body and the gonads : and a *ventral trachea* (*v*) sends branches to the ventral musculature, the nerve-cord and to the legs (in the case of the thoracic segments). A pair of main longitudinal trunks

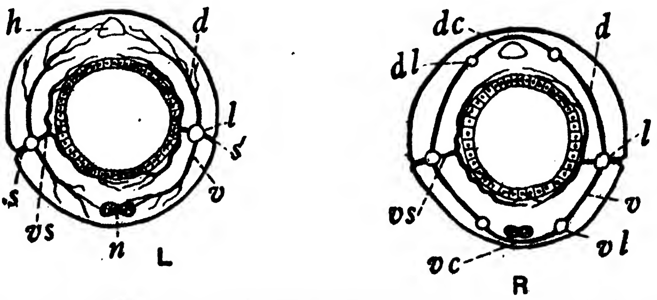

FIG. 27.—DIAGRAMMATIC TRANSVERSE SECTIONS OF THE ABDOMEN SHOWING TWO TYPES OF TRACHEAL SYSTEM

L, with lateral longitudinal trunks, *l* : R, with dorsal *dl*, and ventral, *vl*, longitudinal trunks, together with dorsal, *dc*, and ventral, *vc*, commissural tracheae. *d*, *vs*, *v*, dorsal, visceral and ventral tracheae ; *s*, spiracular trachea ; *h*, heart ; *n*, ventral nerve-cord connected by transverse segmental commissures is generally present. Secondary longitudinal trunks, i.e. dorsal, visceral, and ventral, may also be developed. The wings are supplied by branches from the tracheae of the legs of their segments.

The Air-sacs. In many insects thin-walled sac-like dilations or *air-sacs* occur in large numbers. For the most part they are extremely delicate in structure and are devoid of any special thickening (Fig. 28). In the cockchafer (*Melolontha*) and in grasshoppers (Acrididae) air-sacs are present in large numbers as dilatations of the smaller tracheae. In the House-fly (*Musca*) and in many other Diptera and in bees the main tracheal trunks are dilated to form extensive air-sacs, especially in the abdomen. Air-sacs are mainly developed in swiftly flying insects, and one of their functions is to give increased ventilation to the tracheal system. They respond very rapidly to increase and decrease of pressure resulting from respiratory movements and consequently greatly increase the volume of the inspired and expired air with each respiration.

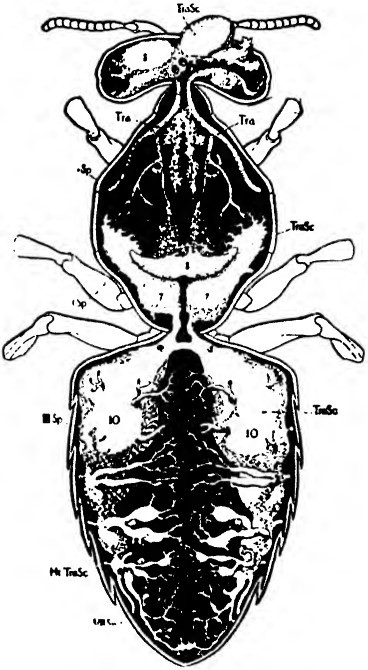

FIG. 28.—TRACHEAL SYSTEM OF WORKER BEE SEEN FROM ABOVE

(One pair of abdominal air-sacs removed and transverse ventral commissures of abdomen not shown.) The air-sacs (Tra.Sc.) are indicated in arabic numerals ; *sp*, spiracles. (*After* Snodgrass, U.S. *Bur. Entom. Tech. Ser.* No. 18)

Types of Tracheal System. Several types of tracheal system are recognized and they depend upon the locations of the functional spiracles (Fig. 29). When the full complement of 10 pairs of spiracles is present, or only a few pairs are closed, the system is said to be *peripneustic* : if only the anterior and posterior pairs of spiracles remain open the system is described as *amphipneustic* : when the anterior pair alone persists it is *propneustic* and when only the posterior pair is present it is *metapneustic*.[1] Frequently the spiracles are all closed

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[1] There are also a few anomalous types of minor importance with a greatly reduced number of functional spiracles. They include the Coccidae with two pairs only (on the thorax) : Thysanoptera with one or two pairs of thoracic spiracles and a pair on the 1st and 8th abdominal segments—and a few other examples. Such exceptions may be included under the term *oligopneustic*.

or are atrophied and the insect is then said to be *apneustic.* This latter condition may be divided into forms which breathe through the skin when they are said to be *dermatopneustic,* and into those that breathe by gills or *branchiopneustic* forms. The primitive system was peripneustic and the other systems are derivatives of that type. Among insects in which some or all the spiracles are closed, especially among larvae, the spiracular tracheae often remain as solid strands or *stigmatic cords.* These cords pass from the longitudinal trunks to points on the cuticle occupied by the original spiracles. Their presence is confirmatory of an original ancestral condition with the full complement of open spiracles. A few insects, including the early instars of endoparasitic Hymenopterous larvae and most Collembola, are devoid of all trace of a tracheal system. Such insects are said to be *atracheate.*

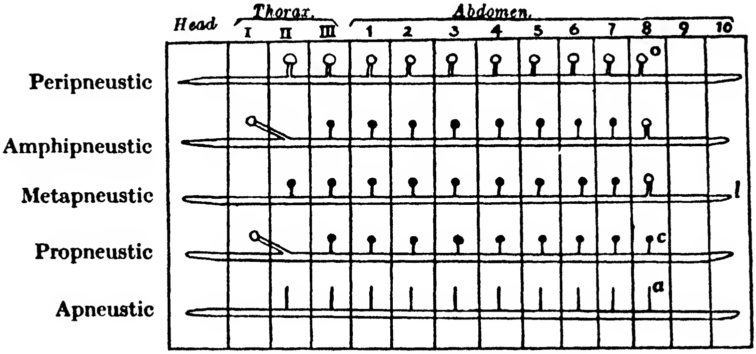

FIG. 29.—TYPES OF TRACHEAL SYSTEM

a, spiracle absent; *c,* spiracle closed; *o,* functional spiracle; *l,* longitudinal tracheal trunk

Respiration. Air enters the tracheal system through the spiracles and is either continuously changed by the physical process of gas diffusion or rhythmically changed by respiratory movements in combination with diffusion. In most larvae and pupae and in the smaller and less active adult insects, diffusion fulfils respiratory needs. Among the larger and more active insects respiratory movements are a regular part of the act of breathing. Expiration is effected by the dorso-ventral muscles of the abdomen, whose contraction flattens the body in Orthoptera and Coleoptera, while among Hymenoptera and Diptera telescopic movements of the abdominal segments result. Inspiration is usually effected by the elasticity of the body-segments as they regain their original contour. While most of the tracheae are circular in cross-section and are, therefore, non-compressible they are on the other hand very extensible in the linear direction. The main tracheal trunks are often oval in cross-section and are readily compressed while the air-sacs are even more prone to collapse. By alternately compressing and dilating the main tracheae, respiratory movements bring about mechanical ventilation of the larger tubes. In some insects it is known that there is a directed air flow in the tracheal system. Among the Acrididae in particular it has been shown that the first four pairs of spiracles are open, while the remaining six pairs are closed, with the result that the former serve for inspiration and the latter for expiration. In the beetle *Dytiscus* it has been estimated that the tracheal system is emptied during strong expiration of nearly two-thirds (64 c.mm.) of its total capacity (107 c.mm.), the remainder being changed by diffusion. While the intake of oxygen is through the spiracles, the elimination of carbon dioxide, owing to its much greater diffusibility through animal tissues, takes place to a considerable extent either through the general integument or, in heavily sclerotized insects, through the membranous regions only. Diffusion accounts for the gaseous exchange in all except the larger tracheae, and the uptake of oxygen by the tissues mostly occurs in the tracheoles. The examination of living insects shows that a variable amount of fluid is present in these tracheal endings, which may be only 0·3μ in diameter. It has been calculated that the force of capillarity in them will represent a pressure of about 10 atmospheres. In other words, a force of this order is needed to prevent a rise of fluid in the tracheoles. According to the theory of Wigglesworth (Fig. 30) the surrounding tissue fluids exert an osmotic pressure of this magnitude and, since this pressure increases during muscular activity, liquid will be absorbed from the tracheoles and air will replace it. In this way the surface from which oxygen can diffuse into the tissues is correspondingly increased. When the muscles

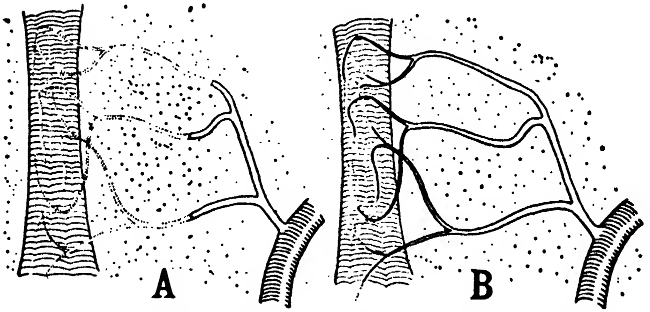

FIG. 30.—TRACHEOLES RUNNING TO A MUSCLE-FIBRE: SEMI-SCHEMATIC (*After* Wigglesworth)

A, muscle at rest; terminal parts of tracheoles (shown dotted) contain fluid. B, muscle fatigued: air extends far into tracheoles are at rest, and the metabolites responsible for the increased osmotic pressure are removed, fluid will again ascend into the tracheoles.

It is especially noteworthy (see p. 60) that no oxygen carrier is known in insect blood and that its oxygen capacity seems to be no greater than can be accounted for by physical solution. An exception to this generalization is found in the aquatic larvae of certain midges of the family Chironomidae, whose blood contains haemoglobin in the plasma. It acts as a carrier and enables the blood to bind chemically enough oxygen for the requirements of the creature when the oxygen tension becomes too low for the necessary amount to be provided by physical solution. Such conditions obtain in the mud of standing water frequented by these larvae.

Respiration in Aquatic Insects. The most complete adaption to aquatic life is found in larvae or nymphs that live submerged and without contact with atmospheric air. Respiration is accomplished by gas diffusion through the thin integument. Common examples are found in fly larvae such as those of *Chironomus* and *Simulium*. In other insects, certain parts of the integument are exceedingly thin-walled and project from the body surface either as lamellae or such as *Dytiscus*, *Notonecta*, &c., come to the surface repeatedly and take in a store of air for use while submerged. In *Dytiscus* this store is lodged beneath the elytra and cannot be displaced by the water. Such an insect remains submerged from 10 to 20 minutes before the contained oxygen is used up. It has been shown that the subelytral air also forms a kind of 'physical gill' capable of extracting dissolved oxygen from the water. Its capacity to act in this way is owing to the invasion coefficient of oxygen between water and air being over three times greater than that of nitrogen. It follows that as the partial pressure of oxygen in the air-store becomes reduced oxygen will diffuse into it from the water rather than nitrogen diffusing out of it. But while some nitrogen will pass into solution in the water, as long as any remains in the air-store dissolved oxygen will diffuse inwards and be available for respiration.

In larvae of beetles of the genus *Donacia* and of certain mosquitoes, &c., the posterior spiracles are modified for piercing the stems of water plants in order to obtain oxygen from the intercellular spaces.

Respiration in Parasites. Endoparasitic insects living in the body-space of their hosts, and thus immersed in blood, show very similar respiratory adaptations to those displayed by aquatic larvae. Thus, in the early instars of parasitic Hymenoptera spiracles are often wanting and respiration is effected by diffusion through the very thin integument. The only available oxygen is held in solution in the blood of the host and diffusion takes place from a region of higher partial pressure maintained in this medium to one of lower partial pressure in the parasite. A metapneustic tracheal system prevails in the larvae of Tachinid flies which are thereby adapted to respire atmospheric air. This they obtain either by perforating the integument of the host or one of its main tracheal trunks, and inserting the spiracular extremity of the body into the opening thus formed. A number of parasites have outgrowths from the caudal end which, in some cases, are comparable with the gills of aquatic forms. They may be well supplied with tracheae and circulating blood and apparently function in extending the surface area available for gaseous exchange. In most cases, however, their respiratory function is either doubtful or not proven.

Biological Indicators of Oxygen Consumption. With an insect larva perhaps only 0·5 mm. long it is very difficult to ascertain by ordinary physical methods whether any particular region of the body is the seat of respiratory activity. In the case of aquatic and endoparasitic larvae various Protozoa, *Bodo*, *Polytoma*, &c., have been used as indicators of oxygen consumption. Advantage is taken of the fact that these organisms are highly sensitive and migrate to a region where the oxygen tension is lower than that in water saturated at atmospheric partial pressure. If a culture of these organisms is run under a coverslip they at once arrange themselves in a zone around an insect at the place where oxygen is being absorbed from the water (Fig. 81). As the oxygen tension falls below the optimum, owing to the respiratory activity of the insect, the Protozoa retreat further and further away from the region or organ concerned. By using this technique Munro Fox has shown, for example, that the pupal gills of *Simulium* are the seat of respiration and that the blood gills of *Chironomus* are not specially active in this way. By means of similar methods Thorpe has shown that the 'tails' of endoparasitic Ichneumon larvae seem to play little or no part in respiration. After dissection from their hosts such parasites are examined under a microscope in Ringer's solution to which a culture of *Polytoma* has been added. On referring to Fig. 81, c, it will be noted that oxygen consumption goes on over the general body surface and that the 'tail', once believed to be of respiratory significance, seems to play no part in this connection. Or, the parasite may be introduced into a culture of luminous bacteria (*B. phosphorescens*) and then examined in total darkness. As oxygen becomes used up by the parasite the luminous zone is

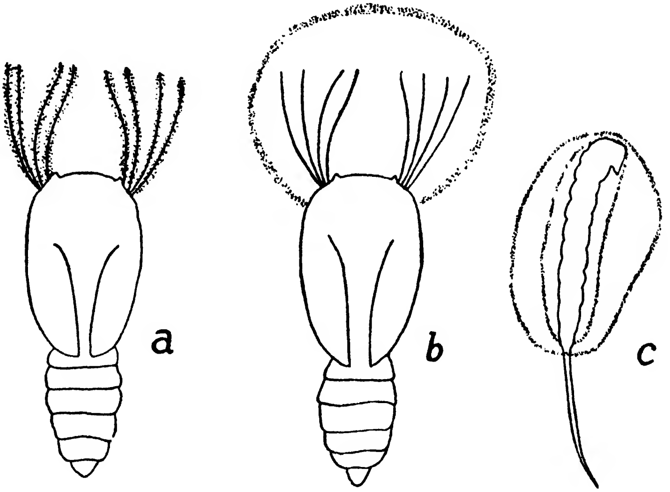

FIG. 81.—DEMONSTRATION OF THE SEAT OF RESPIRATION IN SMALL INSECTS BY THE AID OF BIOLOGICAL INDICATORS

a, pupa of *Simulium* immersed in a culture of *Bodo* which are congregated around the gills; *b*, later, showing the *Bodo* in a band some distance away from the gills (*after* Munro Fox); *c*, larva of an Ichneumon immersed in a culture of *Polytoma*, showing successive positions at which bands of aggregation are formed (*After* Thorpe) gradually limited to the periphery of the culture. Carbon dioxide output, on the other hand, can be investigated on the slide by means of *p*H indicators.

THE CIRCULATORY SYSTEM AND ASSOCIATED TISSUES

The body-cavity in insects is a haemcoele which contains the circulating blood. All the organs and tissues are bathed with this fluid and perform their functions through exchanges with it. The haemocoele in the majority of insects is divided into sinuses by fibro-muscular septa or diaphragms (Fig. 32). The *dorsal diaphragm* is the septum most constantly present: it extends across the abdominal cavity just above the digestive canal and, in this way, divides the haemocoele into a *dorsal* or *pericardial sinus*, containing the dorsal vessel, and a very large *visceral sinus* representing the remainder of the body-cavity. In some insects there is also a *ventral diaphragm* stretching across the abdominal cavity above the nerve-cord and thus demarcating a *ventral* or *perineural sinus*. Pairs of *alary muscles* arise from the abdominal terga and spread out fanwise over the dorsal diaphragm.

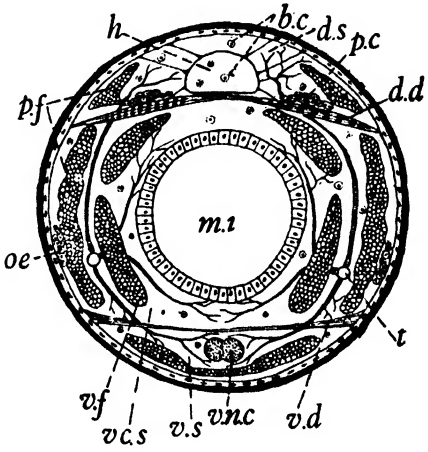

FIG. 32.—SCHEMATIC SECTION ACROSS THE ABDOMEN OF AN INSECT SHOWING HAEMAL SYSTEM AND FAT-BODY

b.c, blood cells; *d.d*, dorsal diaphragm; *d.s*, dorsal sinus; *h*, heart; *m.i*, mid-intestine; *oe*, oenocytes; *p.c*, pericardial cells; *p.f*, parietal fat-body; *t*, main trachea; *vc.s*, visceral sinus; *v.d*, ventral diaphragm; *v.f*, visceral fat-body; *v.n.c*, ventral nerve-cord; *v.s*, ventral sinus

The **dorsal vessel** (Fig. 33) is the main conducting organ of the circulatory system and is divided into the heart and the aorta. The *heart* is a muscular contractile tube situated in the median line of the pericardial sinus just above the dorsal diaphragm. It is held in position by fibrous strands connecting with the body-wall and the diaphragm. As a rule, the heart is a narrow continuous vessel whose sides are perforated with vertical slit-like openings or *ostia*. The margins of the ostia are prolonged inward to form valves which prevent the return of blood from the heart into the pericardial sinus. In other cases the heart shows a series of dilatations or chambers usually corresponding in number to the pairs of ostia and of alary muscles. While there may be a chamber of the heart to each segment of the abdomen and to the 2nd and 3rd segments of the thorax, as in cockroaches, the number of chambers is generally much fewer and may even be reduced to a single terminal enlargement. The *aorta* is the slender anterior prolongation of the dorsal vessel which carries the blood into the head where it opens behind or beneath the brain. The wall of the heart is muscular and is composed of flattened cells whose outer cytoplasm is differentiated into striated muscle fibrils. These cells are bounded externally and internally by a delicate membrane which may be regarded as a sarcolemma. Apart from the aorta there are few closed vessels associated with the circulatory system. Among the most frequent are antennary arteries: in *Blatta* and the hive bee the blood is propelled through these vessels by special *pulsatile organs* situated at their bases. Pulsatile organs are also found in the thorax where they maintain circulation of the blood in the wing veins.

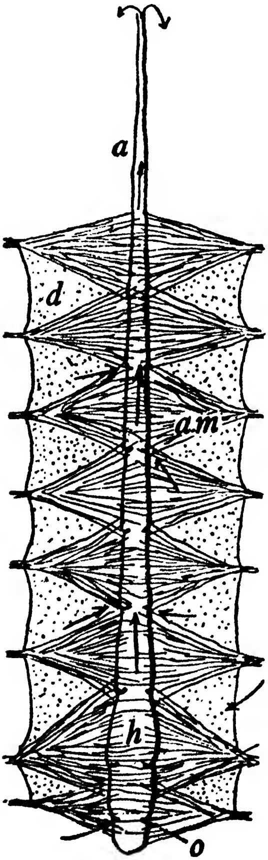

FIG. 33.—DORSAL VESSEL OF A BEETLE—VENTRAL SIDE

***a*, aorta; *a.m*, alary muscle; *d*, dorsal diaphragm; *h*, heart; *o*, ostium. Arrows show course of circulation**

The **blood** or *haemolymph* is either clear or tinged with green or yellow pigment. Suspended in this fluid are numerous colourless blood cells or *haemocytes* (Fig. 34). Various kinds of these cells have been described but several are merely developmental phases of other

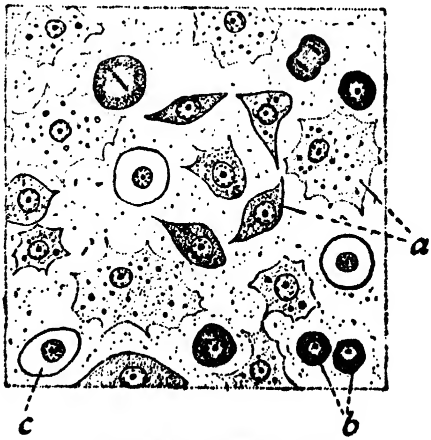

FIG. 34.—HAEMOCYTES

***a*, phagocytes; *b*, proleucocytes; *c*, oenocytoid. (*From* Wigglesworth)**

haemocytes. The more important are (1) *proleucocytes*, small cells with deeply staining cytoplasm, and large nuclei: they are often seen undergoing mitosis and are regarded as young forms of haemocytes. (2) *Phagocytes*, which are basophil and of variable appearance and character: their amoeboid activities enable them to digest tissue debris, bacteria, &c., and they greatly increase in numbers during ecdysis and metamorphosis. These cells also have the property of congregating around and enclosing foreign bodies: they also collect at the site of a wound forming a plug which facilitates healing. (3) *Oenocytoids*, which are rounded cells with acidophil cytoplasm. They bear a resemblance to small oenocytes, but their function is obscure.

The **circulation** of the blood begins in an anterior stream that is maintained by waves of contraction, passing from behind forward, over the heart. During diastole blood is drawn into the heart, through the ostia, under a negative pressure. During systole a positive pressure is set up and the blood is driven forward into the heart-cavity. Here some of it circulates through the antennae, but ultimately the blood enters the visceral sinus after a proportion has circulated through the legs and wing-veins. Undulatory movements of the ventral diaphragm direct a blood flow backward along the perineural sinus. Leaving the latter, through spaces along its sides and posterior end, the blood ascends among the viscera. It then becomes drawn into the pericardial sinus by contractions of the alary muscles. This alters the contour of the dorsal diaphragm and passage of the blood into the sinus occurs through perforations in this membrane (Fig. 85). The property of rhythmical contraction of the heart lies in the muscle fibrils of its walls. This automatism is evident in the isolated heart or even in severed portions of the same since they continue to beat in the usual rhythmic manner. The pulsation rate is influenced by many causes. Thus, it is increased as the temperature is raised: it may vary in different instars of the same insect and it also depends on the activity of the individual insect. It has long been known that in *Sphinx ligustri* the heart beat of the moth is at the rate of 41–50 per minute when at rest and 110–189 during activity. In the larva the rate is highest

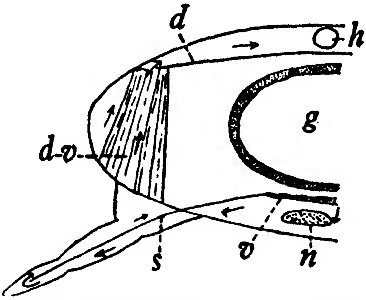

FIG. 85.—CROSS-SECTION OF THORAX OF *BLATTA* SHOWING COURSE OF CIRCULATION

d, dorsal diaphragm; *d-v*, dorso-ventral muscle; *h*, heart; *n*, nerve-cord; *s*, septum; *v*, ventral diaphragm. (*Adapted from* Brocher)

(82–89 per minute) in the early instars and lowest in the pupa when it declines to 10–12 beats per minute, while during hibernation it almost entirely ceases.

The main function of the blood is to convey nutrient substances to the tissues and to transfer waste materials to the excretory organs. Its part in respiration in tracheate forms is small since it does not take up more oxygen than can be accounted for by physical solution and no chemical carrier is known (see also p. 54). The only exception to the latter statement is in larvae of certain midges (Chironomidae) whose blood contains haemoglobin in solution (p. 162). The blood has definite mechanical functions since it provides the means of transferring pressure from one part of the body to another and, in this way, aids in ecdysis and in hatching from the egg and eclosion from the pupa. It also acts as the carrier of hormones from one part of the body to another. In its reaction insect blood is slightly acid with a *p*H of 6·4–6·8. Associated with the circulatory system are the following organs and tissues.

(1) **The Nephrocytes.** These occur as groups of special cells found in localized regions of the insect body. They have the common property of absorbing ammonia carmine, when injected into the haemocoele, and of retaining precipitated carmine in their cytoplasm. On account of this feature they are supposed to have a similar action on natural waste products. They occur very constantly as strands of often binucleate *pericardial cells* on either side of the heart in the pericardial sinus. These cells seem to be analogous with the reticulo-endothelial system of vertebrates and absorb unwanted colloid particles from the blood, but little is known as to what goes on during this process (Fig. 32).

(2) **The Oenocytes.** These are usually large cells often of a wine-yellow colour to which they owe their name. They occur in almost all orders of insects, including larvae, and rank among the largest cells of the body measuring up to about 180μ across. Their large nuclei, eosinophil and dense cytoplasm with an external limiting membrane are characteristic features. They arise from the ectoderm of the embryo as segmental groups of cells situated close behind the invaginations that give rise to the abdominal spiracles (Fig. 32). They may remain associated with the epidermis as in *Blatta* or migrate into the peripheral fat-body (*Locusta, Anopheles*) or come to be in close association with spiracular tracheae (Lepidoptera). Oenocytes show a cycle of morphological changes and secretory activity at the time of moulting, usually increasing greatly in size just before that process: the cytoplasm becomes vacuolated and the cells may become lobed as in *Rhodnius*. It seems probable that they discharge a substance into the blood, possibly a hormone, that is connected in some way or other, at present unknown, with the moulting process.

(3) **The Corpora Allata.** These are a pair of small ductless, glandular bodies that are universally present among insects and their larvae but are not known in other arthropods. They lie near to the oesophagus, a short way behind the brain, and are closely associated with the posterior sympathetic ganglia (Fig. 13). In the embryo they arise as paired invaginations of the ectoderm of either the mandibular or maxillary segment, but ultimately they lose all connection with that cell layer and become wholly internal organs. Corpora allata undergo cycles of histological change and assume appearances of greatest secretory activity at definite periods. Facts of this kind, together with certain experimental evidence, suggest that these bodies, in some insects at any rate, secrete a hormone governing metamorphosis (see also p. 96) and ecdysis (p. 86).

THE DIGESTIVE SYSTEM

The alimentary canal (Fig. 36) is divided into three regions, viz. the *fore-intestine* that arises as an anterior ectodermal ingrowth (stomodaeum): the *hind-intestine* that arises as a similar posterior ingrowth (proctodaeum): and the *mid-intestine, stomach* or *ventriculus* formed as an endodermal sac (mesenteron) connecting the two. These differences in embryonic origin result in marked histological differences in the structure of the mid-intestine as compared with either of the other regions. The fore and hind-intestine, being ingrowths of the integument, resemble the latter histologically and are lined with cuticle.

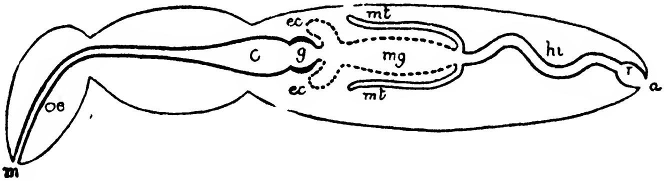

FIG. 36.—DIAGRAM OF THE DIGESTIVE SYSTEM OF AN INSECT

The ectodermal parts are represented by heavy lines and the endodermal parts by broken lines. *m*, mouth; *oe*, oesophagus; *c*, crop; *g*, gizzard; *e.c*, enteric coeca; *m.g*, mid-intestine; *m.t*, Malpighian tubes; *h.i*, hind-intestine; *r*, rectum; *a*, anus

The **Fore-Intestine** begins at the mouth and leads into the pharynx. In chewing insects the mouth is bounded by the labrum above, the labium below and by the mandibles and maxillae on either side. In sucking insects a true mouth is absent, the actual entrance into the digestive system being situated at the apex of the organ of suction. The *pharynx* is recognized by its dilator muscles that pass to the head wall: it is specially well developed in sucking insects. There follows the *oesophagus* and this part is either a simple narrow tube leading to the mid-intestine or, more often, its hind part is modified into a *crop*. In the cockroach the crop is a symmetrical dilation of the oesophagus, but in the blow-fly and most Lepidoptera it is a lateral diverticulum, or food reservoir, joined to the oesophagus by a narrow tube (Fig. 39). The fore-intestine is separated from the mid-intestine by the cardiac sphincter, and at this region it is often modified to form a muscular *proventriculus* or *gizzard*. The crop functions either as a temporary food-chamber from which the food is transferred to the mid-intestine as required or, as in the cockroach, it is the receptacle wherein most of digestion takes place. The *proventriculus* varies greatly in its development. Its main function is that of a sieve occluding the passage of food if not in a sufficiently divided state. Well developed in many chewing insects, in sucking insects it is little more than a valve. In the cockroach and other Orthoptera it has a powerful armature of radial teeth and of circular muscles and serves the additional function of crushing the larger food particles.

Histologically, the fore-intestine consists of a cellular layer, that secretes the cuticular lining, and its outer surface is covered with a basement membrane. External to the latter is a coat of longitudinal muscle-fibres overlaid by circular fibres.

The **Mid-Intestine** is composed of a layer of large epithelial cells bounded externally by a basement membrane. On their inner aspect these cells usually show a *striated border* whose nature has been much discussed (Fig. 37). A layer of minute circular muscle-fibres and external longitudinal muscles is present. In many insects increase in the superficial area of the mid-intestine is achieved by the development of outgrowths or *coeca* that vary in size and number (Fig. 38). A second method is by the folding of the epithelial layer thus giving rise to crypts; both methods may occur in the same species. The epithelial cells of most insects are of one kind, although

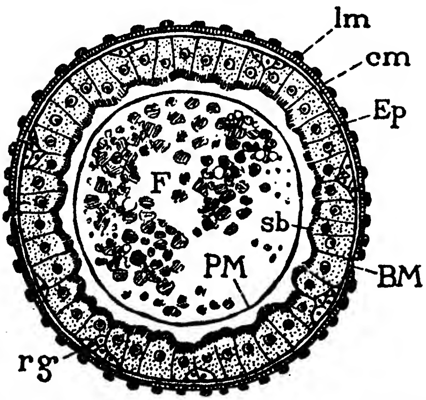

FIG. 37.—DIAGRAMMATIC CROSS-SECTION OF MID-INTESTINE

BM, basement membrane; *cm*, circular muscles; Ep, epithelium; F, food; *lm*, longitudinal muscles; PM, peritrophic membrane; *rg*, regenerative cells; *sb*, striated border. (*From* Snodgrass) individual cells may be in different phases at a given time. Secretion and absorption consequently take place by the same cells. The method of secretion may be (*a*) *merocrine* in which the cells discharge their products through the striated border and without undergoing any marked changes: and (*b*) *holocrine*, which is less prevalent but occurs in Orthoptera and is characterized by the disintegration of the cells during the process. Between the bases of the epithelial cells are small groups of *replacement cells* which divide and provide new epithelial cells (Fig. 37).

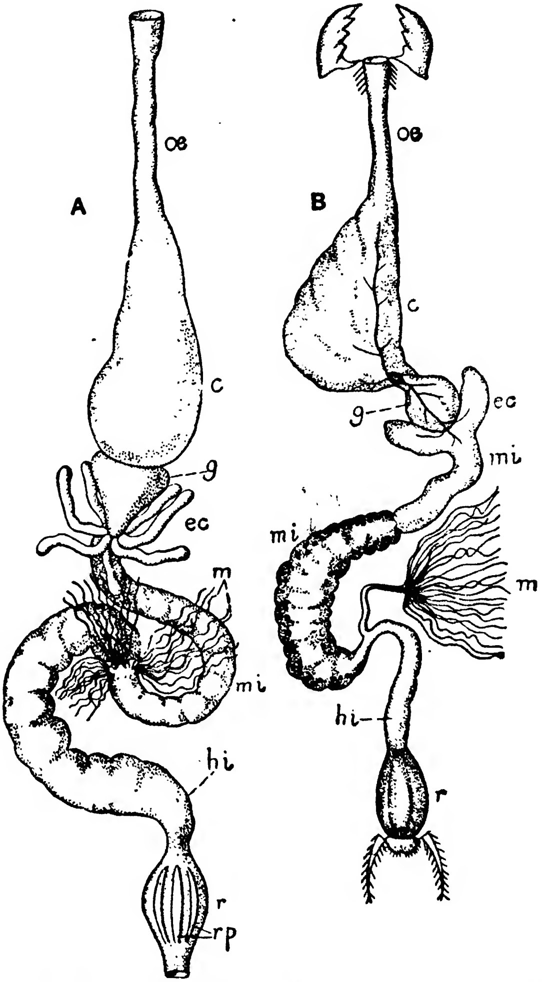

FIG. 38.—A ALIMENTARY CANAL OF *PERIPLANETA AMERICANA*. B, ALIMENTARY CANAL OF *NEMOBIUS SYLVESTRIS* (GRYLLIDAE)

oe, oesophagus; *c*, crop; *g*, gizzard; *e.c*, enteric coeca; *m*, Malpighian tubes; *m.i*, mid-intestine; *h.i*, hind-intestine; *r*, rectum; *r.p*, rectal papillae. (*After* Bordas)

In most insects and their larvae the food is separated from the epithelial lining by the *peritrophic membrane* (Fig. 37) which forms a thin, colourless tube projecting backward to extend into the hind-intestine. It is composed partly of chitin and is supposed to protect the epithelial cells from abrasion. Such an explanation is in accord with the absence of mucous cells that might perform this function. Also, the membrane is absent in many, but not in all, insects that imbibe fluid food including Hemiptera, adult Lepidoptera and numerous blood-sucking forms. The peritrophic membrane is shed through the anus at each moult and is formed either as a secretion of gland cells in the region of the cardiac valve which protrudes into the cavity of the stomach: or, as a product of the epithelial lining of that chamber. It is permeable to digestive enzymes and to the products of digestion.

In the larvae of most Neuroptera-Planipennia and Hymenoptera-Apocrita the stomach is very capacious and does not open into the hind-intestine until the end of larval life. While this feature is of obvious advantage in precluding endoparasitic forms from poisoning their hosts with their excreta, its advantage in free-living neuropterous larvae is not evident.

The **Hind-Intestine** is divisible into a narrow anterior tube or *ileum* and a wider end region or *rectum* which opens exteriorly at the *anus*. Histologically, the hind-intestine consists of the same layers as the fore-intestine, but the cuticular lining is thinner and the circular muscles are internal to the longitudinal layer. In many insects the cellular layer of the rectum becomes greatly thickened to form six longitudinal bands or *rectal papillae*. An important function of these papillae is the maintenance of the proper water-balance by absorbing water from the faeces (see p. 67). A *pyloric sphincter* separates

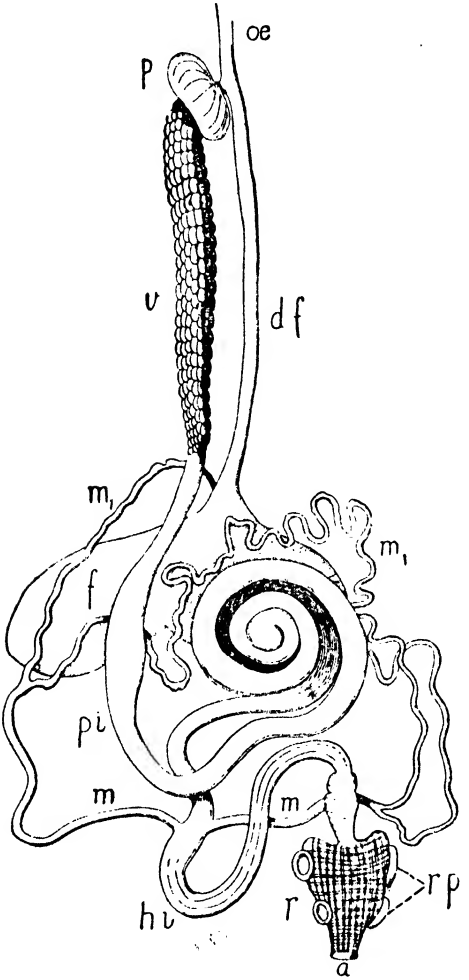

FIG. 89.—ALIMENTARY CANAL OF A MUSCID FLY (CALLIPHORA)

oe, oesophagus; *p*, proventriculus; *v*, ventriculus; *d.f*, duct of food-reservoir, *f*; *p.i*, proximal intestine; m_1, Malpighian tubes which unite to form a common stem (*m*) on either side; *h.i*, hind-intestine; *r*, rectum; *r.p*, rectal papillae; *a*, anus. (*Adapted from* Lowne) the stomach from the hind-intestine and, close to the junction of these two regions, there are outgrowths of proctodaeal origin known as *Malpighian tubes*. These vessels are the principal organs of excretion and are slender blind tubes lying in the haemocoele where they are freely bathed in blood. They vary greatly in number, ranging, for example, from 30 to 120 in Orthoptera and from 4 to 6 among many Holometabola: in the Aphididae and the Collembola these organs are wanting. Each tube is composed of large epithelial cells resting on an external basement membrane, and outside the latter there are commonly muscle fibres. The inner margins of the cells show a *striated border* resembling that of the stomach and there is no cuticular lining.

Salivary Glands are paired glands that discharge their secretion into the mouth-cavity, where it mixes with the food as this is being taken in. Usually these organs are labial glands which originate as paired invaginations of the ectoderm in close association with the developing 2nd maxillae. Their main ducts fuse to form a common outlet discharging on or near the hypopharynx. In many insects the cuticular lining of the ducts is spirally thickened as in tracheae. In caterpillars the labial glands are converted into silk-producing organs and their functions are assumed by the mandibular glands.

Physiology of the Digestive System. Almost every kind of organic substance is utilized as food by some or other insects and the feeding organs show a wider range of adaption than any other parts of the body. A cockroach (*Blatta* or *Periplaneta*) being omnivorous shows a very generalized type of nutrition. All the usual enzymes are present, as in man, excepting those of the pepsin type, that need a strongly acid medium; the chief proteolytic ferment resembles pancreatic trypsin.

The gut contents usually have a *p*H ranging between 6 and 7, but it naturally varies with the diet. The salivary glands secrete an abundant amylase which mixes with the food, but carbohydrate digestion is completed in the stomach. Its enzymes include amylase, invertase, maltase, protease and lipase which hydrolyse, respectively, starch, cane-sugar, maltose, proteins, and fats. These secretions pass forward into the crop where most of digestion takes place: only fluid matter passes through the gizzard into the stomach where absorption goes on.

In *Glossina* and other blood-sucking insects the salivary glands secrete an anti-coagulin but no digestive enzymes. Abundant protease is produced in the stomach where carbohydrate-splitting enzymes are absent except for a weak amylase. The reverse obtains in the blow-fly (*Calliphora*), where proteolytic enzymes are weak, whereas amylase, invertase and maltase are all active. In adult butterflies and moths digestion is even more specialized since their food is mainly the nectar from flowers. Almost the only enzyme in the saliva and stomach is invertase, which enables them to hydrolyse the large amount of cane-sugar taken in. Whereas most leaf-feeding insects appear to leave the cellulose component unutilized, some wood-feeding forms are able to use this constituent. Thus, certain Cerambycid larvae secrete a true cellulase and can invade the heartwood of trees, whereas others from which cellulase is absent attack only the sapwood, feeding upon the contained starch and sugar.

Micro-Organisms and Nutrition. Various kinds of micro-organisms such as bacteria, bacteroids, protozoa, yeasts and other fungi occur in intimate relationship with many insects (Fig. 40). In wood-feeding termites and the cockroach *Cryptocercus*, of similar habit, intestinal protozoa are the chief agents for breaking down cellulose. The termites can live for a long time on pure cellulose, but when deprived of their protozoa, either by raising the temperature to 36° C. for 24 hours or by increasing the oxygen tension of the air by 3½ atmospheres, they die in 3 to 4 weeks when fed upon their usual diet. Other insects contain specific micro-organisms that are transmitted from one generation to another in various ways. These organisms may be lodged in special cells or *mycetocytes* which, in many cases, are grouped to form an organ termed the *mycetome* as in Homoptera and Anoplura. While they have been cultured outside the insect body in a few instances, conclusive information as to their function has been lacking. In the case of the human louse, *Pediculus*, it has been possible to remove the micro-organisms by centrifuging the egg, when the resulting nymphs die within one week and excision of the mycetome in the female prevents egg-production. These facts suggest that the micro-organisms provide some essential vitamin or growth-promoting substance. In support of this conclusion is experimental evidence that certain constituents present in yeast are required by various insects for normal growth and that in the blow-fly larvae these substances are produced by bacteria.

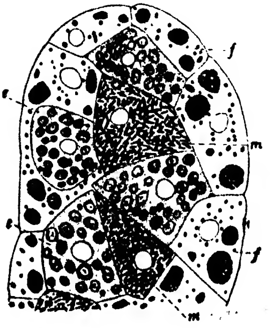

FIG. 40.—LOBE OF FAT BODY FROM *BLATTA ORIENTALIS.* × 650
e, excretory cell with concretions ; *f*, fat cell ; *m*, mycetocyte containing bacteroids. (*Adapted from* Gier, 1936)

THE EXCRETORY ORGANS AND FAT-BODY

The chief excretory organs are the **Malpighian tubes** (p. 65), but other tissues, that will be mentioned later, are believed to aid in dealing with waste products among various insects. The Malpighian tubes remove excretory matter by absorption from the blood and discharge such substances into the hind intestine. Nitrogen is mainly excreted as uric acid or as its salt ammonium urate: urea is only present in very small quantities and guanin, which is important in Arachnida, is not known in insects. While many species of insects live in surroundings providing sufficiency of water to allow of uric acid being excreted in solution, very many others have to conserve water. This happens especially in desert forms and in species living in dried timber or infesting stored grain, flour and other products. In such cases most of the water from the food is reabsorbed and results in the precipitation of the uric acid as crystalline spheres. There are several physiological types of Malpighian tubes, but detailed knowledge of their individual œconomy is lacking. It is believed that these tubes absorb sodium or potassium acid urate in water solution and, as this fluid passes towards the rectum, most of the water and base (as sodium or potassium bicarbonate) are reabsorbed. As suggested by Wigglesworth, this would result in the precipitation of free uric acid. There is consequently a continuous circulation through the excretory system, resulting in the same water and base being repeatedly used in carrying uric acid from the body.

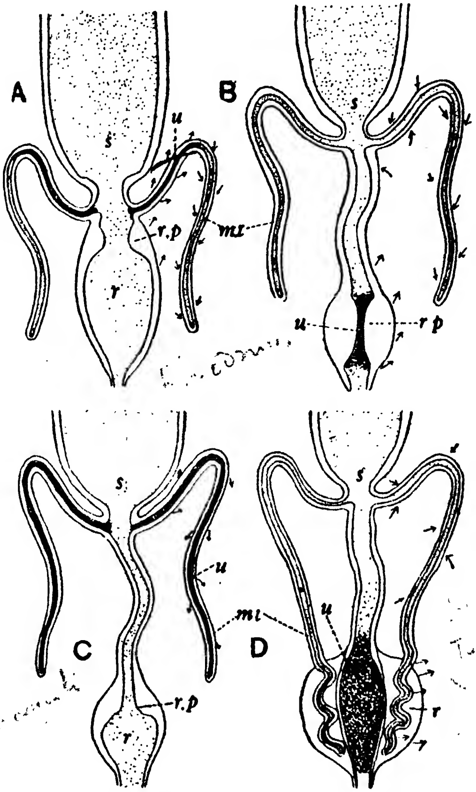

FIG. 41.—DIAGRAMS OF DIFFERENT TYPES OF EXCRETORY SYSTEM IN INSECTS

(*Adapted from* Wigglesworth. Explanation in the text.) *m.t*, Malpighian tubes; *r*, rectum; *r.p*, rectal papillae; *s*, mid-intestine; *u*, zone of precipitation of uric acid. The arrows indicate presumed course of circulation of water and base

In some insects such as the blood-sucking bug *Rhodnius* (Fig. 41, A) uric acid in clear solution is secreted in the distal two-thirds of the

Malpighian tubes, while precipitation in crystalline form takes place in the proximal part of each tube where absorption of water and base occurs in the cells. In *Lepisma*, Orthoptera, Neuroptera and many Coleoptera (Fig. 41, B) the Malpighian tubes only contain fluid while precipitation of a white crystalline mass of uric acid takes place in the rectum through whose walls water absorption is carried out. In mosquitoes and Muscid flies (Fig. 41, C) the Malpighian tubes contain solid uric acid throughout their length and a method of precipitation occurs different from that found in *Rhodnius*.

In many Coleoptera and the larvae of Lepidoptera the distal parts of the Malpighian tubes are closely attached to the walls of the rectum. This device seems for the purpose of facilitating water conservation by using the combined absorptive capacity of the rectum and Malpighian tubes. In the mealworm (*Tenebrio*) (Fig. 41, D), where such an arrangement obtains, the Malpighian tubes only contain clear fluid and the rectum is mainly occupied by a dry mass of uric acid, apparently precipitated by the almost complete absorption of the available water.

Other excretory products include calcium salts that are sometimes taken into the body in quantities greatly above requirements. They are present in the Malpighian tubes either as amorphous granules or less frequently as solid spheres or as crystals. The most general compound is calcium carbonate, which is usually stored during larval life and often used in various ways during metamorphosis, disappearing by the time the imago is reached. Many dipterous larvae contain calcium carbonate either in the Malpighian tubes or in special cells of the fat body: in phytophagous larvae of the family Agromyzidae the calcium occurs as laminated bodies or ‘calcosphaerites’ that are well seen in those of the celery fly (*Acidia heraclei*) and other species. At metamorphosis the calcium carbonate dissolves in the blood and becomes deposited on the inner wall of the puparium. Many larvae of the Cerambycidae (p. 143) line the pupal burrow with lime and also close it with an operculum composed of similar material. In the Phasmidae the chorion of the eggs is hardened by becoming impregnated with calcium.

In addition to the Malpighian tubes an excretory function, as will be mentioned later, is also performed by the fat-body. Other cells termed **nephrocytes**, and especially those known as **pericardial cells** (p. 60), have long been regarded as accessory excretory organs, but it is uncertain whether their chief function is in this capacity. Nephrocytes occur in most Arthropoda and have the common property of absorbing ammonia carmine injected into the blood and retaining its precipitate in their cytoplasm. They are supposed to have a similar action on waste products present in the blood and thereby act as storage cells.

Fat-body (Fig. 32) is present in all insects and is derived from the mesoderm of the walls of the embryonic coelomic cavities. It sometimes shows a segmental disposition and occurs as loose strands, sheets and lobes of tissue. Generally there is a visceral layer around the gut and a peripheral layer beneath the integument. Since the fat-body lies in the haemocoele it is immersed in blood which also circulates through the interspaces of this tissue. It would appear, therefore, that the fat-body is well adapted for its main function—the separation from the blood and the storage of reserve materials. These include fat, proteins and glycogen, but little is known of the various processes involved in their elaboration. In the newly hatched insect the cells of the fat-body are rounded, with a homogeneous cytoplasm free from vacuoles or inclusions. During growth these cells increase in size, become vacuolated and their boundaries are then hard to see; nuclear changes are also involved. In a starved insect the reserve food materials mentioned may become used up, but normally they are drawn upon at certain periods only, i.e. during the change from larva to pupa, during hibernation, and to some extent at each ecdysis. In adult insects the fat-body is often more developed in the female, where it provides nutriment for egg development.

The fat-body also performs an excretory function. In Collembola, Hymenopterous larvae, Orthoptera, &c., special *excretory cells* containing deposits of urates are present among the ordinary cells of the tissue (Fig. 40). The excretory cells serve in the main as storage cells until their products are eliminated at the time of pupation. In Collembola, which lack Malpighian tubes, urate concretions are deposited and increase in size throughout life: much the same is stated to occur in the cockroach, where the Malpighian tubes apparently do not eliminate uric acid.

THE REPRODUCTIVE SYSTEM

The reproductive system, whether male or female, is a group of organs often of great complexity. As a convenience the external sexual organs or genitalia were considered in a previous chapter (p. 21) and the internal organs remain to be described. Their primary parts are derived from the mesoderm and, in addition to these, secondary or ectodermal parts are almost invariably present.

The Female Organs

The primary or mesodermal parts of the reproductive system in the female are a pair of sex glands or *ovaries* and two *lateral oviducts* opening to the exterior by a pair of *gonopores* located just behind the 7th abdominal sternum. This primitive condition is only retained among may-flies, but it is passed through as a developmental phase in most insects. The paired oviducts join a secondary ectodermal *median oviduct* that usually opens by a single gonopore into a wider passage or *vagina* whose orifice is on the hind border of the 9th sternum. In addition, other ectodermal parts are usually present and include a *spermatheca* (or *receptaculum seminis*) and a pair of *accessory glands* (Figs. 42 and 43).

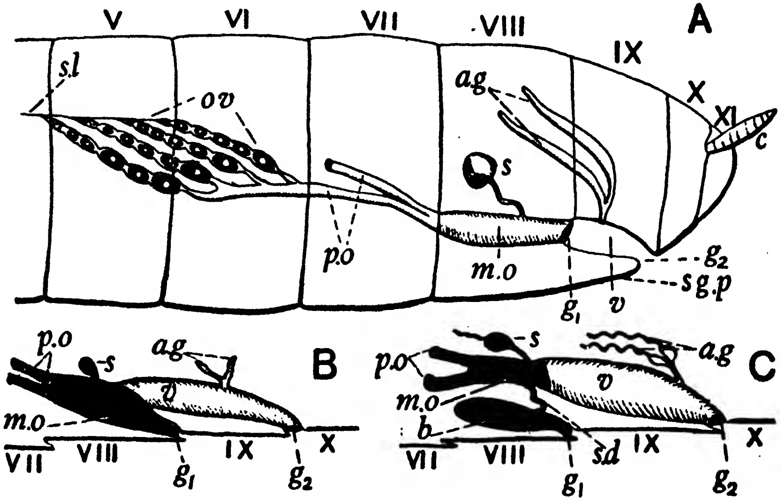

FIG. 42.—FEMALE REPRODUCTIVE SYSTEM: SCHEMATIC

A, typical system in an Orthopterous insect. B, developmental stage and, C, mature condition in Lepidoptera. In B and C homologous parts are similarly shaded. *a.g*, accessory glands; *b*, bursa copulatrix; *c*, cercus; g_1, primary gonopore; g_2, secondary gonopore; *m.o*, median oviduct; *ov*, ovary; *p.o*, paired oviduct; *s*, spermatheca; *s.d*, seminal duct; *sg.p*, subgenital plate; *s.l*, suspensory ligament; *v*, vagina. The numerals refer to the respective segments

The Ovaries. The essential feature of the insect ovary is its division into separate *egg-tubes* or *ovarioles* which open into the corresponding lateral oviduct. The primitive number of ovarioles is uncertain, and usually 4 to 8 of these tubes compose an ovary. In Hymenoptera they may exceed 200, while an even larger number is present in the queens of many termites. Reduction to a single ovariole also occurs and is found, for instance, among viviparous flies. A typical ovariole (Fig. 43) consists of a *terminal filament*, a *germarium* and a *vitellarium.* The terminal filaments of all the ovarioles of a side are usually united to form a *suspensory ligament.* The *germarium* is always terminal and contains the primordial *germ cells* or *oögonia* which later become differentiated into *oöcytes* and *trophocytes* (or nurse cells). The *vitellarium* is formed by the backward extension of the wall of the germarium. The *oöcytes* are liberated in order of their age into the vitellarium, the lowest of these cells being the first discharged. The growth of the oöcytes distends the egg-tube into a series of follicles or egg-chambers each lined by a definite *follicular epithelium*. Ovarioles are divisible into three types as follows (Fig. 43):

1. The *panoistic type* is devoid of trophocytes, the developing oöcytes being nourished by products elaborated from the blood by the follicular epithelium. This is the primitive type of egg-tube and is found in Apterygota, Orthoptera and other of the lower Pterygota.
2. The *polytrophic type* shows successive chambers containing oöcytes and trophocytes. It is found in most of the Endopterygota.
3. The *acrotrophic type* has the trophocytes remaining in the germarium but connected with the developing oöcytes by means of progressively lengthening protoplasmic strands that convey nutriment to them. This type is found in Hemiptera and in some Coleoptera. The trophocytes in Types 2 and 3 apparently obtain nourishment from the blood and pass it on to the oöcytes which elaborate from it the substances forming the yolk.

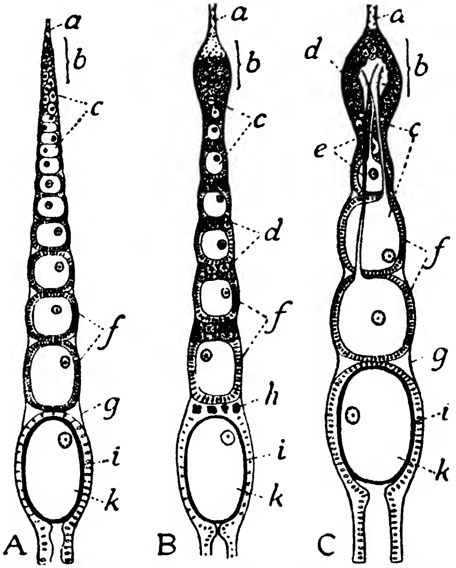

FIG. 43.—THE THREE CHIEF TYPES OF OVARIES, DIAGRAMMATIC. (*After* Weber)

A, panoistic type. B, polytrophic type. C, acrotrophic type. *a*, terminal filament; *b*, germarium *c*, oöcytes; *d*, nurse cells; *e*, nutritive cords; *f*, follicular cells; *g*, membranous coat; *h*, degenerated nurse cells; *i*, chorion; *k*, egg

The Genital Ducts and Accessory Organs. As previously mentioned, the primitive oviducts are paired mesodermal tubes opening just behind the 7th sternum. These become connected with an ectodermal ingrowth forming the median oviduct which opens on the hind border of the 8th sternum. The aperture does not usually communicate directly with the exterior, but is concealed in a chamber formed by an inflection of the body-wall of the 9th segment (Fig. 42). This chamber is the *vagina* and its floor is formed by the subgenital plate which is a backward extension of the 7th (Blattidae) or 8th sternum (Acrididae). In Lepidoptera (Fig. 42, B, C) there are generally two sexual openings. Owing to the absence of the subgenital plate the orifice behind the 8th sternum is external. It leads into the *bursa copulatrix*, which is an outgrowth of the median oviduct. A *seminal duct* connects the bursa and probably represents the remainder of the original median oviduct. While the aperture behind the 8th sternum is the true *gonopore* or copulatory pore, the second opening is that of the vagina on the 9th segment and through it the eggs are discharged to the exterior. The *spermatheca* opens on to the dorsal wall of the median oviduct or of the vagina. The spermatozoa received during mating are stored in this sac and are later liberated over the eggs after the latter have passed down the oviduct. A gland is commonly associated with the spermatheca and in such cases the spermatozoa are bathed in its secretion.

The *accessory glands* (or *colleterial glands*) open into the vagina and they commonly secrete an adhesive substance for attaching the eggs to an external object or for cementing them in a mass. In *Blatta* the secretions of the two glands produce the horny non-chitinous oötheca or egg-containing capsule.

The Male Organs

The mesodermal parts of the male reproductive system are a pair of sex glands or *testes* and two lateral ducts or *vasa deferentia*. The last-named join a median ectodermal passage termed the *ductus ejaculatorius*, which usually opens to the exterior on the *penis* (p. 21). In addition to these essential parts there is frequently a pair of *vesiculae seminales* or sperm reservoirs, formed by the enlargement of a part of each vas deferens. *Accessory glands* of ectodermal origin are also commonly present (Fig. 44).

The Testes. Each testis is composed of tubules or *follicles* variable in number, which open by narrow passages or *vasa efferentia* into the vas deferens of their side. The testis is covered outwardly by an *epithelial sheath* or peritoneal sheath : the latter name is in general use, but is open to objection since there is no peritoneal cavity (or coelom). Each follicle is lined by epithelinum resting on a basement membrane, and it is from the cells of this lining that the primordial germ cells are derived. A succession of zones, in which the germ-cells are in different stages of development, are to be distinguished. At the apex of a follicle is the *germarium* or *zone* *of spermatogonia* which comprises primordial germ-cells among numerous somatic cells. Lower down each spermatogonium becomes surrounded by somatic cells to form a cyst. By the repeated division of a spermatogonium from 64 to 256 *spermatocytes* are produced. In the next zone, or *zone of maturation*, the spermatocytes undergo reduction division so that their chromosome number is halved : each spermatocyte ultimately produces four *spermatids*. There follows a *zone of transformation* in which the spermatids, still enclosed in cysts, are converted into *spermatozoa* ; the latter break through the cyst wall by lashing movements of their flagella. At first the spermatozoa adhere by their heads into bundles, but they ultimately become free.

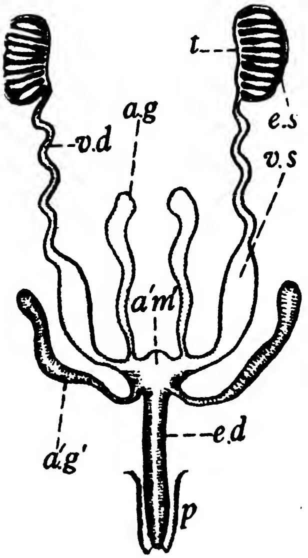

FIG. 44.—MALE REPRODUCTIVE SYSTEM : SCHEMATIC

a.g, accessory gland (mesadene) ; *a'.g'*, do. (ectadene) ; *a'm'*, mesodermal vesicle formed by union of ampullae (*am* in Fig. 45) ; *e.s*, epithelial sheath ; *p*, penis. Other lettering as in Fig. 45

The Genital Ducts and Accessory Parts. In may-flies the genital ducts remain separate and each enters the penis of its side. From this generalized condition is derived the typical system in which a median ectodermal ingrowth gives rise to the *ductus ejaculatorius*. Where the vasa deferentia join the anterior extremity of this canal their ends become enlarged ampullae (Fig. 45, A) which unite to form a mesodermal vesicle. The *accessory glands* are of two kinds. Thus, in *Blatta* and most other Orthoptera numerous glands (*a.g*) arise from the vesicle just mentioned and, since they are of mesodermal origin, they are classed as *mesadenia* (Fig. 45, B). In other insects from one to three pairs of accessory glands may occur, and those arising from the ectoderm of the ductus ejaculatorius are termed *ectadenia*. In many cases the accessory glands produce substances that go to the formation of a kind of capsule or *spermatophore* that encloses the spermatozoa. It is deposited in the bursa copulatrix or in the vagina of the female during mating, the spermatozoa ultimately becoming freed. Spermatophores vary in form and structure and several may be produced during a single mating. They are prevalent in Orthoptera (including *Blatta*), Lepidoptera and other orders. *Vesiculae seminales* are found in many insects and are developments of the vasa deferentia. In *Blatta* they take the form of numerous outgrowths of the mesodermal vesicle (Fig. 45) already mentioned and, owing to the degeneration of the testes in the adult, spermatozoa are only found in the vesiculae seminales.

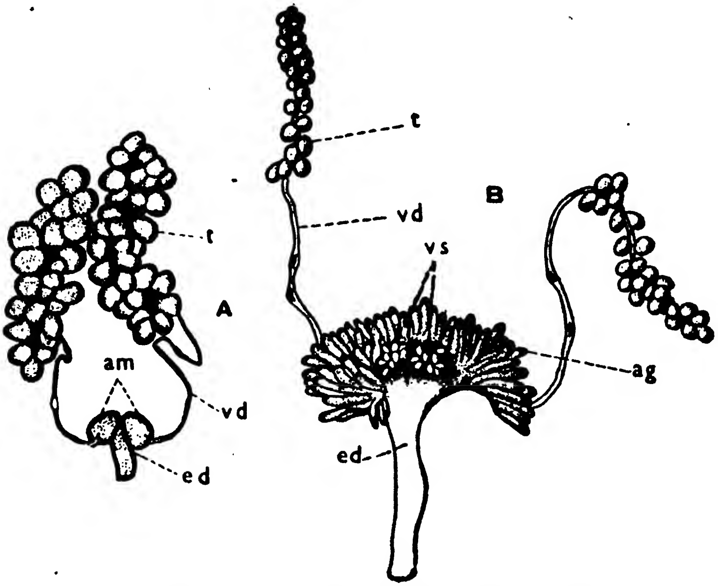

FIG. 45.—*BLATTA ORIENTALIS*, MALE ORGANS
B, ventral view of reproductive organs of adult male. A, the same of 6th instar nymph (equally magnified). *am*, ampullae ; *a.g*, accessory gland ; *e.d*, ductus ejaculatorius ; *t*, testis ; *v.d*, vas deferens ; *v.s*, vesicula seminalis. (*Adapted from* Qadri, 1938)

Reproduction

Reproduction in insects is ordinarily dependent upon the meeting of individuals of opposite sexes resulting in copulation and the fertilization of the ovum by the spermatozoon. Most insects are oviparous, i.e. they lay eggs that hatch after deposition. Exceptions to these generalizations are, however, frequent and are dealt with below.

Viviparity. Some insects produce either larvae or nymphs instead of laying eggs and are said to be viviparous. This condition is due to the retention of the eggs within the body of the female until the contained insects have emerged. It is most frequent in Diptera and Hemiptera. In some Coccidae and in various flies the eggs hatch almost immediately after oviposition : such insects are sometimes described as being 'ovoviparous'. In most cases of viviparity the embryos are nourished by the yolk within the eggs which, it may be added, are devoid of a chorion. In aphides, for example, the developing eggs lie in the ovarioles and the agamic generations are hatched as young nymphs. In flies the eggs pass into the vagina which is specially developed as a uterus wherein they undergo development. The young larvae are deposited in the first or later instar. In other cases only a single larva develops at any one time in the uterus, where it is nourished by products of the accessory glands which are discharged near its mouth. This happens in the Tsetse flies (*Glossina*) and in the Sheep Ked (*Melophagus*: Fig. 46, D), where the larva is deposited when fully grown and pupation occurs shortly afterwards.

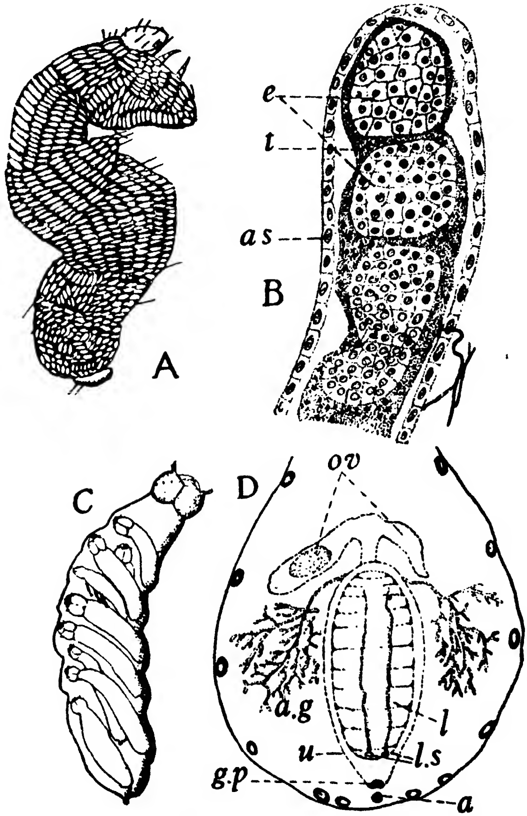

FIG. 46.—TYPES OF REPRODUCTION

A, remains of larva of *Plusia gamma* distended with pupae of the polyembryonic parasite *Litomastix* (*after* Silvestri). B, portion of a polyembryonic chain derived from a single egg of a Chalcid parasite dissected from its host; *a.s*, adventitious sheath produced by host; *e*, embryos surrounded by trophamnion, *t* (*after* Marchal). C, paedogenetic larva of *Micromalthus* with daughter larvae ready to emerge (*from a drawing by* H. E. Hinton). D, viviparity in *Melophagus*, ventral aspect of abdomen seen as a transparent object, showing *l*, growing larva, in uterus, *u*; *a.g*, accessory gland; *a*, anus; *g.p*, gonopore; *ov*, ovaries; *l.s*, larval spiracles

Sex Determination. As in other animals, the male among insects can be distinguished from the female by differences in the sex chromosomes. In most insects the male is the heterogametic sex. Among Orthoptera, Hemiptera-Homoptera and certain members of other orders the X-chromosome is unpaired in the male and present in duplicate in the female (Fig. 47, B). More often the X-chromosome is paired with one that differs from it morphologically. Such a dissimilar pair forms the X- and Y-chromosomes and occurs in most Diptera (*Drosophila*, &c.), Coleoptera, Hymenoptera and Hemiptera-Heteroptera (Fig. 47, A). Among Lepidoptera, as in birds, the female is the heterogametic sex. In *Ephestia*, for example, the X-chromosome is unpaired in the female and the genetic constitution of the male is XX (Fig. 47, D); in the Gipsy moth (*Lymantria*) the female has the XY constitution (Fig. 47, C).

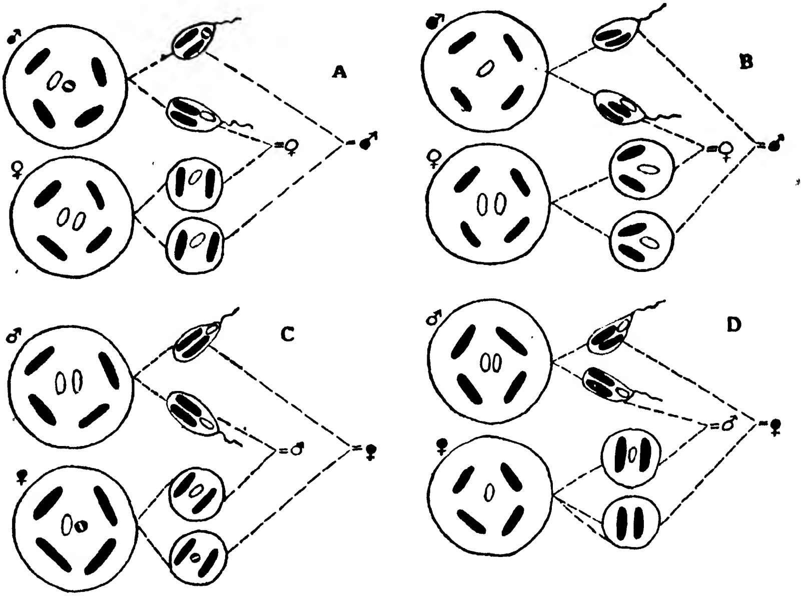

FIG. 47.—DIAGRAM OF BEHAVIOUR OF SEX CHROMOSOMES

In A and B the male is heterogametic: two kinds of sperms and one kind of egg are produced. In C and D the female is heterogametic: two kinds of eggs and one kind of sperm are produced. (The heterogametic sex is indicated by the heavier black symbol.) For simplicity, an arbitary number of four autosomes has been taken

Among insects, castration, even of very young larvae or nymphs, usually has no effect upon sexual characters or behaviour. Nor has the implantation into the castrated individual of the gonads of the opposite sex. As a general rule, therefore, it is concluded that hormones do not influence the sexual characters and that the origin of such secretions is not in direct relation with the gonads.

Parthenogenesis. Closely connected with sex determination is the production of individuals from unfertilized eggs, or parthenogenesis. Many insects that develop parthenogenetically have *diploid* somatic cells owing to the failure of the reduction division (meiosis). Less often reduction takes place and the individuals are *haploid*. In the former type the progeny may be either male or female (aphides), whereas in haploid parthenogenesis males alone result (hive bees and other Hymenoptera). Agamic reproduction is a constant feature in many Hymenoptera: among certain Gall-flies (Cynipoidea) and Saw-flies males are unknown. Cyclic parthenogenesis is well displayed in aphides where there is a regular sequence of agamic generations in which females only are produced. Later in the year gamic males and females appear and, after mating, eggs are laid which give rise to the agamic broods of the next year (see also p. 127). The change from the agamic to the sexual method of reproduction is largely activated by season, which apparently influences chromosome behaviour. With a sufficiently high temperature and an abundance of suitable plant hosts the parthenogenetic generations have been prolonged, in captivity, over a period of four years without the appearance of any gamic forms.

Paedogenesis. Paedogenesis is reproduction by the immature animal and is a rare phenomenon. A well-known example is in the Gall-midge *Miastor* (Cecidomyidae), whose larvae give rise asexually to daughter larvae in varying numbers, thus involving parthenogenesis and viviparity. The progeny eat their way out of the parent larva and reproduce in a similar manner. This process may go on for several generations until pupa-producing larvae develop that give rise to normal males and females. These mate and the paedogenetic cycle is restarted by larvae that issue from the fertilized eggs. Paedogenesis of a very similar kind also occurs in larvae of the beetle *Micromalthus* of N. America and S. Africa (Fig. 46, c.)

Polyembryony. Polyembryony is the production of two or more individuals, instead of one, from a single egg. It happens in cases of identical twins in man, in certain armadillos and in Polyzoa, but assumes its extreme development among parasitic Hymenoptera. While apparently many thousands of species of the latter seem potentially capable of this method of sexual reproduction, it is only known to occur in small number belonging to diverse groups. The essential feature of the process is the separation of the blastomeres of the egg into groups of cells or morulae, each of which grows into an adult insect. Very early in development the egg develops a surrounding sheath or *trophamnion* (Fig. 46, B), which absorbs food material from the tissue fluids of the host and passes it on to the growing embryo. This covering accommodates itself to the increasing size of the polygerminal mass which, in extreme cases, forms a tortuous chain of embryos blocking the haemocoele of the host. The latter, in order to withstand this heavy drain on its system, becomes increasingly ravenous until it finally succumbs. The simplest cases of polyembryony are in *Platygaster* (Proctotrypoidea) whose species parasitize the Hessian fly and its allies. In *P. hiemalis* some of the eggs produce single embryos while the others divide and give rise to two individuals. In various other parasites embryonic fission results in the production of 8 or 10 to 50, 120 or more individuals from a single egg: they are always of the same sex, the sex being dependent upon whether or not fertilization took place. An extreme phase is reached in the Chalcid parasite, *Litomastix truncatellus*, of the common Silver Y moth (*Plusia gamma*), where the division of a single egg produces up to about 1,000 individuals (Fig. 46, A).

III. EMBRYOLOGY, GROWTH AND METAMORPHOSIS

A. EMBRYOLOGY

The Ovum. A typical insect egg (Fig. 48, A) is covered by an outer shell or *chorion* that is variously sculptured or ornamented. It is secreted by the follicular epithelium and is composed of a scleroprotein without any chitin. Beneath the chorion is the *vitelline membrane*, which is a product of the egg itself. Insect eggs usually contain a large amount of *yolk* that lies within the meshes of a protoplasmic reticulum. The yolk occupies a central position and, as in other arthropods, the insect egg is of the centrolecithal type, being enclosed in an outer layer of protoplasm or *periplasm*. The germinal vesicle is at first centrally placed, but, in preparation for fertilization, moves towards the periphery of the ovum, which undergoes *maturation* or *oögenesis*. This process does not differ in essentials from what obtains in most animals. The germinal vesicle divides twice and the daughter nuclei thus produced are expelled from the ovum as the *polar bodies*. Maturation results in reduction of the original chromosome material to half the amount present in an ordinary somatic cell. Owing to the impenetrable nature of the chorion, and the fact that it is secreted before fertilization of the egg, provision for the entrance of the spermatozoon becomes necessary. This is ensured by the presence of one or more specialized pores or canaliculi forming the *micropyle*. The latter is generally situated at the anterior pole of the egg or that pole which lies in the ovariole directed towards the head of the parent insect.

The Blastoderm and Germ Band. After fertilization, the resulting segmentation nucleus divides and many of the nuclei thus produced pass outward to form, with the periplasm, a continuous cell layer or *blastoderm*. Others remain behind, surrounded by contiguous cytoplasm as *yolk cells*. Before the blastoderm is complete some of the dividing cells pass to the posterior pole of the egg (Fig. 48, B) forming the *primordial germ cells* ; this happens in many insects but in others the germ cells are not apparent until later. As development proceeds, the blastoderm thickens along the mid-ventral line, and, in this way, forms the *germ band* (Fig. 48, C), which is destined to produce all the tissues of the embryo. The rest of the egg consists chiefly of yolk enclosed by the *extra-embryonic blastoderm*.

Developmental Physiology (Fig. 49). Two centres control the beginnings of embryonic organization in the ovum. Near the posterior pole there is an *activation centre* which governs formation of the germ band. This centre apparently produces a chemical substance which permeates the egg from behind forward and initiates

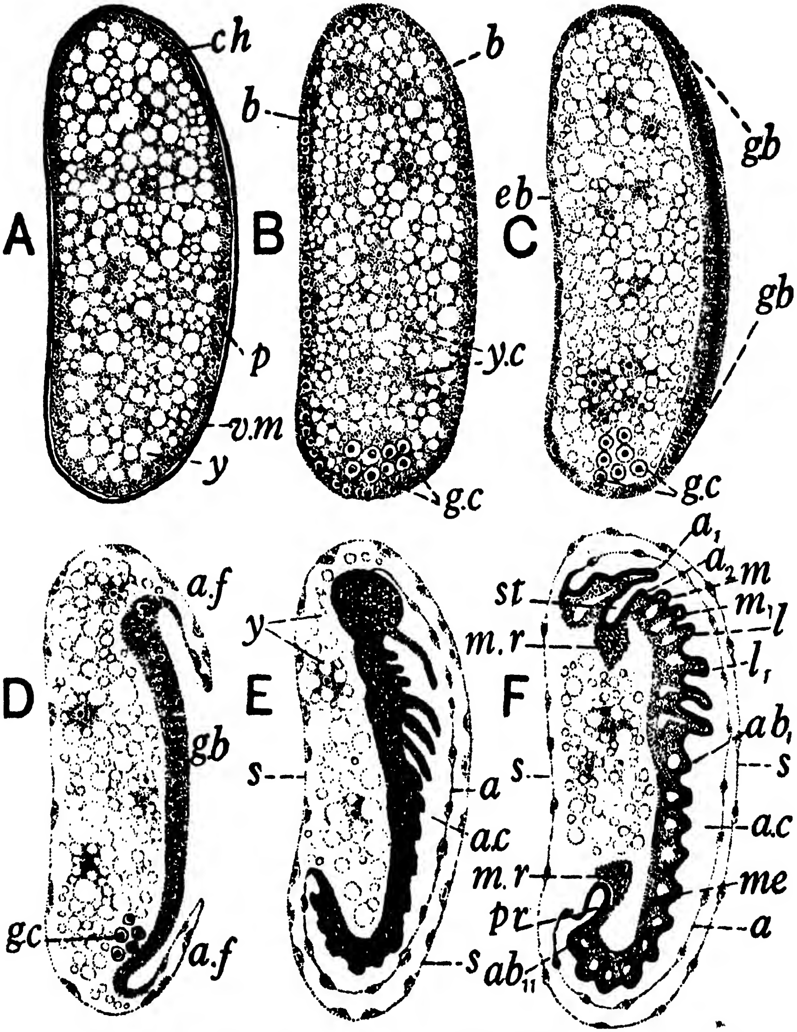

FIG. 48.—SUCCESSIVE STAGES IN THE EMBRYOLOGY OF AN INSECT

A, cleavage and migration of nuclei to the periplasm (*p*). B, formation of blastoderm (*b*). C, development of the germ band (*g.b*). D, developing amniotic folds (*a.f*). E, embryo enclosed in the amniotic cavity (*a.c*). F, section through the same. Other lettering: *a*, amnion; a_1, 1st antenna; a_2, 2nd antenna; ab_1, 1st abdominal appendage; ab_{11}, 11th do.; *ch*, chorion; *eb*, extra embryonic blastoderm; *g.c*, primordial germ cells; *l*, labium; l_1, 1st thoracic limb;. *m*, mandible; m_1, maxilla; *me*, mesoderm; *m.r*, mesenteron rudiment; *pr*, proctodaeum; *s*, serosa; *st*, stomodaeum; *v.m*, vitelline membrane; *y*, yolk; *y.c*, yolk cells. (In B–F the chorion and vitelline membrane have been omitted).

embryo formation. Its destruction or removal prevents formation of the germ band. It must be stressed that the activation centre is not a visibly distinct area and its existence has been determined as the result of experimentation. Towards the middle of the region where the future germ band develops there is a *differentiation centre.* It occupies a position corresponding with the thorax of the future embryo and it is from this centre that visible differentiation of form begins. The differentiation centre only comes into action after the product of the activation centre has reached it. Once the differentiation centre has performed its function the egg becomes unalterable or, in other words, it is incapable of 'regulation'. The process of differentiation comes about at different stages of development in different insects. Thus, in the egg of the dragon-fly *Platycnemis*, regulation is possible up to a late stage in blastoderm formation. In other words, the various regions of the egg can at first be altered from their normal course of development. Thus, ligaturing the egg across the middle results in the formation of two complete but dwarf individuals. On the other hand, the eggs of *Drosophila* and other Diptera are fully differentiated at the time of laying. Localized injuries induced, for example, by ultra-violet light cause corresponding injuries in the larvae. Such eggs are highly 'mosaic' and have already passed the stage when 'regulation' is possible at the time they were laid. In *Platycnemis* it will be noted the 'mosaic' condition is not reached until the late blastoderm stage. In the hive bee perfect larvae of reduced size develop from a ligatured egg provided it is not more than 12 hours old. These larvae develop from both

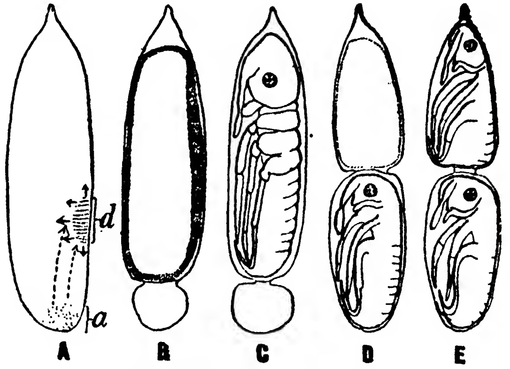

FIG. 49.—REGULATION OF DEVELOPMENT IN *PLATYCNEMIS*. (*Based upon* Seidel)

A, undeveloped egg with positions of the activation centre, *a*, and the differentiation centre, *d*, indicated. B, egg ligatured at an early stage just in front of the activation centre: no embryo develops and only extra-embryonic blastoderm is formed. C, the ligature has been applied at a later stage than B, and after the activation centre has become operative and the differentiation centre has become functional. D, dwarf embryo produced by ligaturing the egg in front of the functional differentiation centre: in the upper half of the egg only extra-embryonic blastoderm is developed. E, an egg later than D, but in the same stage as C when ligatured across the middle and giving rise to double dwarfs parts of the ligatured egg, irrespective of the position of the ligature. If, on the other hand, a 24-hour-old egg be ligatured, the larger part will develop into a defective larva, lacking those organs under the control of the other part. The hive bee therefore presents a type intermediate between *Platycnemis* and *Drosophila.*

Embryonic Membranes and Gastrulation. Sooner or later the germ band becomes enclosed by *amniotic folds* that arise from its edges. These folds grow towards one another so as to meet and fuse, thus enclosing the germ band within a space known as the *amniotic cavity* (Fig. 48, D and E). Of the covering membranes thus formed the outer layer or *serosa* is continuous with the *extra-embryonic* *blastoderm* and the inner membrane or *amnion* is continuous with the margins of the germ band. These two membranes, and the cavity they enclose, function as an insulating cushion that protects the growing embryo from injury.

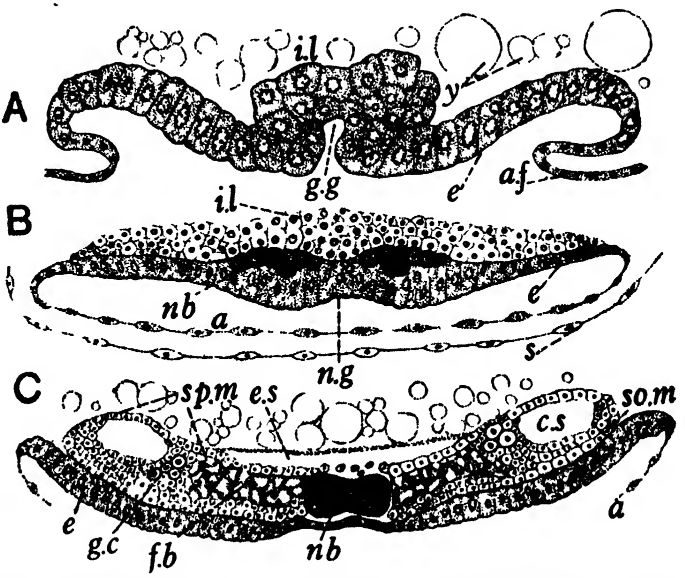

FIG. 50.—TRANSVERSE SECTIONS THROUGH THE GERM BAND OF AN INSECT AT SUCCESSIVE STAGES OF DEVELOPMENT

A, formation of gastral groove (*g.g*) and inner layer (*i.l*). B, beginnings of neural groove (*n.g*) and ventral nerve cord (*n.b*). C, development of coelom sacs (*c.s*) and beginning of separation of the embryo from the yolk resulting in the formation of the epineural sinus (*e.s*). Other lettering: *a*, amnion; *a.f*, amniotic fold; *e*, ectoderm; *f.b*, fat-body; *g.c*, primordial germ cells; *s*, serosa; *so.m*, somatic layer of mesoderm; *sp.m*, splanchnic layer of mesoderm; *y*, yolk

During growth of the amniotic folds *gastrulation* takes place as a ventral furrow-like ingrowth on the middle line of the germ band. It begins at the site of the future stomodaeum and gradually extends to the caudal end of the germ band. Its cells become deployed as an inner or *lower layer* beneath the outer layer or *ectoderm* (Fig. 50). According to some authorities the lower layer gives rise to both *mesoderm* and *endoderm*, but others claim that there is no true endoderm in insects and consequently the inner layer is the equivalent of only the mesoderm of other animals.

Segmentation. Very early in development the two-layered germ band or embryo, as it may now be termed, becomes divided by transverse furrows into a series of segments which ultimately number 20 in all. Segmentation is a gradual process beginning anteriorly and extending backward (Fig. 51). The embryo is at first divisible into a *protocephalic* or *primary head region* and a *protocormic* or *primary trunk region*. In this phase the embryo most likely represents an ancestral stage in insect evolution in which there was a 3-segmented head and a many-segmented trunk. As development progresses the first three protocormic segments become added to the protocephalic region. The next three body segments are grouped to form the thorax and the remaining segments, i.e. eleven, together with the telson, constitute the abdomen. Each of these, excepting the first segment and the tail piece or *telson*, develops a pair of out-growths or *embryonic appendages* (Fig. 51). The 1st or ocular segment is formed of the large *procephalic lobes*. The 1st pair of appendages or antennae belongs to the 2nd segment, while the very small 2nd pair, which represents the crustacean 2nd antennae, is transitory and soon disappears. The 3rd, 4th and 5th pairs grow respectively into the mandibles, maxillae and labium. The next three pairs of embryonic appendages are usually larger and more conspicuous: they are the fore-runners of the thoracic legs. Finally, there follow eleven pairs of abdominal appendages of which the last pair becomes the cerci and the remaining pairs are usually resorbed before hatching. The presence of these evanescent limb rudiments can only be interpreted as being an indication of a many-legged ancestral stage. The number of abdominal segments varies in the adults among different groups of insects since some of the end somites tend to disappear.

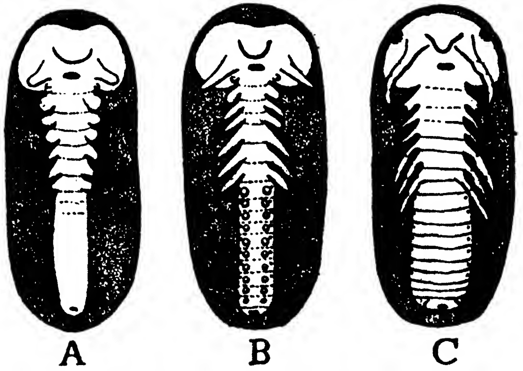

FIG. 51.—VENTRAL SIDE OF DEVELOPING EMBRYOS IN, A, PROTOPOD, B, POLYPOD, AND, D, OLIGOPOD STAGES

Mesoderm. The cells of the lower layer become arranged, for the most part, in two longitudinal bands which are shortly afterwards marked off into divisions or segments corresponding with those bearing the appendages (Fig. 48). Most of these mesodermal segments acquire, in generalized insects, a pair of cavities or *coelom sacs*. The dorsal or splanchnic wall of these sacs gives rise to the gonads, visceral muscles and fat-body, while the ventro-lateral or somatic wall produces the muscles of the body and the appendages. The *body-cavity* begins as the *epineural sinus* or space that is mainly formed by the separation of the yolk from the embryo in the mid-ventral region (Fig. 50, c). This process extends laterally and upward, and results in the epineural sinus and most of the coelom sacs becoming confluent, thus forming the permanent body-cavity. The *primordial germ cells* soon migrate forward, and, after separating into two groups, they penetrate into the gonads, where they become located.

Nervous System. Shortly after gastrulation the central nervous system develops as a pair of longitudinal *neural ridges* of the ectoderm that are separated by a median *neural groove* (Fig. 50, B). The neural ridges become segmentally constricted into *neuromeres* or primitive nerve ganglia, while their intersegmental portions give rise to the connectives. It will be noted that the whole of the nervous system and the sense organs are ectodermal in origin and that their fundaments become separated from the outer ectoderm which forms the body-wall (Fig. 50, c). The first three neuromeres, viz. the *proto-*, *deuto-* and *tritocerebrum*, amalgamate to form the *brain*, while the succeeding three cephalic neuromeres fuse to become the *sub-oesophageal ganglion*. The neuromeres that follow develop into the thoracic and abdominal ganglia.

Alimentary Canal. An ingrowth of the ectoderm, just behind the antennae, forms the *stomodaeum* or embryonic fore-intestine and a corresponding posterior ingrowth or *proctodaeum* gives rise to the hind-intestine (Fig. 48, F). The *mesenteron rudiments* are groups of cells closely associated with the stomodaeal and proctodaeal ingrowths, and some authorities claim that they are consequently ectodermal in origin. Others maintain that they are derived from the anterior and posterior ends of the inner layer and represent the endoderm of most animals. These cells multiply and grow towards each other and, finally, enclose the yolk in the form of a complete tube—the *mesenteron* or embryonic mid-intestine. By the disappearance of the walls separating the mesenteron, from the stomodaeum and proctodaeum respectively, a through passage is established in the alimentary canal.

The Malpighian tubes arise as ectodermal outgrowths of the proctodaeum, close to its union with the mesenteron. The *salivary* *glands* arise as paired ectodermal ingrowths at the sides of the labial segment. During development they become drawn into the mouth-cavity, where they fuse and open by a common duct on the hypopharynx.

Tracheal System. The tracheae develop from paired lateral ingrowths, near the bases of the appendages, on the meso- and meta-thorax and on the first eight abdominal segments. The mouths of these invaginations become the *spiracles* and, at their inner ends, anterior and posterior longitudinal extensions meet and fuse to form the main tracheal trunks.

Later Phases of Development. The embryo always forms on the ventral surface of the egg but, in the lower insects (Exopterygota), it becomes invaginated into the abundant yolk that is present in these forms. This process results in the embryo traversing an arc so that its ventral surface now faces the dorsal side of the egg. After a period of diapause it begins to reverse its position and ultimately regains the ventral side of the egg. These movements of the embryo during development are termed *blastokinesis*, but the significance of the process is obscure. The germ band forms the ventral part of the developing insect and, in order to complete the embryonic body, the margins begin to grow upward. The final result is the completion of the embryo on the dorsal side and the details of the process differ among different insects. The upward growth involves not only the ectoderm or body-wall but also the epineural sinus and the mesoderm, while the developing mid-intestine ultimately encloses the yolk. The embryonic membranes later rupture and, becoming contracted, are finally resorbed.

B. GROWTH AND METAMORPHOSIS

Hatching. When ready to emerge from the egg an insect has to force its way through the chorion in order to reach the outer world. In many cases the chorion is torn open by means of provisional structures known as hatching spines or egg bursters. These are located on the head, or other part of the body, where they may remain until the insect has undergone its first moult. In other instances, notably among Anoplura and Hemiptera-Heteroptera, a preformed egg-cap or operculum is pushed open to allow of the insect emerging. The force used in hatching is chiefly muscular activity but, as a preliminary, an insect may swallow air or the amniotic fluid and the resulting increase in bulk and turgidity play their part in the process.

Growth. Growth in an insect is in cycles alternating with periods when moulting (p. 86) takes place. The actual mode of growth may be by cell-multiplication either with or without any increase in cell size. In other cases growth is by increase in the size of the individual cells of organs or parts, no cell-division taking place. Tissues or parts growing by this method are frequent in the Holometabola, where they are usually subjected to histolysis during the pupal stage. Organs, &c., that grow by cell-multiplication are not, as a rule, subjected to dissolution and are carried over into the adult insect. Where growth is expressed as increase in cell size the changes are often very striking. Thus, in the life of larvae of Tachinid flies the cells of the fat-body have been noted to increase in diameter from 17μ to 290μ and the oenocytes to increase from 15μ to 85μ. Growth in insects is biologically similar to growth in most other animals. It is in general heterogonic or, in other words, parts of the body grow at rates peculiar to themselves and may be higher or lower than the growth rate of the body as a whole. The change involved is expressed by the statement that the logarithm of the dimension of the part is proportional to the logarithm of the dimension of the whole, and when these measurements are plotted on a double logarithmic grid a straight line is obtained.

Ecdysis. Every insect, during its growth, sheds its skin one or more times, this process being known as *moulting* or *ecdysis*, and the cast-off skin is termed the *exuviae.* The special feature of insect growth centres around this phenomenon of moulting, which provides the only means for any increase in surface area or change of form of the exoskeleton. While growth is the most important factor that determines moulting, it is not exclusive. Collembola moult after attaining sexual maturity when all growth has ceased, and some insects moult repeatedly during starvation, but the meaning is obscure.

The initiating factor in moulting is the secretion of a hormone into the blood. The source of this hormone appears to be the corpora allata (p. 61). In some cases blood from an insect, near to the moulting stage, has been transfused into another individual in a normal condition, with the result that an accelerated moulting has followed.

Prior to ecdysis an insect ceases to feed and may become, for a time, quiescent. Owing to recent growth the epidermal cells become greatly elongated and often thrown into folds which results in the old cuticle being separated from them. A thin new covering, composed of epicuticle and exocuticle, becomes formed and a moulting fluid is discharged into the narrow space separating the old from the new cuticle (Fig. 52). The fluid is the product of epidermal *moulting glands* that become functional at this time, and it has the property of liquefying the endocuticle. It does not attack the epicuticle or exocuticle of the new skin which function as interposing layers between the moulting fluid and the developing endocuticle. The old skin, thus reduced to epi- and exocuticle, is now ready to be cast off.

The insect, by contracting its abdominal muscles, increases the pressure of blood in the thorax. The tergal region comes to bulge upward until the old skin ruptures along a predetermined line of weakness. This line is marked by the absence of exocuticle: it commonly runs mid-longitudinally along the back of the thorax. Many insects swallow air, or water in the case of aquatic forms, and thereby enhance the disruptive force employed. When the skin has split the insect escapes gradually by peristaltic movement, often aided by gravity, since many insects suspend themselves head downward during the moulting process. As it issues from the old skin, the limbs are withdrawn from their coverings and the creature escapes with a soft and pliant cuticle. It swallows considerable quantities of air (or water) and by this means again increases its bulk. Many of the muscles remain for the time in a state of contraction and, in this way, pressure of the blood serves to expand the wings and other parts to their full dimensions. The cuticle hardens and darkens, processes which appear to be effected by an oxidative change since neither takes place in an atmosphere of nitrogen. In may-flies and many moths the only function of the digestive canal is to receive air for the purpose mentioned. If the crop of a newly-moulted cockroach be perforated with a needle, air escapes and distension of the new cuticle is prevented. If the wings of newly emerged insects be pricked, blood is seen to issue freely and their proper expansion cannot be attained.

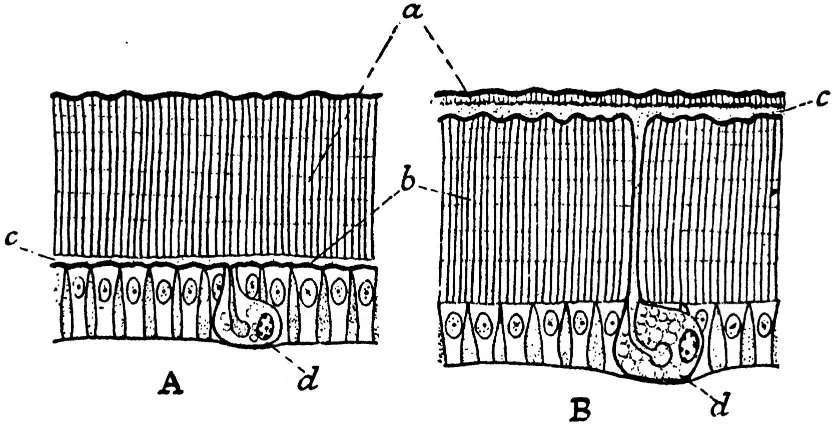

FIG. 52.—MOULTING OF A CUTICLE IN WHICH AN EXOCUTICLE IS WANTING
(*Modified after* Wigglesworth)

A, new epicuticle formed; digestion of old endocuticle scarcely begun. B, digestion and absorption of old endocuticle almost complete. *a*, old cuticle; *b*, new cuticle; *c*, moulting fluid; *d*, moulting gland

Instar **and** ***Stadium*****.** The intervals between the ecdyses are known as stages or *stadia*, and the form that is assumed by an insect during a particular stadium is termed an *instar*. When an insect issues from the egg it is in its first instar: at the end of this stadium the first ecdysis occurs and the insect then assumes its second instar. The final instar is the fully grown insect which is the adult or *imago*. While the number of instars is usually fixed, or only varies within narrow limits in most insects, there are wide ranges of difference. Thus, among the cyclorraphous Diptera there are three larval instars, while in the Plecoptera more than thirty nymphal instars may be passed through. In caterpillars of various moths the number ranges between about three and nine in different species.

Metamorphosis. One of the most characteristic features of insects is that they usually issue from the eggs in a condition morphologically different from that assumed in the imago: the subsequent growth involves changes of form that are known as *metamorphosis*. Some insects (i.e. Apterygota, p. 100) emerge from the eggs in a phase resembling miniature adults and the change of form from instar to instar is too slight and gradual to merit the term metamorphosis. Such insects are, for this reason, known as *Ametabola*. All other insects pass through a metamorphosis and, in contradistinction to ametabolous forms, are termed *Metabola*. The orders coming under this category are divisible into two series: Hemimetabola and Holometabola.

The *Hemimetabola* comprise all the lower orders or those with external wing-growth (Exopterygota, p. 100). They undergo simple metamorphosis, often described as being *direct* or *incomplete*. Owing to the presence of abundant yolk the immature insects are hatched from eggs in a relatively advanced phase of development and are termed *nymphs*. A nymph prefigures the imago in its general structure and body-form. It usually adopts the same mode of life as its parents, frequenting the same habitat and feeding upon similar food. Its mouth-parts usually show unimportant structural differences from their final condition, and compound eyes, often accompanied by dorsal ocelli, are the prevailing visual organs. During the early ecdyses nymphs undergo but slight change of form, but soon rudiments of wings and genitalia appear (Fig. 53). The final transformation comprises little or no important morphological change other than the acquisition of these organs in the fully developed condition. Physiologically, the main changes are in the increasing development of the gonads and their products up to maturity.

In the Ephemeroptera, Odonata, and Plecoptera the nymphs are exceptional in being aquatic, while the imagines lead an aerial life. In possessing special respiratory organs, and other adaptive modifications, the nymphs of these three orders show evolutionary divergence from the adults. The final transformation into the imago consequently involves more drastic morphological change than is usual among Hemimetabola.

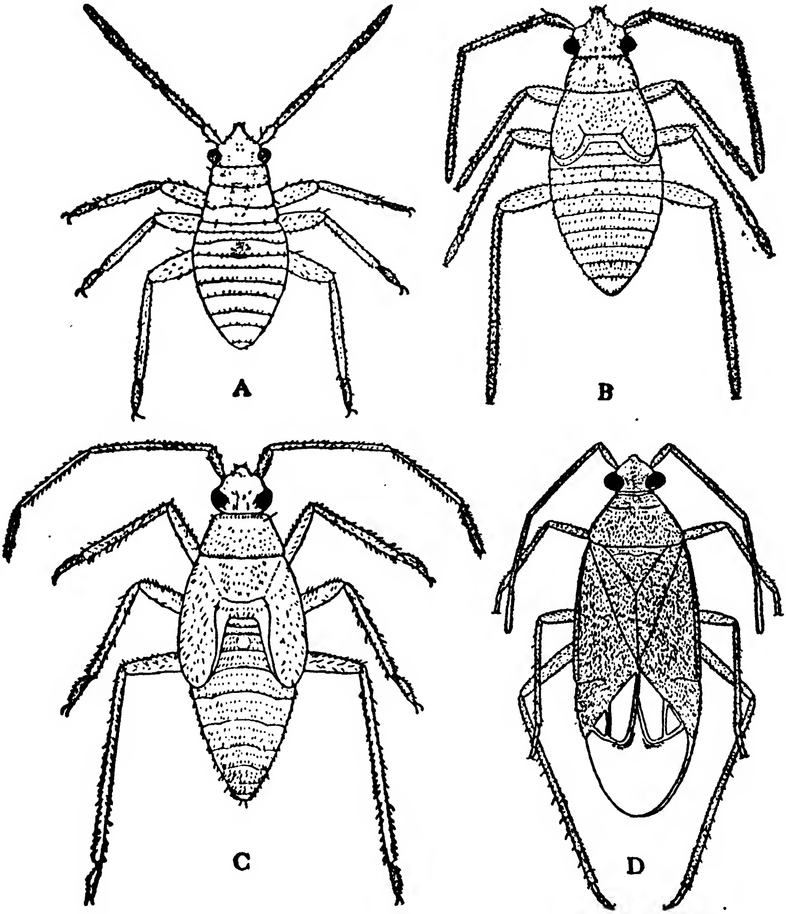

FIG. 88.—INCOMPLETE METAMORPHOSIS OF AN HEMIPTERON (*LYGUS PABULINUS*)
A, nymph, 2nd instar. B, do., 4th instar. C, do., 5th instar. D, imago (*From* Petherbridge and Thorpe)

Some Hemiptera, notably Aleurodidae and male Coccidae (p. 127), show evident *tachygenesis* or shortening of development. The functional nymphal instars are reduced to three or fewer, growth being completed as quiescent, non-feeding pupae of a rudimentary kind. Such a type of life-cycle represents a definite approach to the holometabolous condition.

The *Holometabola* include all the higher orders of insects (Endopterygota, p. 100) or those in which the developing buds of the genitalia, wings and other appendages lie concealed beneath the body-wall. They undergo complex metamorphosis often referred to as being *indirect* or *complete*. As a rule the embryo is large in relation to the amount of yolk present in the egg which results in the insect hatching in a relatively early stage of morphological growth known as a *larva*. In general, a larva differs fundamentally in form, structure and behaviour from the imago. The mouth-parts and other appendages usually show profound differences in structure and function. The prevailing visual organs are lateral ocelli. Throughout larval life the gonads are in a very rudimentary stage. Divergence of evolution has become so pronounced among most types of larvae that transformation into the imago has involved the intercalation of an intermediary stage or *pupa* in the ontogeny.

Larval Types (Fig. 54). Although embryonic development is a continuous process, and no stage is sharply marked off from another, three successive phases are recognizable in the embryonic growth of all the more primitive insects. These are the protopod, polypod and oligopod phases (Fig. 51). In the Holometabola the larvae are hatched in one or other of such stages and consequently leave the egg earlier in development than nymphs.

The *protopod type* (Fig. 54, A) is found in the early instars of endoparasitic Hymenoptera. The eggs are almost devoid of yolk and transparent and the larvae consequently issue at a very early stage in ontogenetic development. Their survival is only possible on account of their being surrounded by an abundance of yolk or haemolymph within their hosts. Thus the primary larva of the Proctotrypoidea is little more than a precociously emerged embryo. The abdomen is unsegmented and the thoracic limbs are rudimentary outgrowths : the nervous and respiratory systems are undeveloped and the digestive canal is little more than a mesenteric sac.

The *polypod type* (Fig. 54, B) is well seen in the caterpillars of the Lepidoptera and Symphyta (saw-flies). The essential feature is the retention of abdominal limbs. The digestive, nervous and respiratory systems are more or less complete. Such larvae constitute the 'eruciform' type of earlier writers.

The *oligopod type* (Fig. 54, C) is the prevailing form in Coleoptera and Neuroptera. Larvae of this kind have well-developed sense organs, antennae and thoracic legs, but other than cerci, abdominal limbs have disappeared. They are often described as *campodeiform* from their resemblance to *Campodea* and its allies. The typical oligopod larva is a predator, but many transitional or adaptive forms (Fig. 54, D), often showing different habits, lead to the apodous type.

The *apodous type* (Fig. 54, E) is devoid of all true locomotory appendages and has been derived, in most cases, from the oligopod phase as the result of degeneration. Such larvae live amidst plentiful food or where very little locomotory activity is required to find it. Sensory organs are, consequently, much reduced or to a great extent atrophied. Apodous larvae are characteristic of Diptera, of the aculeate and parasitic Hymenoptera and of weevils among Coleoptera.

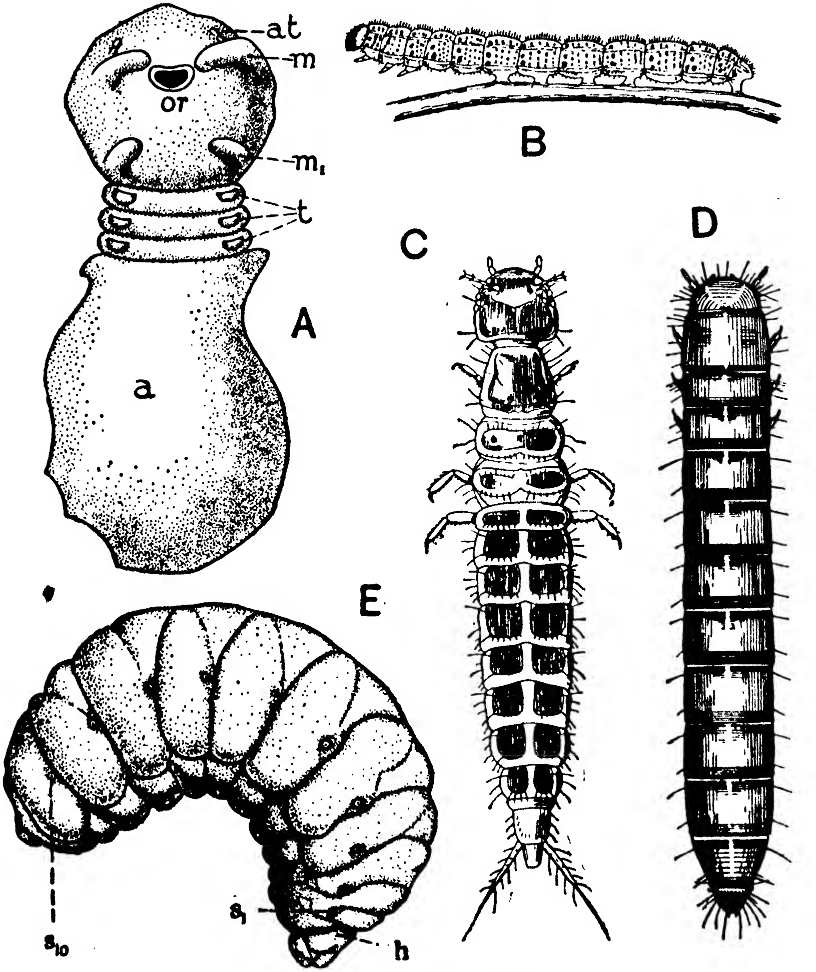

FIG. 54.—LARVAL TYPES

A, protopod (Proctotrypoidea). B, polypod (Lepidoptera). C, oligopod (Coleoptera, Staphylinidae). D, do. (*Tenebrio*). E, apodous (Hymenoptera : hive bee). (A *from* Kulagin, E *from* Nelson). *a*, abdomen ; *at*, antenna : *m*, mandible ; m_1, maxilla : *h*, head : s_1, s_{10}, spiracles ; *t*, thoracic limbs ; *or*, mouth

Prepupa and Pupa. In Holometabola the larval instars are preparatory to the development of the pupa, whereas in Hemimetabola the nymphal instars are preparatory to the development of the imago. In the higher orders tachygenesis has prevailed to the extent that the nymphal instars of the lower forms have become abbreviated and represented by the prepupa and pupa. The beginnings of this process are to be noted among some of the Hemiptera (p. 127) and in Thysanoptera (p. 122). The prepupal and pupal instars represent the abbreviated recapitulation, or passing through, of ancestral nymphal stages. During evolution the nymphal stadia have acquired a quiescent condition, feeding only taking place during the antecedent larval period. This changed phase became necessary in order to provide for the larval organization to become remodelled to a greater or less degree in accordance with the very different needs of the future imago.

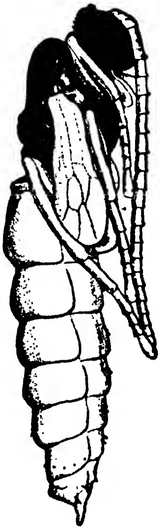

FIG. 55.—EXARATE OR FREE PUPA OF A HYMENOPTERON (ICHNEUMONIDAE): LATERAL VIEW

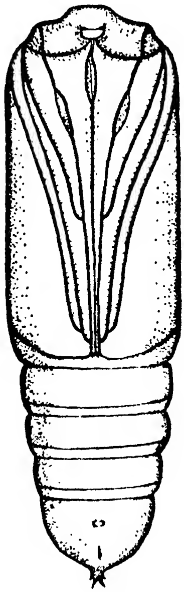

FIG. 56.—OBTECT PUPA OF A LEPIDOPTERON (NOCTUIDAE): VENTRAL VIEW

FIG. 57.—COARCTATE PUPA OF A DIPTERON (ANTHOMYIDAE): DORSAL VIEW

The *prepupa* is marked by cessation of feeding and it is usually in this instar that the cocoon is produced: among Diptera it is the stage in which the puparium is formed. The prepupa bears the general facies of the late larva, but is more contracted in form and loses any pigmentation that may be present. Towards the end of the stadium changes of body-form supervene, also the eyes and legs of the future insect may show the first external signs of development. Among some of the saw-flies the prepupa is preceded and followed by an ecdysis, but usually only the second of these moults is undergone, the first being suppressed.

The *pupa* (Fig. 55) is a quiescent or resting instar: at this stage the wings and appendages become everted from their epidermal pouches and become evident externally. The prevailing type is known as the *exarate* or *free pupa* that is characterized by the appendages being free from any secondary attachments to the body and by the abdominal segments being movable. Among Neuroptera the pupae are often active and able to crawl about in order to facilitate the free eclosion of the imagines. In other orders such movements are much less pronounced, or no longer take place as in most Diptera, Coleoptera, and Hymenoptera.

In the *obtect* type (Fig. 56), found in most Lepidoptera, the wings and appendages are glued to the body and most or all of the abdominal segments become immovable. In the Diptera Cyclorrhapha the last larval exuviae persists and, undergoing contraction and other changes, becomes a hardened barrel-like case or *puparium* that protects the exarate pupa within. Such a type of protected pupa is said to be *coarctate* (Fig. 57).

Pupal Protection. Great vulnerability and lack of means of defence render special means for pupal protection necessary. Most pupae are concealed in some way or other and also guarded against extreme changes of weather. Many larvae burrow beneath the soil and make pupal cells of earthen particles held together by silk or other secretion. A number of insects construct cocoons of silk alone which, in the silk-worm and other moths, is secreted by the labial glands: in Neuroptera the silken material is a product of the Malpighian tubes. The exposed pupae of butterflies are usually protectively coloured; a cocoon is also wanting in the Chalcidoidea and in most flies.

Some pupae are provided with a varied armature of hooks or spines to facilitate emergence of the imagines from the cocoons: others have provisional mandibles for making their exit. In beetles and Hymenoptera emergence from the pupa occurs in the cocoon or cell and the adults gnaw their way out by means of their jaws.

Internal Metamorphosis. Among hemimetabolous insects the internal and external developmental changes are gradual and direct. The organs of the nymph become transformed into those of the imago with little change other than increase in size and limited structural elaboration. In the holometabolic life-cycle a variable degree of dissolution of the larval organs and tissues takes place during the pupal stage—the process being known as *histolysis*. Simultaneously they become gradually replaced by the organs of the adult insect, this generation of new tissues being termed *histogenesis*. The two processes intergrade and involve a gradual, successive transformation

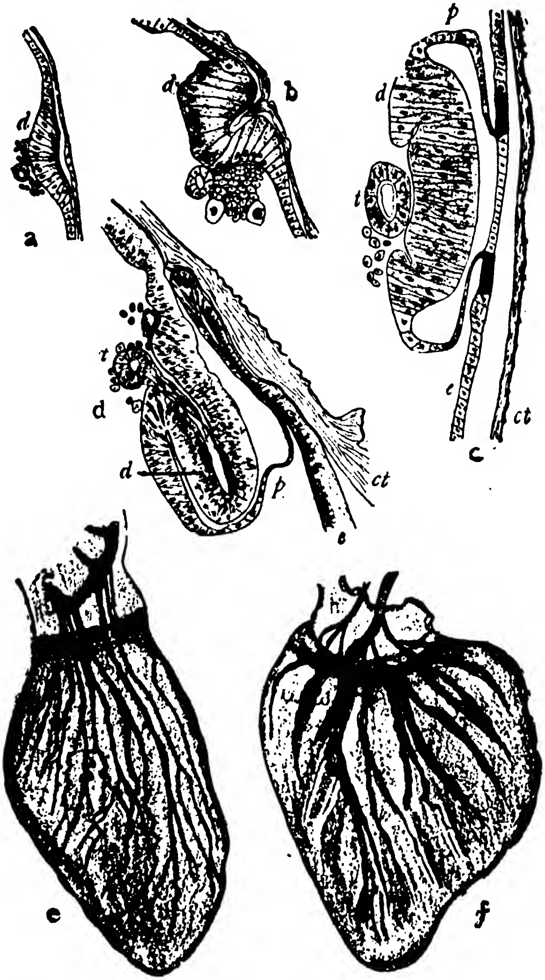

FIG. 58.—SUCCESSIVE STAGES IN THE DEVELOPMENT OF A WING-BUD OF *PIERIS*

a-d, sections of wing-bud ; *e*, *f*, surface views of fore- and hind-wings to show tracheation ; *ct*, cuticle ; *d*, wing-bud ; *e*, hypodermis ; *p*, peripodial membrane ; *t*, tracheae. (*From* Comstock, *after* Mercer)

without destroying the continuity of the parts concerned. In most of the lower orders of the Holometabola relatively little histolysis takes place and a considerable proportion of the larval organs pass over, with only slight modification, into the imago. Among Hymenoptera and Diptera, on the other hand, histolysis and histogenesis are processes of considerable complexity. While some organs, including the Malpighian tubes, fat-body and certain of the muscles, may be subjected to but slight modification, the epidermis, digestive system, other muscles, the glands, &c., are often wholly new formations. The heart, nervous system and much of the tracheal system often undergo great changes in the pupa without being subjected to any histolysis, In such cases they pursue an uninterrupted course of growth and differentiation.

There is much controversy regarding the *modus operandi* of histolysis. In many instances some or all the larval tissues that are subjected to the process undergo autolysis—possibly by means of enzymes appearing in the blood at this time. Among such Diptera as *Calliphora*, on the other hand, where the changes are great, phagocytes play an active part in histolysis by absorbing and digesting the disintegrating tissues. The products of histolysis are discharged into the blood where they provide the energy for the reconstructive process or histogenesis.

The primary elements in histogenesis are undifferentiated cells termed *histoblasts*, which retain the potentialities of embryonic tissue and function as self-differentiating growth-centres of the various organs and parts. Until metamorphosis sets in the histoblasts remain dormant. When they become functional they undergo cell-division and form the *imaginal buds* (imaginal discs) or rudiments of the future organs. In the higher Diptera (Cyclorrhapha) the imaginal buds are already laid down in the embryo : in other insects they appear in the larva. Those of the wings, legs, genitalia, &c., arise as slight folds or thickenings of the epidermis and come to lie in pockets (Fig. 58). In the pupa they become everted from their pockets and appear outside the body. The imaginal buds of the epidermis, the different regions of the digestive canal, the glands, main tracheal trunks, &c., are little more than nests of cells localized in the walls of these organs.

Hypermetamorphosis. When an insect, during its development, passes through two or more different larval instars it is said to undergo *hypermetamorphosis*. This process is characteristic of certain parasitic groups and is usually accompanied by a marked change in the mode of life. The sequence of larval types displayed during hypermetamorphosis follows, in the main, the corresponding embryonic phases of normal development. Thus, the first instar is very commonly an active oligopod larva that seeks out its host. In the second instar it usually becomes a parasite and this change of regime leads to its transformation into an inert maggot-like larva with vestigial thoracic legs and correlated modifications. This instar may be followed by an apodous stage. The foregoing sequence of larval forms is well shown in the life-cycle of the Melöidae or oil beetles. Hypermetamorphosis occurs also in all Strepsiptera, in the Mantispidae among Neuroptera, and in many endoparasitic Hymenoptera. In some of the last-named the yolkless eggs disclose a protopod larva which is followed by polypod and apodous instars.

Pupal Metabolism. The outwardly inert pupa is in reality the seat of intense biochemical change. As a general rule, reserves of fat and glycogen accumulate in the fat-body towards the end of the larval period. During the pupa these stores are extensively drawn upon and provide much of the energy for pupal metabolism. The curve of energy production during pupal life is characteristically U-shaped, being high at the beginning and end of the instar with a low intervening period. This kind of curve is obtained when O_2 uptake, CO_2 production or heat production are plotted but its significance is not evident. It has been suggested that the degree of metabolism, as expressed by the curve, is the measure of the amount of active tissues present—those of the larva at the beginning and those of the imago at the end of the instar.

Initiation of Metamorphosis. Many hypotheses have been put forward to account for the onset of metamorphosis. Recent experimental work has given a new interpretation based upon chemical differences in the blood. It appears probable that, as in moulting, initiation of the change into the pupa is due to the discharge of a hormone into the blood. Thus if young nymphs of the bug *Rhodnius* receive a transfusion of blood from 5th-stage nymphs that are in the process of moulting to become adults, they undergo precocious metamorphosis. Also, if the larva of the blow-fly *Calliphora* be ligatured less than 16 hours (at about 20° C.) before normal pupation, formation of the pupa and puparium occurs on both sides of the ligature. If the ligature be applied earlier than about 16 hours before, pupation only occurs in the anterior half of the animal (Fig. 59). Injection of blood from a pupating *Calliphora* into the pos-

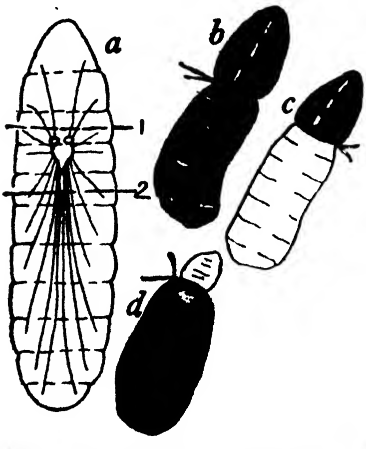

FIG. 59.—PUPATION IN *CALLIPHORA*
a, *Calliphora* larva, showing nerve centre and positions of ligatures (1, 2); *b*, ligature at 2 and less than 16 hours before pupation; *c*, more than 16 hours before pupation; *d*, ligature at 1 and more than 16 hours before pupation. (*From* Fraenkel)

terior part of a non-pupating larva will cause this region to pupate. Other evidence of a somewhat similar kind has been obtained by experiments with caterpillars and it is concluded that a hormone (or hormones) is involved and that its source is in close association with the brain. Whether the hormone is actually secreted by gland-cells present in the brain itself or by the corpora allata requires much further investigation.

Diapause. A *diapause*, or arrestation of growth, may take place at any stage of development. It is a condition of suspended metabolism that may be induced by various environmental causes such as cold, dryness, heat, &c. As a rule the dormancy ends when the cause no longer operates. This kind of arrested development is often regarded as a state of quiescence rather than a true diapause. The eggs of *Locusta*, for example, may be kept in such a state for many months so long as moisture be withheld, but on application of the requisite humidity development goes on. In other cases dormancy of a more deeply-seated kind prevails and results from an inborn rhythm. Such a condition commonly occurs in regions with a well-defined cold season and is known as hibernation. Thus, the autumn-laid eggs of the silkworm-moth (*Bombyx mori*) enter into a true diapause and will not hatch under moderately warm conditions. This fact is well known to silkworm rearers, who subject the eggs to 0° C., or thereabouts, for several months, which is essential before the application of warmth. The winter diapause, or hibernation of certain fly larvae, may be interrupted, and pupation induced, several months ahead of time, by allowing such larvae to become parasitized or by subjecting them to some kind of shock such as sudden change of temperature, by pricking with a needle, centrifuging, &c. In some species of moths the pupal diapause may last for several years, and it is very difficult to ‘ break ’ this dormancy before the required time. The most probable hypothesis in regard to diapause is that it results from failure of growth hormones to function owing to various causes. The stimuli which ‘ break ’ the diapause are regarded as evoking the re-activity of the hormones in question.

IV. NOMENCLATURE AND CLASSIFICATION

WHERE two kinds of animals differ from each other in some definite but relatively minor structural character or characters, they are said to be of distinct *species*. Species are grouped into genera, a *genus* being an assemblage of species showing evidence in common characters of close relationship. Genera in their turn are classed into the higher category of a *family*, whose components all display the same important characters. An *order* comprises all those families that show major features that link them together into a single natural assemblage. To continue, on the ascending scale, orders collectively form a *class* or major division of the animal kingdom, while classes are grouped on the basis of common fundamental characters into a *phylum*. Certain intermediate grades are also adopted, the most noteworthy being the *subfamily* or group of genera forming a section only of a family: the *superfamily*, or smaller group of families than an order, and the *suborder*. It will suffice to give one example, viz. *Formica rufa* Linné.

SPECIES : *rufa* Linné
GENUS : *Formica* Linné
SUBFAMILY : Formicinae
FAMILY : Formicidae
SUPERFAMILY : Formicoidea
SUBORDER : Apocrita
ORDER : Hymenoptera
CLASS : Insecta
PHYLUM : Arthropoda

As the American taxonomist G. F. Ferris has remarked, classification deals with concepts only. An order, a family or a genus are purely taxonomists ideas as to how the aggregates termed species may be grouped together so as to show their relationships. The first step in the classification of any group of animals is to have these animals named so as to allow of future reference. The system of naming in universal use is binomial, i.e. each kind of animal bears two names, one generic and the other specific. It dates from the publication of the 10th edition of the *Systema Naturae* of Linnaeus (Linné) in 1758, when binomial nomenclature was first definitely established for zoology. During the subsequent growth of this science nomenclature has become a matter of great complexity and, in order to regulate the procedure to be followed, a Code of Rules of Nomenclature has been adopted since 1901 by international sanction of zoologists.

The Rules of Nomenclature lay down that scientific names of animals must be Latin or latinized words, or considered and treated as such when not of classical origin. The name of a family is formed by adding the suffix *idae*, and of the subfamily by adding *inae* to the stem of the name of the type genus ex., *Blatta*, Blattidae. No rules are laid down for names in higher categories than that of a family. A generic name is a substantive in the nominative singular. The name of a species must be either an adjective agreeing grammatically with the generic name, ex., *Musca domestica*: or a substantive in apposition with the generic name, ex., *Stratiomys chamaeleon*: or a substantive in the genetive, ex., *Psila rosae*: geographic names and names of persons when used as specific designations are also expressed in the genetive, ex, *Peripatus novae zealandae*, *Termes horni*. When the name of the author is quoted after a specific name it follows without mark of punctuation, ex., *Tabanus rusticus* Linn. When a species is transferred to a genus, other than that in which it was originally placed, the name of the author of that species is then given in parenthesis, thus: *Fasciola hepatica* Linn. has become *Distomum hepaticum* (Linn.): it will be noted that the specific name conforms grammatically with the new generic name. The valid name of a species or genus is that name under which it was first properly designated and no name published prior to the 10th Edition of the *Systema Naturae* is valid. A generic or specific name that has been replaced on account of its being invalid is known as a *synonym*. It may be also noted that the specimens from which the published descriptions of species are drawn up are called *types*: they are of various categories and have received special names. The importance of types being carefully preserved is obvious when it is realized that a large amount of existing taxonomic work is dependent upon access to them for its ultimate clarification. Descriptions which, at one time, were deemed sufficient so often, in later years, prove inadequate in the light of more exact and discriminating standards. The type is then the final appeal in matters of doubtful identity.

The Classification of Insects. In striving after a natural system of classification of insects, the characters of most importance in diagnosing the main divisions are (1) the presence or absence of wings and their main features, (2) the mouth-parts and their changes in ontogeny, (8) metamorphosis, and (4) characters afforded by the antennae and tarsi. Orders of most importance to the elementary student are indicated *.

Subclass APTERYGOTA

Apterous insects, the wingless condition being primitive, with slight or no metamorphosis.

Order	1	Diplura*	Order	3	Protura
„	2	Thysanura*	„	4	Collembola

Subclass PTERYGOTA

Winged insects which are sometimes secondarily apterous: metamorphosis very varied, rarely slight or wanting.

Division 1. Exopterygota (= Hemimetabola)

Insects passing through a simple and sometimes slight metamorphosis, rarely accompanied by a pupal instar. The wings develop externally and the young are generalized nymphs.

Order	5	Orthoptera*	Order	11	Odonata*
„	6	Isoptera*	„	12	Psocoptera
„	7	Plecoptera	„	13	Anoplura
„	8	Embioptera	„	14	Thysanoptera
„	9	Dermaptera	„	15	Hemiptera*
„	10	Ephemeroptera*			

Division 2. Endopterygota (= Holometabola)

Insects passing through a complex metamorphosis always accompanied by a pupal instar. The wings develop internally and the larvae are usually specialized.

Order	16	Neuroptera*	Order	21	Strepsiptera
„	17	Mecoptera	„	22	Hymenoptera*
„	18	Trichoptera	„	23	Diptera*
„	19	Lepidoptera*	„	24	Aphaniptera
„	20	Coleoptera*			

ORDER I. DIPLURA (*diplos*, double; *oura*, a tail)

SMALL, EYELESS, MOSTLY UNPIGMENTED INSECTS WITH MONILIFORM ANTENNAE PROVIDED WITH SEGMENTAL MUSCLES. MOUTH-PARTS FOR BITING, ENTOGNATHOUS. ABDOMEN TERMINATING WITH VARIABLY DEVELOPED CERCI OR UNJOINTED FORCEPS: NO MEDIAN TAIL FILAMENT: STYLI AND USUALLY PROTRUSIBLE VESICLES PRESENT. NO OVIPOSITOR: TARSI 1-JOINTED. *Bristle-tails.*

About 400 species of Diplura are known. They are denizens of the soil but also frequent decaying vegetable matter of various kinds. The largest forms (Japygidae) measure up to 50 mm. long,

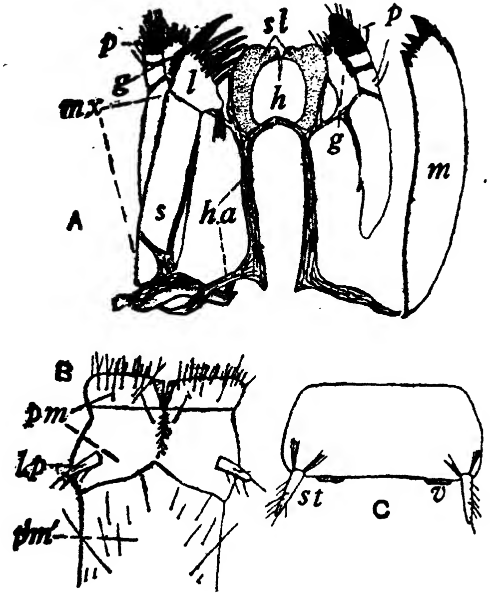

FIG. 60.—DIPLURA

A, *Japyx*, mouth-parts. B, labium. *C*, *Campodea*, 4th abdominal sternum. *c*, cardo; *g*, galea; *h*, hypopharynx; *h.a*, hypopharyngeal apodeme; *l*, lacinia; *m*, mandible: *mx*, maxilla; *lp*, labial palp; *p*, maxillary palp; *pm*, prementum; *p′m′*, postmentum; *s*, stipes; *sl*, superlinguae; *st*, stylus; *v*, protrusible vesicle

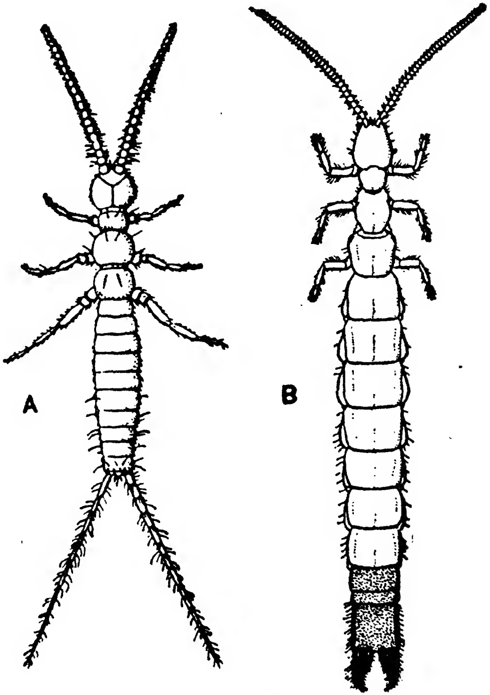

FIG. 61.—A, *CAMPODEA*. B, *JAPYX*

but an average is 2 to 5 mm. in length. Excepting Japygidae, with their darkened sclerotized forceps, these insects are unpigmented. While often included in the Thysanura, Diplura are obviously a separate group coming nearest to the ancestral insects. The multiarticulate antennae, provided with segmental muscles, separate the order from all other insects and link it with the Myriapoda. The mouth-parts (Fig. 60) are entognath to the extent that the mandibles and maxillae lie in pockets from which they are protruded when feeding Styli are present on abdominal segments 1 to 7 or 2 to 7, and protrusible vesicles are usual on segments 2 to 7 (Fig. 60, c). External genitalia are very little developed or wanting. Malpighian tubes are represented by papillae or are absent: while only 3 pairs of spiracles are present in Campodeidae, 9 to 11 pairs occur in other families. There are three families, the *Projapygidae* being the most primitive: their short-jointed cerci are traversed by the ducts of special glands. The *Japygidae* are all forcipate and the *Campodeidae* (Fig. 61) have long fragile cerci: only the last-named insects occur in Britain where they number about half a dozen species.

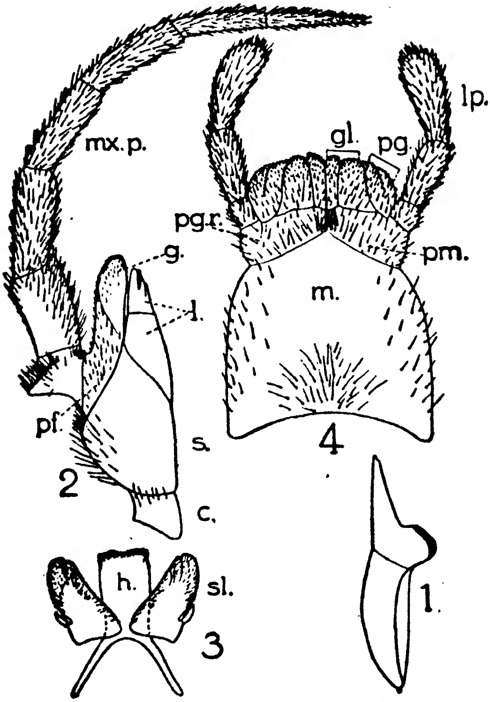

FIG. 62.—MOUTH-PARTS OF *PETROBIUS MARITIMUS*

1, Mandible. 2, Maxilla: *pf*, palpifer. 3, Hypopharynx (*h*) and superlinguae (*sl*). 4, Labium: *m*, postmentum. Other lettering as in Fig. 4

ORDER II.

THYSANURA

(*thusanos*, a fringe; *oura*, a tail)

SMALL INSECTS USUALLY WITH COMPOUND EYES AND OFTEN WITH SCALES. ANTENNAE LONG, SETACEOUS AND DEVOID OF SEGMENTAL MUSCLES. MOUTH-PARTS FOR BITING; NORMAL AND ECTOGNATHOUS. ABDOMEN WITH LONG CERCI, 11TH SEGMENT FORMING A MEDIAN TAIL FILAMENT: STYLI AND PROTRUSIBLE VESICLES PRESENT, OVIPOSITOR LONG. TARSI 3–4 JOINTED. ***Bristle-tails.***

These insects mostly occur under stones, logs or among dead leaves, but a few live differently. Thus, *Lepisma saccharina* and some related species, together with *Thermobia furnorum*, inhabit dwellings and bakehouses, while *Petrobius maritimus* lives just above tide mark on rocky coasts: various other Thysanura occur in nests of ants and termites. The mouth-parts resemble those of Orthoptera and have little in common with their counterparts in Diplura (Fig. 62). Genitalia are well developed, but neither the limb bases nor the styli of the 9th abdominal segment enter into their formation. Consequently, the long annulate ovipositor is 4-valved only (Fig. 63, D) and there are no claspers in the male (Fig. 63, C). Malpighian tubes are well developed but variable in number, and there are 9 or 10 pairs of spiracles. About 650 species are known and they are grouped into two families. The *Machilidae* are the more primitive and they show certain convergent resemblances to higher Crustacea. The abdominal sterna and limb-bases are separate (Fig. 63): styli

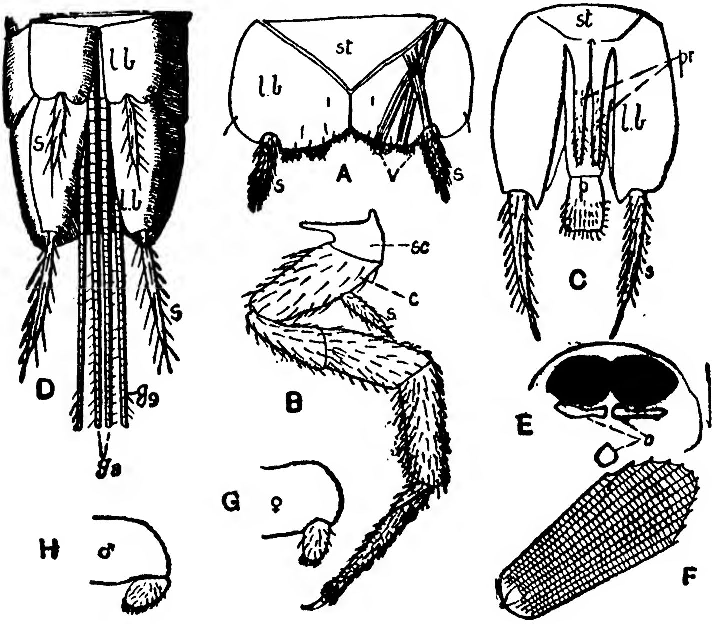

FIG. 63.—THYSANURA, ETC.

Petrobius: A, 5th abdominal segment, ventral; B, left leg of 3rd pair; C, male genitalia; E, eyes; F, body scale. *Machilis:* D, ovipositor and associated segments (cerci omitted). *Campodea:* G, H, half of 1st abdominal sternum of female and male respectively. *c*, coxa; g_8, g_9, gonapophyses or valves of 8th and 9th segments; *l.b*, limb base; *o*, ocelli; *p*, penis; *pr*, parameres; *s*, stylus; *st*, sternum; *sc*, subcoxa; *v*, protrusible vesicles are borne on segments 2 to 9 and usually on the coxae of the 2nd and 3rd legs (Fig. 63, A). The *Lepismidae* connect the Thysanura with the Blattidae. Styli are confined to abdominal segments 7 to 9 or 8 and 9 and there are usually no protrusible vesicles.

ORDER III. PROTURA (*protos*, first ; *oura*, a tail)

MINUTE COLOURLESS INSECTS WITHOUT EYES OR ANTENNAE : MOUTH-PARTS ENTOGNATHOUS, FOR PIERCING. ABDOMEN OF 11 SEGMENTS AND A DEFINITE TELSON, CERCI ABSENT.

These minute creatures seldom attain more than 1 mm. in length ; they are widely distributed and about 12 species have been found in Britain. They are local and need looking for in moist soil, in turf, beneath bark of trees, under stones, &c. On eclosion from the egg Protura have eight abdominal segments and three more are added later, this kind of post-embryonic growth or *anamorphosis* being found in no other insects. Antennal functions are performed by the front legs, which are held forward. Organs, apparently homologous with the post-antennal organs of Collembola, are present one on either side of the head. The mouth-parts show basic resemblance to those of some of the Collembola. Rudiments of limbs are borne on the 1st three abdominal segments and are evidently homologous with the pair on the 1st segment of *Campodea* (Fig. 63, G, H). The legs have 1-jointed tarsi and single claws. Tracheae are only slightly developed as in *Eosentomon*, or are absent as in *Acerentomon* ; two pairs of spiracles occur in the tracheate forms. About 50 species of Protura are known. The order is, apparently, a divergent offshoot from the ancestors of insects : nothing is known of the embryology.

ORDER IV. COLLEMBOLA (*kolla*, glue ; *embolon*, a peg)

VERY SMALL INSECTS WITH ENTOGNATHUS, BITING MOUTH-PARTS : ANTENNAE 4–SEGMENTED : TARSI WANTING. ABDOMEN OF 6 SEGMENTS SOMETIMES FUSED TOGETHER : 1ST SEGMENT WITH A SUCKER-LIKE VENTRAL TUBE, 4TH USUALLY WITH A FORKED SPRINGING ORGAN. *Springtails.*

Collembola (Fig. 64) rarely exceed 5 mm. long and occur from the poles to the equator. They are often immensely abundant as individuals and occur on and below the ground, among herbage, in decaying matter, under bark, in nests of ants and termites, &c. An acre of meadow has been found to support nearly 230,000,000 of these insects from the surface to a depth of nine inches. The eyes are typically eight ocelli on each side, but may be wanting : just behind the antenna there is often a characteristic *post-antennal* *organ.* The mouth-parts resemble those of Diplura and, when feeding, they are partly extruded from pockets within the head: well-developed superlinguae are present. The antennae, like those of Diplura, have intrinsic muscles—a feature shared by no other insects. The abdomen usually bears three pairs of persistent appendages, and those of the 1st segment are fused to form the *ventral tube,* which is probably an organ for absorbing moisture from surfaces. A *furcula* or springing organ is borne on the 4th segment and, when not in use, is retained beneath the abdomen by a 'catch' or *retinaculum* formed by the reduced appendages of the 3rd segment. External genitalia are wanting and the sexes are almost always alike. Except in *Sminthurus* and its allies tracheae are wanting (see p. 48); there are no Malpighian tubes and excretion is performed partly by the fat-body and partly by the periodic shedding of the cells of the stomach. The gonads have the germarium lateral in position and ovarioles are undeveloped. Segmentation of the egg is total and there is no amnion or serosa. The order is divided into the suborders **Arthropleona** (Fig. 64, A), with cylindrical body and without evident fusion of its segments, and **Symphypleona** (Fig. 64, I) with globular body and with the thoracic and first four abdominal segments closely amalgamated. About 2,000 species of Collembola are known: several rank as injurious, the most important being *Sminthurus viridis,* which is a pest of clover and lucerne. Collembola have no close affinity with other insects and, in many characters, they are related to the Myriapoda.

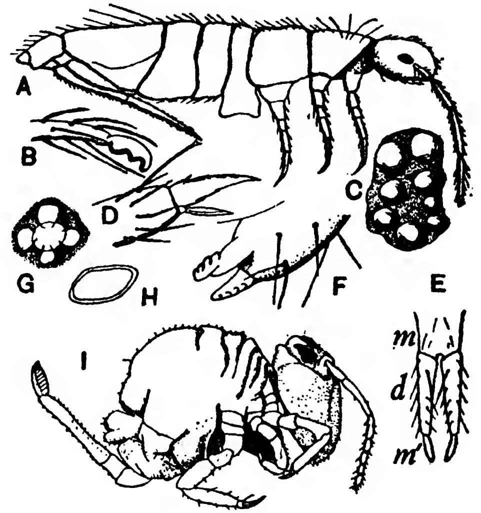

FIG. 64.—COLLEMBOLA

A, *Entomobrya.* B, do., apex of furcula. C, eyes of left side. D, apex of tibia with claw. E, *Sminthurus,* furcula: *m,* manubrium; *d,* dens; *m',* mucro. F, *Isotoma,* retinaculum. G, *Hypogastrura,* postantennal organ. H, *Isotoma,* postantennal organ. I, *Sminthurides.* (*After* Willem)

ORDER V. ORTHOPTERA (*orthos*, straight; *pteron*, a wing)

FORE WINGS MODIFIED INTO TEGMINA: HIND WINGS WITH A LARGE PLICATED ANAL LOBE. MOUTH-PARTS FOR BITING, LIGULA 4-LOBED: CERCI AND OVIPOSITOR PRESENT. *Cockroaches*, *Crickets*, *Locusts*, *Grasshoppers*, &c.

In this order are included about 20,000 species, of which only 32 inhabit Great Britain. The common cockroach, *Blatta orientalis* L., whose female has aborted wings, and the American cockroach *Periplaneta americana* (L.), a species winged in both sexes, are cosmopolitan. The Orthoptera are divisible into four superfamilies, whose relationships are indicated below.

A. Cursorial insects with 5-segmented tarsi, segmented cerci and a reduced ovipositor concealed by the subgenital plate formed by the 7th abdominal sternum: the eggs are enclosed in a special capsule or oötheca. BLATTOIDEA.

B. Cursorial or, more often saltatorial, insects with variably segmented tarsi and unsegmented cerci: ovipositor usually well developed and not concealed: subgenital plate formed by the 8th abdominal sternum: eggs not in an oötheca.

I. Legs subequal in size: tarsi 5-segmented. PHASMOIDEA.
II. Hind femora much enlarged: tarsi 1- to 4-segmented. ACRIDOIDEA.

C. Cursorial insects with long ovipositor, segmented cerci and 5-segmented tarsi: subgenital plate undeveloped. GRYLLOBLATTOIDEA.

The BLATTOIDEA include the Blattidae (cockroaches) and the Mantidae (praying mantises). In habits the former are omnivorous and the latter are predaceous, feeding upon other insects (p. 119). The PHASMOIDEA include the family Phasmidae that comprise the stick insects (Fig. 65, A) and leaf insects. As their names imply, they bear a striking resemblance in form and colour to sticks, stems and leaves and, thus protected, they remain immobile during daylight. The ACRIDOIDEA comprise the short-horned grasshoppers or Acrididae, the long-horned grasshoppers or Tettigoniidae and the crickets or Gryllidae. Stridulation is a characteristic feature among the males of these insects and there are tympanal organs present in both sexes (Fig. 15). The Acrididae mostly stridulate by friction between the tegmina and hind femora: the tympanal organs are on either side at the base of the abdomen. The species are vegetarian: those termed locusts migrate, at times, considerable distances in large swarms and rank among the most injurious of all insects (Fig. 65, c). The Tettigoniidae and Gryllidae stridulate by means of the two tegmina: The tympanal organs are on the fore tibiae. Their members are less

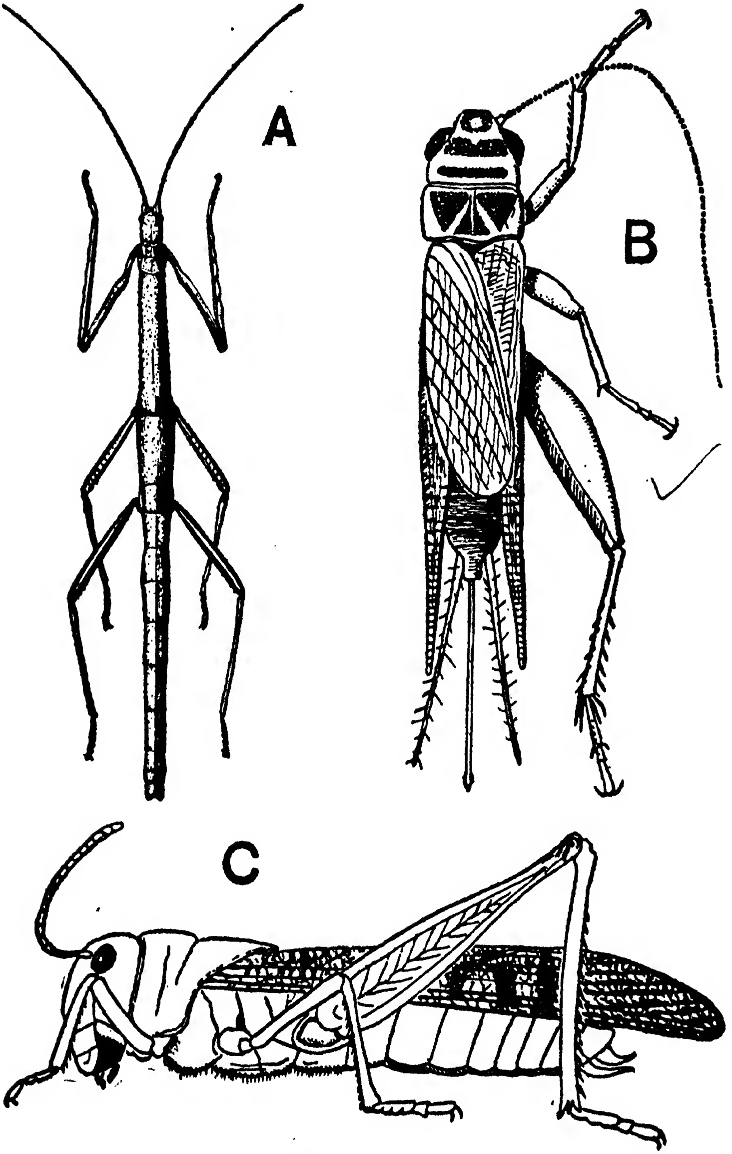

FIG. 65.—ORTHOPTERA
A, Stick Insect (*Carausius*), female (Phasmidae). B, Cricket, female (Gryllidae).
C, Locust, female (Acrididae)

predominantly vegetarian than those of the Acrididae. The long unsegmented cerci of the Gryllidae (Fig. 65, B) will separate that family from the Tettigoniidae. The GRYLLOBLATTOIDEA comprise the family Grylloblattidae with the single genus *Grylloblatta*. They are the most primitive of all Orthoptera and combine features of both A and B given above. The few known species are apterous and occur in the mountains of North America and Japan.

APPENDIX

The Phases of Locusts. Each species of locust has the capacity to develop into forms or *phases* that differ from one another both structurally and biologically. At one extreme these insects may occur in the migratory phase (*phasis gregaria*), when they are highly destructive to vegetation : at the other extreme they may be in the solitary phase (*phasis solitaria*), when they behave after the manner of ordinary grasshoppers and are relatively harmless. These two phases were formerly considered to represent separate species, but are now known to be modifiable and to be connected by intermediate forms that constitute the *phasis transiens.*

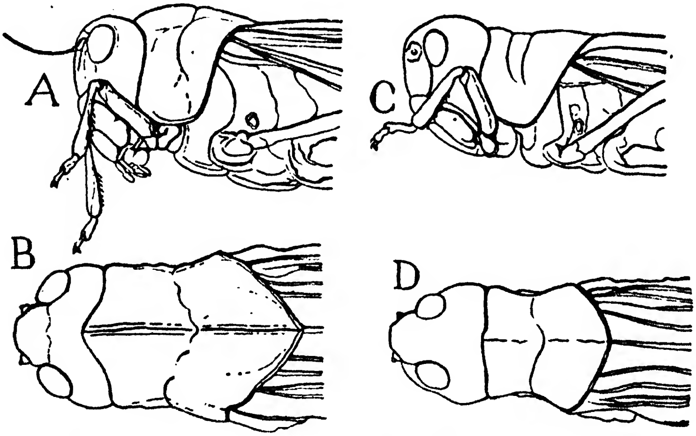

FIG. 66.—FORM OF THORAX IN PHASES OF THE LOCUST (*LOCUSTA MIGRATORIA MIGRATORIOIDES*)
A, B, phasis solitaria. C, D, phasis gregaria. (*After* Faure)

Among the best known species are the Migratory Locust (*Locusta migratoria*) of the Old World ; the Desert Locust (*Schistocerca gregaria*) of Africa and Western Asia, and the Brown Locust (*Locustana pardalina*) of South Africa. *Locusta migratoria* may be taken as an example. In the phasis gregaria it is characterized by the black and orange nymphal coloration, that develops independently of the nature of the environment. The adults have the pronotum laterally constricted and without a dorsal carina : the hind femora are relatively shorter and the tegmina longer than those of individuals in the solitary phase. In the phasis solitaria the nymphal coloration is plastic with a marked tendency to simulate that of the immediate environment. In the adult the pronotum is longer, it is not laterally constricted and bears a dorsal carina (Fig. 66).

The phase theory has been subjected to experiment, and given suitable temperature, humidity and food it is possible to control the phase that develops. Individuals reared from the egg in separate containers assume evident solitaria characters, whereas those reared collectively in large numbers show strong gregaria features: under less crowded conditions they develop into the phasis transiens. The typical or ancestral form of the species is displayed by the solitary phase and the differences shown by individuals in the migratory phase are perhaps due to their great activity. Intense muscular action brings about changes in the form of the pronotum and it is probable that the characteristic black and orange nymphal pigmentation results as a by-product of a high rate of metabolism. Out in the field the migratory phase only develops in specific breeding areas where a particular combination of ecological factors prevail. For this reason the destruction or modification of these areas will eliminate the conditions favouring the development of this phase and thereby open the way for countering the tendency to form migratory swarms. The latter, it may be added, do not arise as the result of food shortage, but appear to be connected with the maturation of the gonads and the dispersal of the species. The resultant progeny of these swarms develop into solitaria or transiens individuals should their environment be different from the original breeding grounds.

ORDER VI. ISOPTERA (*isos*, equal; *pteron*, a wing)

SOCIAL INSECTS LIVING IN LARGE COMMUNITIES: SOFT BODIED AND GENERALLY PALE COLOURED. MOUTH-PARTS FOR BITING, LIGULA 4–LOBED: CERCI VERY SHORT. EITHER WITH TWO PAIRS OF ELONGATED SIMILAR WINGS, WHICH ARE SOON SHED, OR WITHOUT WINGS. APTEROUS FORMS WITH RUDIMENTARY EYES OR NONE AND MAINLY OF TWO TYPES, VIZ SOLDIERS WITH LARGE HEADS AND JAWS OR A POINTED ROSTRUM AND WORKERS WITH NORMAL HEADS AND JAWS. *Termites* or *White Ants.*

The members of this order are, structurally, closely allied to the Blattidae. All termites are social and polymorphic and live as highly organized colonies in nests or *termitaria.* The primitive species merely tunnel into wood, but others form special nests, often of great size, and composed of earth and wood mixed with faecal matter and saliva. Five chief *castes*, composed of individuals of both sexes, may occur in a species. These castes comprise functional reproductive forms of three kinds and sterile forms of two principal kinds. The usual reproductive caste is the fully-winged or *macropterous* form (Fig. 67). At suitable times individuals of this caste swarm from the nest, cast their wings and, after mating, found new colonies. Brachypterous and apterous forms may also occur and are, functionally, supplementary reproductive castes. In the more specialized termites only a single fertilized female is present in a colony. This individual, which may be derived from any of the three castes just named, undergoes remarkable post-metamorphic growth and may reach 4½ inches long. In the sterile castes the gonads are greatly reduced and non-functional in both sexes. The members are divisible into *workers* and *soldiers* (Fig. 68). The *workers* are the most numerous individuals in a colony: they build the nest and keep it provisioned. Owing to their gnawing propensities they have earned for the termites their notoriety as destroyers of woodwork and other materials. The *soldiers* act as defenders of the nest and usually have large sclerotized heads and jaws. In the specialized genus *Nasutitermes* they are replaced by *nasute forms* with pyriform heads drawn out into a rostrum, and very small jaws. A *frontal gland* discharging a defensive secretion through a *frontal pore* is commonly present. This type of chemical warfare is specially developed in the nasute forms, which emit a pungent secretion through the rostrum. The lower termites feed on wood and harbour a rich Protozoan fauna in the hind intestine. The most characteristic of these organisms belong to the order Polymastigina of the Mastigophora, whose only known host, other than termites, is the wood-feeding cockroach *Cryptocercus* of North America. Functionally, the Protozoa are symbionts which produce enzymes that split up the cellulose of the wood into assimilable products: termites sterilized of their Protozoa are unable to digest

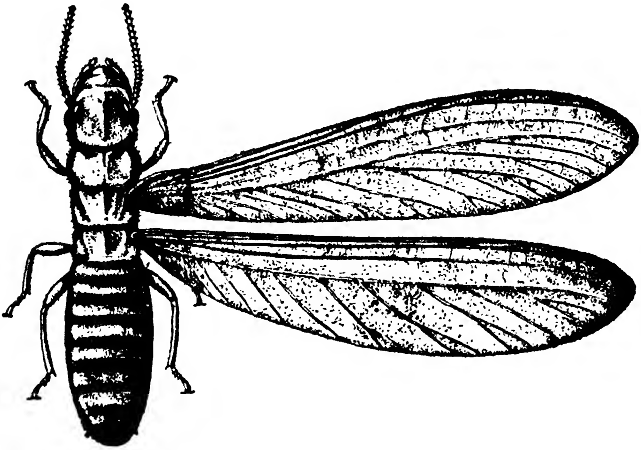

FIG. 67.—MACROPTERUS FORM OF *CALOTERMES*. (*From* Banks and Snyder)

wood. The higher termites feed on fungi, humus and organic matter from the soil. About 2,600 species of Isoptera are known. The few European forms are found in southern parts of that continent: about 55 species occur in North America, but most termites are denizens of the tropics.

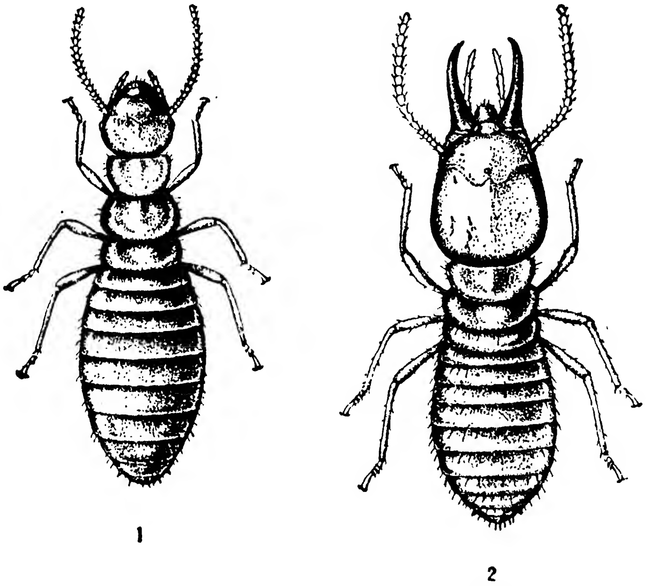

FIG. 68.—*PRORHINOTERMES SIMPLEX*
1, worker; 2, soldier. (*After* Banks and Snyder, *U.S. Nat. Mus. Bull.*, 108)

ORDER VII. PLECOPTERA (*plekein*, to fold; *pteron*, a wing)

SOFT-BODIED INSECTS USUALLY WITH LONG THREAD-LIKE ANTENNAE AND CERCI: TARSI 3-JOINTED. WINGS MEMBRANOUS, HIND PAIR WITH A PLICATED ANAL LOBE. MOUTH-PARTS FOR BITING, LIGULA 4-LOBED. NYMPHS AQUATIC WITH FILAMENTOUS TUFTED GILLS. *Stone-flies.*

This small order includes some 700 species, of which only about 80 occur in Great Britain. They are more closely related to the Orthoptera than to any other living order, but the wings have important venational differences and tegmina are undeveloped: also, there is no ovipositor. Stone-flies are weak fliers seldom found far from the streams inhabited by their nymphs. The latter are largely carnivorous and breathe by filamentous gills: these are usually disposed in tufts near the bases of the legs, cerci, &c., (Fig. 69), but in the family Eustheniidae of Australia and New Zealand, pairs

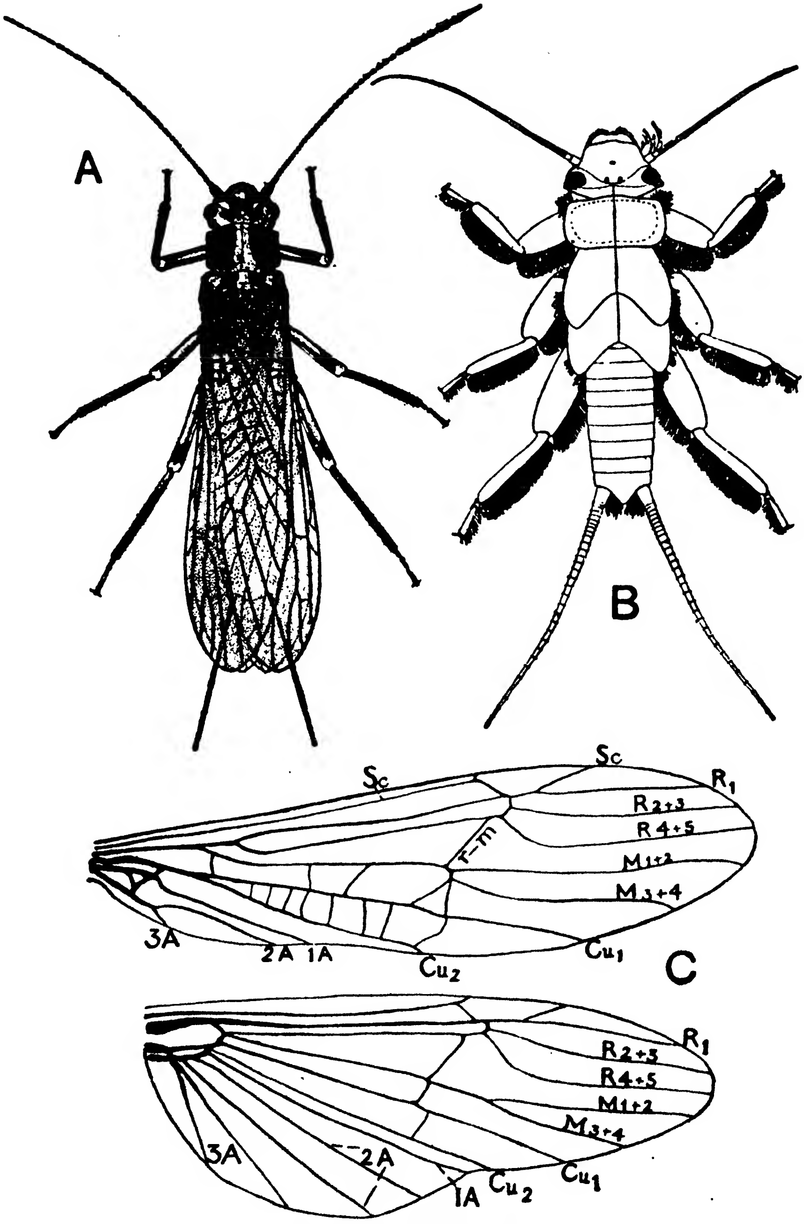

FIG. 69.—PLECOPTERA

A, ***Isoperla.*** **B, a Perlid nymph. C, right wings of** ***Nemoura.*** **(A and B** ***adapted from*** **Frison)**

of lateral gills are situated on the abdominal segments. Nymphal life is often long and, in *Perla*, may last nearly four years: during that time more than 30 instars may be passed through.

ORDER VIII. EMBIOPTERA (genus, *Embia*; *pteron*, a wing)

ELONGATED SOFT-BODIED INSECTS LIVING IN SILKEN WEB-LIKE TUNNELS. TWO PAIRS OF EQUAL-SIZED LONG, SMOKY WINGS USUALLY WITH SIGNS OF VENATIONAL DEGENERATION. MOUTH-PARTS FOR BITING, LIGULA 4-LOBED: TARSI 3-JOINTED, 1ST JOINT OF ANTERIOR PAIR GREATLY SWOLLEN: CERCI 2-SEGMENTED. FEMALES APTEROUS. *Web-spinners.*

The members of this small order live in silken tunnels beneath stones or loose bark of trees. They are semi-social and several individuals, along with nymphs and eggs, inhabit one tunnel system. The silk is produced by numerous glands lodged in the inflated 1st joint of the anterior tarsi: the ducteole from each gland discharges ventrally at the apex of a corresponding bristle. These glands are present in individuals of both sexes and of all ages. Except in the primitive genus *Clothoda*, the 10th abdominal segment and the cerci are modified asymmetrically in the male for pairing. About 140 species are known and they occur throughout the warmer regions of the world. One or two species only are found in South Europe and fewer than 20 inhabit the warmer parts of the United States. The Embioptera are rather an isolated order and appear to be nearer related to the Isoptera than to any other insects.

ORDER IX. DERMAPTERA (*derma*, skin; *pteron*, a wing)

FORE WINGS REPRESENTED BY SMALL TEGMINA: HIND WINGS LARGE, MEMBRANOUS AND COMPLEXLY FOLDED. MOUTH-PARTS FOR BITING, LIGULA 2-LOBED: BODY TERMINATED BY FORCEPS. *Earwigs.*

This order numbers about 1,000 species. *Forficula auricularia* is the common Earwig of Europe which has become established in North America and New Zealand. It is omnivorous in habit and the female shows parental care for the eggs and young nymphs. The forceps are modified cerci and, in some forms, are present as many-jointed appendages during the immature stages. *Arixenia* and *Hemimerus* are aberrant, wingless ectoparasites of bats and the rat *Cricetomys*, respectively, in the tropics.

ORDER X. EPHEMEROPTERA (*ephemeros*, living a day; *pteron*, a wing)

SOFT-BODIED INSECTS WITH LARGE EYES, MINUTE ANTENNAE AND ATROPHIED MOUTH-PARTS. WINGS MEMBRANOUS, LONGITUDINALLY PLICATED, HIND PAIR SMALL OR EVEN ATROPHIED. CERCI SLENDER,

MANY-JOINTED, USUALLY ACCOMPANIED BY A MEDIAN CAUDAL FILAMENT. NYMPHS AQUATIC, WITH PLATE-LIKE OR FILAMENTOUS TRACHEAL GILLS. *May-flies.*

The Ephemeroptera (Fig. 70) are known as may-flies, many of which live only a few hours as imagines—hence the ordinal name; this feature is compensated by the lengthy nymphal life which may last three years. The venation is very primitive with all the main

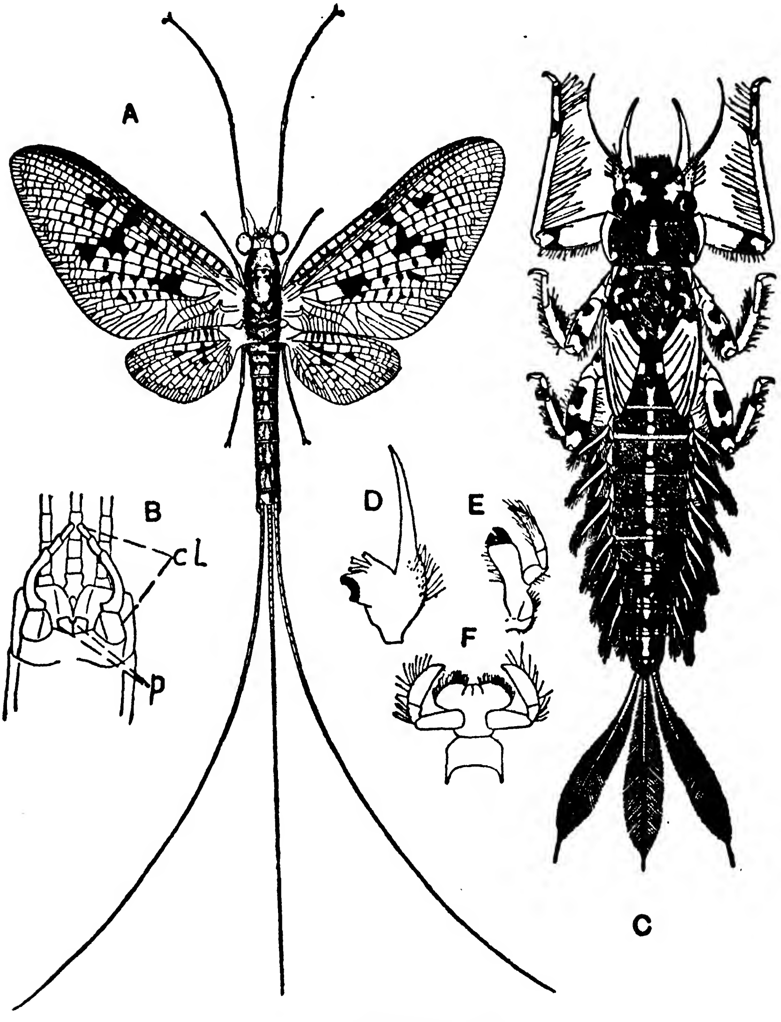

FIG. 70.—EPHEMEROPTERA

A, *Ephemera*, male. B, genitalia; *cl*, clasper; *p*, penes. C, *Polymitarcys*, nymph. D, mandible of same. E, maxilla. F, labium. (*Adapted from* Needham) veins and their branches present: unlike most recent insects the media consists of both MA and MP. The characteristic plication of the wings enables both convex and concave veins to be easily identified. Between the forked branches of the main veins *intercalary veins* are present as in Odonata. While the hind wings are largest in Siphloneuridae, in other families they are much reduced or even atrophied as in *Chloeon* and *Caenis*. The legs are useless for walking and only enable these creatures to cling to objects while resting. The first winged stage is the *subimago* which resembles the imago except for a translucent pellicle which covers the whole insect, giving it a dullish appearance. After undergoing an ecdysis, unique among insects, the true imago is assumed and is recognisable by its clear shining appearance and full coloration. May-flies take no food as imagines: the alimentary canal remains in a thin-walled condition and is used for taking in air, the mid-intestine acting as an aerostatic organ. The nymphs are essentially phytophagous and like the imagines have long cerci and usually a median caudal filament. They inhabit lakes, ponds and streams and present notable adaptive modifications. Burrowing forms (*Ephemera*, *Hexagenia*) have cylindrical bodies and fossorial fore-legs. Species inhabiting swift streams have flattened bodies and hooked spines for clinging to rocks (*Iron*, *Epeorus*). Inhabitants of sandy streams have the gills covered by opercula formed by the upper lamellae of the first pair: the branchial chamber thus formed is guarded by hair-fringes against the entry of particles suspended in the water (*Caenis*, *Tricorythus*). About 40 species of may-flies occur in Great Britain and over 400 kinds are known in North America. The order has not been much studied and probably fewer than 1,000 species are known in the whole world.

ORDER XI. ODONATA (*odous*, gen. *odontos*, a tooth)

LARGE INSECTS WITH VERY ELONGATED BODIES, LARGE EYES, AND MINUTE ANTENNAE. MOUTH-PARTS SPECIALIZED AND STRONGLY TOOTHED: CERCI SMALL, 1-SEGMENTED. TWO PAIRS OF MEMBRANOUS, GLASSY WINGS EACH WITH A PTEROSTIGMA AND NUMEROUS CROSS-VEINS. NYMPHS AQUATIC: LABIUM MODIFIED INTO A RETRACTIBLE PREHENSILE ORGAN. *Dragon-flies*, *Damsel-flies*.

All Odonata are predators and devour insects of various kinds which they seize while in flight. The capture is effected by the legs, which bear a spiny armature for the purpose on the femora and tibiae. The prothorax is very small, but the meso- and meta-thorax have conspicuously enlarged pleurites that slant steeply backward. This results in the terga and wings being pushed posteriorly, while the sterna become situated far forward (Fig. 72, A). The legs, in consequence, lie close behind the mouth and are thus enabled readily to seize the prey: they are unfitted for locomotion and the tarsi are 3-jointed. The venation shows no close affinity with that of other insects, and the wings, like those of may-flies, are incapable of being folded over the back. Each wing (Fig. 71, A) bears a pterostigma and vein Sc ends in a conspicuous *nodus* (*n*) or incision, near the middle of the costal margin. The division of the wing area into numerous quadrate cells by a multitude of cross-veins is also a characteristic feature. The abdomen is composed of 10 segments with vestiges of an 11th segment. The male genital armature is unique in being located on the ventral side of the 2nd segment. The gonopore, however, lies on the 9th segment and the semen is transferred to the penis. During pairing the clasping organs at the apex of the abdomen of the male are used to seize the female by the prothorax: the female then curves her abdomen so as to bring the genital opening in contact with the penis. The whole process occurs while the insects are in flight (Fig. 72, A). There are usually marked colour differences between the sexes and the female

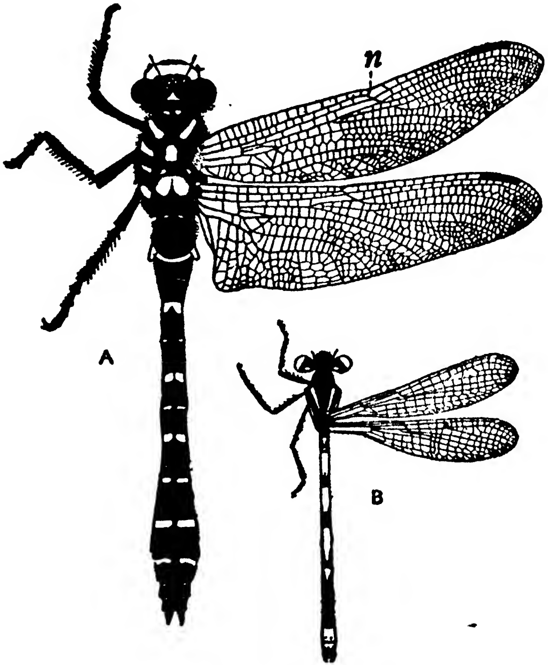

FIG. 71.—ODONATA
A, Anisopterid dragon-fly; *n*, nodus. B, Zygopterid dragon-fly

often has a short 3-valved ovipositor. Oviposition may be *endophytic*, i.e. the eggs are inserted into slits cut by the ovipositor in aquatic plants : or, *exophytic*, i.e. the eggs are dropped freely in the water or superficially attached to vegetation. The nymphs are always aquatic and prey upon small Crustacea, insects, &c. They are somewhat sluggish and more or less protectively coloured. Their most characteristic feature is the modification of the labium into a prehensile organ or 'mask' (Fig. 72, D). This organ is hinged between the pre- and post-mentum and stowed away between the legs : when a victim is seized the mask is suddenly extended with great rapidity and the prey impaled on the spines of the labial palpi.

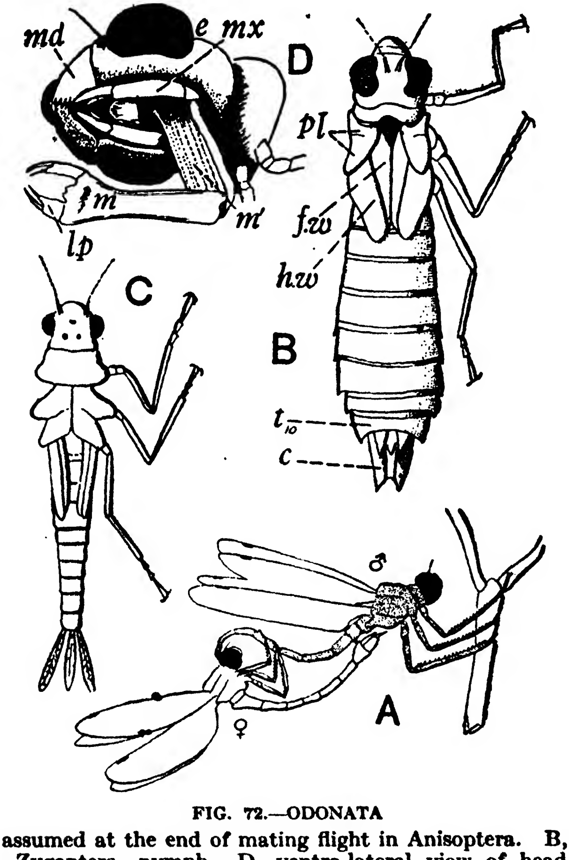

FIG. 72.—ODONATA

A, position assumed at the end of mating flight in Anisoptera. B, Anisoptera, nymph. C, Zygoptera, nymph. D, ventro-lateral view of head of dragonfly nymph with mask (*m*,*m′*) half retracted. *c*, cercus ; *e*, compound eye ; *f.w*, fore wing ; *h.w*, hind wing ; *l.p*, labial palp ; *m*, prementum ; *m′*, post mentum ; *md*, mandible ; *mx*, maxilla ; *pl*, pleura of meso- and metathorax ; t_{10}, 10th abdominal tergum. (A, after Meisenheimer)

Dragon-flies are divided into two main suborders (Fig. 71), viz. (1) The **Zygoptera**, which have very slender bodies ; the two pairs of wings are alike with narrow bases and are held vertically above the abdomen when at rest. (2) The **Anisoptera**, which have stouter bodies, have the hind wings broader basally than the fore wings and the two pairs are held horizontally in repose. The nymphs of the Zygoptera (Fig. 72, C) are slender in form and the body is terminated by three elongate caudal gills. In the Anisoptera (Fig. 72, B) the nymphs are of more robust build ; caudal gills are absent, but there is an elaborate system of tracheal gills that project in longitudinal rows into the cavity of the rectum. About 3,500 species of dragon-flies are known : of these, over 360 species occur in North America and 43 species are found in Great Britain.

APPENDIX

Predatism. A predator is an animal of carnivorous habit that seeks out and devours its prey. This kind of behaviour prevails among very diverse groups of insects and the prey consists of members of their own or other classes of invertebrates. In conformity with this mode of life certain structural adaptations are manifested in (1) the legs, (2) the mouth-parts, and (3) the sensory organs. In some cases adaptive changes in behaviour are also evident.

Many predators use their legs for seizing their victims and for holding them while they are being devoured. Thus, in dragon-flies and adult Diptera of the family Asilidae, or robber flies, all three pairs of legs are used for this purpose, these limbs being notably elongated and spiny. In the water-bugs (*Notonecta*, &c.) the fore-legs alone are adapted for seizing and holding the prey : they are held well in front of the head and terminate in sharp prehensile claws. In the Mantidae, and in the neuropterous family Mantispidae, the prey is caught and impaled by means of the combined femora and tibiae of the fore-legs. It will be noted that the femur bears a ventral channel flanked by a double series of spines. The tibia is adapted to close in this groove after the manner of the blade of a pocket-knife, its sharply toothed edge acting in conjunction with the femoral spines in impaling the prey. In these two families, and in various others that use the fore-legs for capturing their prey, the coxae of the limbs concerned are notably elongated (Fig. 5, D) so as to throw the legs forward and also allow of increased freedom of movement. Other predators have projecting sharply pointed mandibles for seizing their victims, as is well shown in larvae of ground beetles (Fig. 83), of *Dytiscus* and of most Neuroptera (Fig. 78). In dragon-fly nymphs, as already noted, the labium is modified into a prehensile organ or mask (Fig. 72, D).

The sensory organs of many predators are highly developed, especially the compound eyes—a feature well seen, for example, in the Mantidae, Odonata, Carabidae, and Asilidae. When the prey are few and far between, and therefore requiring agile search, the legs of predators are adapted for running (Carabidae); or the predators are strong rapid fliers (Odonata, Asilidae). In cases where the specific prey is abundant and sedentary the legs and sense organs of such predators are not specially developed, since in most cases very little searching for their victims is required. Larvae of Neuroptera and of hover flies or Syrphidae, together with the Coccinellidae, come under this category and they develop from eggs laid in close proximity to the aphides, &c., that form their food.

The mandibles, and sometimes the maxillae also, of predators are sharply pointed and adapted for piercing: they may also be toothed as in Odonata, being thus adapted for lacerating and tearing. In the Asilidae, together with other predaceous flies, and also in many water bugs, the mouth-parts are developed into a rigid horny proboscis.

A considerable number of predators lie in wait for their prey, suddenly pouncing upon it when within reach. This adaptive habit is well seen among dragon-fly larvae and Mantidae: the members of these two groups are usually cryptically coloured and thereby allow unwary prey to come within easy reach. Others, such as the larvae of tiger beetles (Cicindelidae), and those known as ant-lions (Myrmeleonidae), construct pits to ensnare their prey, while carnivorous trichopterous larvae, that bear no cases, make web-like snares for entangling their victims.

ORDER XII. PSOCOPTERA (genus *Psocus*; *pteron*, a wing)

VERY SMALL SOFT-BODIED WINGED OR APTEROUS INSECTS WITH BITING MOUTH-PARTS. VENATION REDUCED AND SELDOM WITH CROSS VEINS: FORE WINGS WITH PTEROSTIGMA. TARSI 2-OR 3-SEGMENTED, CERCI USUALLY ABSENT. *Book-lice* and allies.

This order (Fig. 73) is divided into two suborders, of which the

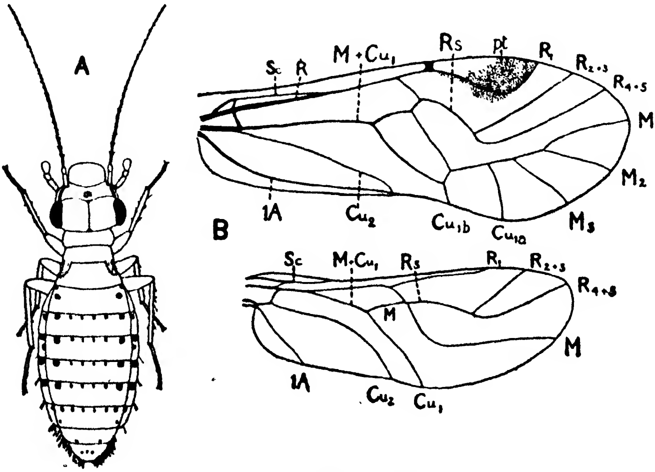

FIG. 73.—PSOCOPTERA

A, *Atropos pulsatoria* (*from* Tillyard). B, *Psocus*, right wings

Psocida are world-wide in distribution and include the vast majority of the species (about 800). They have long multiarticulate filiform antennae, the maxillae are single-lobed, each ensheathing an elongate rod or 'pick', and there are no cerci. These insects are known as book-lice, since several kinds often occur among books, &c., in little-used rooms: others are found among stores of cereal products, or of straw or chaff, but more usual habitats are among vegetation or on the bark of trees, lichens, old palings, &c. They are more or less gregarious and lay their eggs in groups covered with silken threads. The rod-like 'pick' is of uncertain homology and is probably used for rasping off fragments of bark or other plant tissues.

The **Zoraptera** live beneath bark in decaying wood or in termitaria in the warmer parts of the world, including parts of the United States; fewer than a dozen species are known. Their antennae are moniliform and 9-segmented, the maxillae are 2-lobed, and 1-segmented cerci are present. They live in colonies which often contain both winged and apterous individuals: the wings are shed as in termites. The apterous forms are blind and resemble workers of the last-named insects. The venation, however, is nearest to that of the Psocida. Little is known of the economy of these insects and they are grouped under the one genus *Zorotypus.*

ORDER XIII. ANOPLURA (*anoplos*, unarmed; *oura*, a tail)

VERY SMALL, TOUGH-BODIED, FLATTENED APTEROUS INSECTS ECTOPARASITIC ON BIRDS AND MAMMALS. ANTENNAE SHORT, 3- TO 5- SEGMENTED: EYES REDUCED OR NONE. MOUTH-PARTS EITHER FOR BITING OR PIERCING: LEGS SHORT WITH STRONG SINGLE OR PAIRED CLAWS: CERCI ABSENT. *Bird-lice* and *Sucking-lice.*

Anoplura number about 2,200 species: they live in all stages on warm-blooded animals, fastening their eggs to the hair or feathers, as the case may be. Lice from closely related hosts form well-defined groups that are themselves of close relationship, thus suggesting that, to a considerable extent, host and parasite evolution has taken place simultaneously. Two well-defined suborders are recognized. The **Mallophaga** or *bird-lice* are chiefly avian parasites: they are much less often found on mammals. The prothorax is free and distinct and the thoracic spiracles are ventral. The mouth-parts are of a modified biting type and the food consists of fragments of skin or feathers: sometimes they may take exuding drops of blood. It is possible that Mallophaga are derivatives of original nest-inhabiting Psocida that came to live an ectoparasitic life. Among members of the suborder the chicken mite *Menopon pallidum* is notorious: species of *Trichodectes* live on dogs, cats, and other domesticated animals.

The **Siphunculata** or *sucking-lice* are a smaller suborder numbering little more than 200 species. They are to be distinguished by the thoracic segments being fused and by the spiracles of this region being dorsal in position. All species are blood-sucking parasites of mammals. The highly modified mouth-parts are used for piercing and in front of the head is a small retractile tube or haustellum armed with denticles. When everted the denticles anchor the insect to the skin of the host. A pair of stylets, said to be derived from the labium, passes through the haustellum and pierces the skin. These stylets are enclosed in a sheath-like pharyngeal tube which is inserted into the puncture and the action of the pharyngeal muscles pumps blood into the gut of the louse. The original mandibles and maxillae are stated to be atrophied. *Pediculus* includes species found on man and the higher apes. The best known is *P. humanus* of man, with its subspecies, known respectively as the Head Louse (*capitis*) and the Body Louse (*humanus* s. str.). The human louse is the vector which transmits from man to man the pathogenic agents of epidemic typhus, relapsing fever and trench fever. *Phthirus pubis* is the Crab Louse of man, while *Haematopinus* has common species infesting the pig, horse, and ox.

ORDER XIV. THYSANOPTERA (*thusanos*, a fringe; *pteron* a wing)

MINUTE SLENDER INSECTS WITH SHORT 6- TO 9-SEGMENTED ANTENNAE AND VERY NARROW WINGS WITH LONG HAIR FRINGES. MOUTH-PARTS STYLET-LIKE, FOR RASPING. TARSI VERY SHORT ENDING IN A VESICLE: CERCI ABSENT: AN INCIPIENT PUPAL STAGE PRESENT. *Thrips.*

Thysanoptera frequent many kinds of plants besides being found in decaying wood, fungi, &c. About 1,500 species are known and they occur all over the world. While rarely exceeding 4 mm. long, these insects are very abundant as individuals. Being sap-feeders, a number are enemies of cereals and other cultivated crops such as peas and fruit trees: their attacks on the flowers often lead to sterility or to the fall of the fruit. The head bears a ventral cone or short rostrum that is formed by the labrum above, the labium below and laterally by the plates of the maxillae. The rostrum thus encloses the mandibles, the two maxillae and the hypopharynx. The mandible, which is a stout stylet, is the left one, its counterpart being vestigial. Each maxilla consist of a palpus-bearing plate, together with a slender 2-segmented stylet articulating with it. During feeding the rostrum is closely applied to a leaf; the tissues are lacerated and broken up by the three stylets named and then sucked up through the rostrum by the pumping action of the fore-intestine. During growth four instars commonly occur, the 3rd and 4th instars being the prepupa and pupa, respectively. Both these instars are resting nymphal stages in which no food is taken, and they commonly occur in the soil. External buds of the wings and appendages are evident, and these instars foreshadow the holometabolous condition of the higher insects. While Thysanoptera form an isolated order they are nearer related to Hemiptera than to any other group.

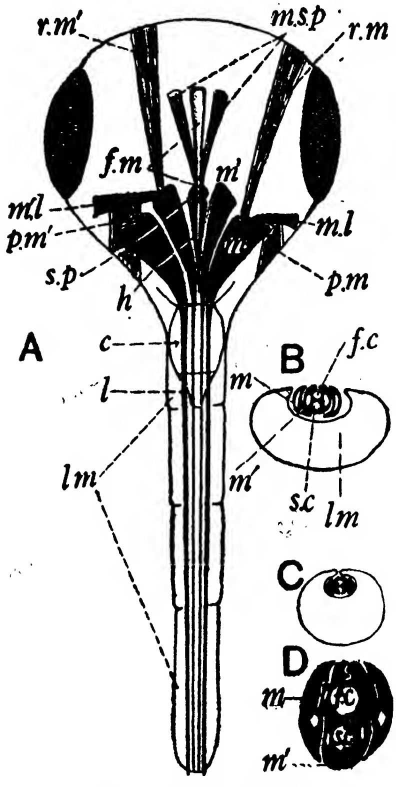

FIG. 74.—HEMIPTERA

A, simplified diagram showing feeding mechanism of a plant bug (Heteroptera), anterior view. B, transverse section of mouth-parts, just in front of labrum. C, transverse section of mouth-parts near apex of labium. D, transverse section of mouth-stylets of *Anasa tristis* (Heteroptera), showing method of interlocking (*from* D. G. Tower, 1914). *c*, clypeus; *f.c*, suction canal; *h*, hypopharynx; *m.l*, mandibular lever; *m'.l*, maxillary lever; *m.s.p*, muscles of salivary pump; *p.m*, protractor muscle of mandible; *p.m'*, do. of maxilla; *s.c*, salivary canal. Other lettering as in Fig. 75

ORDER XV. HEMIPTERA

(*hemi*, half; *pteron*, a wing)

WINGS VERY VARIABLY DEVELOPED WITH REDUCED OR GREATLY REDUCED VENATION: FORE PAIR OFTEN MORE OR LESS CORNEUS: APTEROUS FORMS FREQUENT. MOUTH-PARTS FOR PIERCING AND SUCKING WITH MANDIBLES AND MAXILLAE STYLET-LIKE AND LYING IN THE PROJECTING GROOVED LABIUM: PALPI NEVER EVIDENT. AN INCIPIENT PUPAL INSTAR SOMETIMES PRESENT. *Plant-bugs, Cicadas, Leafhoppers, Aphides, Scale insects.*

This order includes about 40,000 species and is the largest among Exopterygota. Its members are best recognized, in cases of doubt, by the mouth-parts, which are very constant in their essential structure. The wings present no common venational or other features and, furthermore, are often absent. The mouth-parts are adapted for piercing plant tissues and extracting the sap. The labium or rostrum projects downward from the head and forms a grooved channel within which lies two pairs of needle-like stylets. At the base of the labium the groove is absent and the stylets are roofed over in this region by the labrum. The mandibles form the outer (or anterior) pair of stylets and the maxillae are lodged between. The maxillary stylets interlock so as to enclose an anterior or suction canal and a posterior or salivary canal (Fig. 74). Just before the maxillae diverge in the head a narrow *food meatus* enters the suction canal. The common salivary duct opens into a salivary pump which discharges the salivary secretion at the apex of the hypopharynx into the salivary canal. The mandibles are the chief piercing organs and the maxillae are afterwards inserted into the puncture. Ordinarily, the stylets are forced into the tissues by their protractor muscles, being guided by the labrum and the grooved labium. As they gradually penetrate, bringing the head nearer the leaf surface, the labium becomes shortened by being bent or looped (Fig. 75, D). In the scale insects and white flies the stylets may exceed the length of the whole insect and when retracted, are coiled within an internal pouch or *crumena* (Fig. 75, E). The four stylets are interlocked to function as a single structure : they are inserted into the plant partly by the action of the protractor muscles and partly by means of a muscular clamp, near the apex of the labium, which alternately grips and releases the stylets after the manner of forceps. Hemiptera feed by drawing the sap into the food meatus by the action of a muscular sucking pump : it then enters the pharynx and passes into the mid-intestine. In virtue of their universal sucking propensities many Hemiptera cause a vast amount of direct or indirect injury to cultivated plants. Certain aphides and leafhoppers also convey highly destructive virus diseases from plant to plant during feeding. Especially noteworthy are diseases of potatoes, tobacco, maize and sugar-cane that are transmitted in this manner.

Hemiptera are divided up into two main groups that are often regarded as separate orders, viz. the Heteroptera and Homoptera. The **Heteroptera** or plant bugs, have the fore wings usually modified into hemelytra (Fig. 75, C) and, while at rest, they overlap flat on the abdomen : also the base of labium is separated from the anterior coxae by a sclerotized area of the head wall. The majority of the members of this suborder are plant feeders and among them are a number of injurious species. These include the Chinch-bug (*Blissus leucopterus*) of the United States, the cotton stainers (*Dysdercus*) of the tropics and the apple Capsid (*Plesiocoris rugicollis*) of Europe (Fig. 75, A). A propensity for animal food has been acquired in the predaceous family Reduviidae, and most aquatic bugs, which imbibe the body fluids of insects and other small animals. Bed-bugs (*Cimex*) and the Reduviid *Triatoma* comprise blood-suckers of man. A number of Heteroptera are aquatic in habit and include the water boatmen (Notonectidae) (Fig. 75, F), water scorpions (Nepidae), giant water-bugs (Belostomatidae), and others, which are familiar examples.

The **Homoptera** have the fore-wings either leathery or membranous but of uniform consistency, and they are folded roof-like along the sides of the body. The labium arises far back on the head or even between the fore coxae. Associated with Homoptera are three characteristic features in their economy, viz. the almost continuous discharge of a sugary waste product or ' honey dew ' from the anus, especially notable in aphides : the prevalent excretion of wax either in a powdery form or as threads : and the presence in the

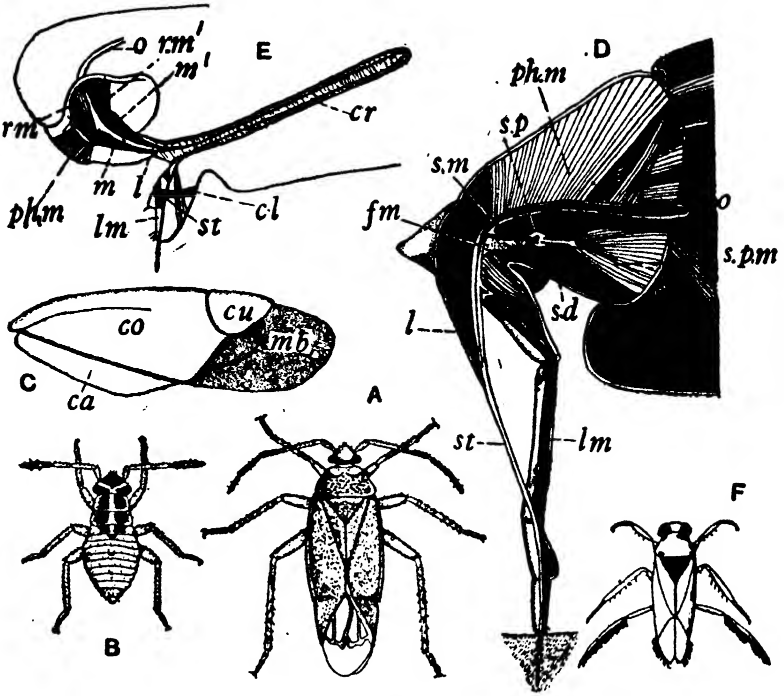

FIG. 75.—HEMIPTERA

A, *Plesiocoris rugicollis* (Capsidae). B, 1st instar nymph of same. C, hemelytron of a Capsid. D, section through the head of *Graphosoma* (Heteroptera), showing position of labium during feeding. E, *Pseudococcus* (Coccidae), lateral view of head showing position of stylets in crumena. F, *Notonecta*. (A and B *from* Petherbridge and Husain : D and E *adapted from* Weber, 1930). *ca*, clavus : *cl*, clamp muscle ; *co*, corium ; *cr*, crumena ; *cu*, cuneus ; *f.m*, food meatus ; *l*. labrum ; *lm*, labium ; *m*. mandibular stylet ; *m'*, maxillary stylet ; *mb*, membrane ; *o*, oesophagus ; *ph.m*, dilator muscles of pharynx ; *rm*, retractor muscle of mandible ; *rm'*, do. of maxilla ; *s.d*, salivary duct ; *s.m*, salivary meatus ; *s.p*, salivary pump ; *s.p.m*, dilator muscles of salivary pump ; *st*, stylets abdomen of a peculiar tissue—the *mycetom* which harbours microörganisms supposedly symbiotic in function. Among the different families of Homoptera the cicadas (Cicadidae) are well known for the shrill sounds emitted by the males, and the lantern-flies (Fulgoridae) are large tropical insects usually of brilliant coloration. The frog-hoppers (Cercopidae) are small insects whose nymphs live within a frothy exudation which is believed to prevent dessication and also afford protection from enemies. The abdominal spiracles open into a ventral cavity formed by the downgrowth of the tergites and pleurites which meet beneath the sterna. This cavity is closed anteriorly, but air enters posteriorly through a kind of valve. The actual frothing results from the fluid, exuded from the anus, forming a film over this valve and becoming blown into bubbles by air expelled through the latter. The Cicadellidae (or Jassidae) are leafhoppers and the Aleyrodidae are the white flies whose bodies and wings are dusted with a powdery wax. The final nymphal instar in Aleyrodidae is followed by an incipient pupa, with external wing-buds, and enclosed in the persistent nymphal skin.

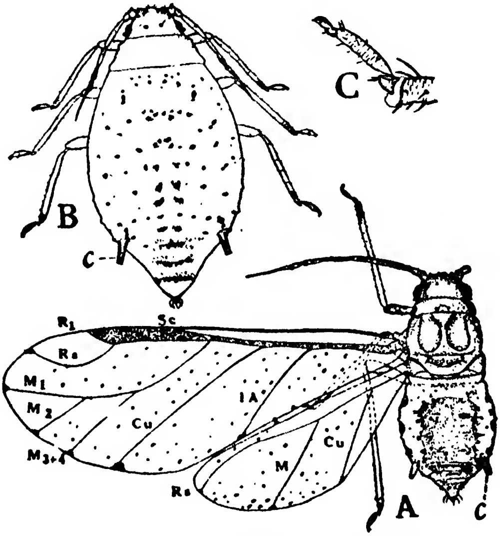

FIG. 76.—*ANURAPHIS TULIPAE*
A, winged viviparous female. B, wingless do. C, tarsus of 3rd leg; *c*, cornicle
(*Adapted from* J. Davidson)

The *Aphidae* (Fig. 76) are an immense family, including many destructive species. They all pass through a more or less complex life-cycle on one or more plant hosts and are commonly termed 'green-fly' or plant-lice. The Aphidinae comprise the greater number of the species: they bear a pair of short dorsal tubes or cornicles on the abdomen through which blood and wax-laden corpuscles are exuded. In this subfamily the asexual generations are viviparous. Winter is usually spent in the egg, which is commonly laid on a woody plant termed the *primary host*. In the spring an apterous agamic female (*fundatrix*) hatches out which produces very similar offspring (*fundatrigeniae*), but soon winged agamic females (*migrantes*) develop and these fly to some herbaceous plant or *secondary host*. All through the summer new generations of winged or wingless agamic females (*alienicolae*) are produced on the secondary

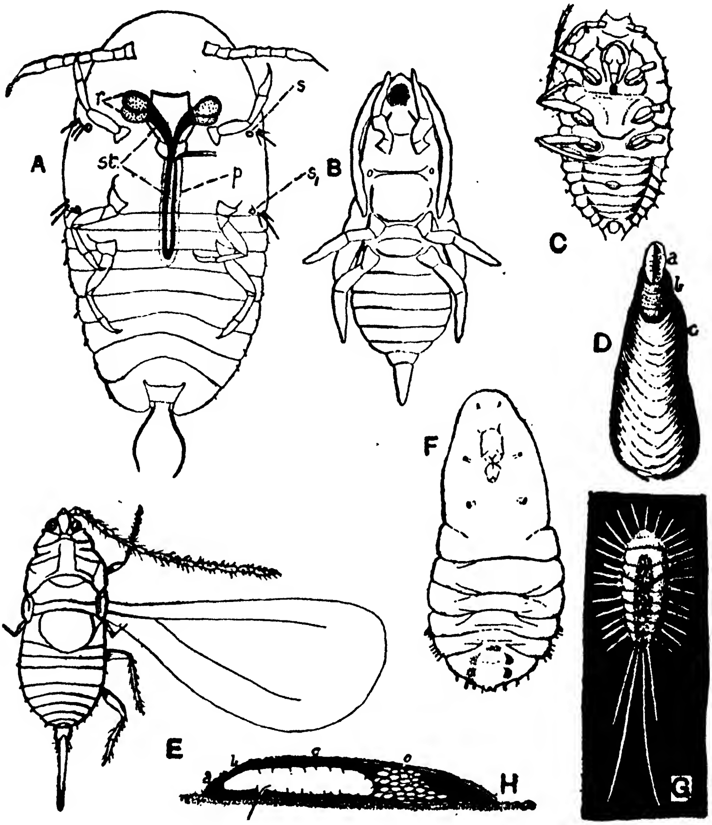

FIG. 77.—COCCIDAE

A, 1st instar of *Coccus hesperidum*, ventral, × 110. B, *Lepidosaphes fulva* male pupa, ventral, × 48. C, *Pseudococcus longispinus* young adult female, ventral, × 28. D, *Lepidosaphes ulmi* female scale, dorsal, × 16. E, *Aspidiotus limonii* male, × 48. F, *Lepidosaphes ulmi* female removed from scale, ventral, × 37. G, *Pseudococcus longispinus* female in natural state on a leaf, × 4. H, *Lepidosaphes ulmi*, longitudinal section of female, × 16. (Figs. D and H original; remainder *adapted from* Berlese.) *a*, scale of 1st instar; *b*, do. of 2nd instar; *c*, do. of adult; *o*, eggs; *p*, crumena; s, s_1, spiracles; *st*, mouth-stylet host, the winged forms relieving overcrowding by flying to other plants. In early autumn winged alienicolae known as *sexuparae* fly to the primary host and produce gamic males and females (*sexuales*). After mating, eggs are laid and the cycle is thus completed. Members of the subfamily Phylloxerinae undergo a more complex life-cycle and differ from the Aphidinae in that the cornicles are absent and reproduction is never viviparous. The genus *Phylloxera* is an important enemy of the vine and *Adelges* affects Coniferae. Its gamic generation always occurs on spruce (*Picea*) and the agamic forms on *Larix*, *Pinus*, *Abies*, &c. The *Coccidae* (Fig. 77) include the scale insects and mealy bugs. They rank among the most highly modified of all insects and are notable for their extreme sexual dimorphism. In the mealy bugs the insect is covered with a fine waxy exudation, while in the true scale insects the ‘ scale ’ is a covering formed by the persistent exuviae of the previous instars glued together with a dermal secretion. Many Coccids are well known injurious insects, and the more important include *Lepidosaphes ulmi*, the Mussel Scale (Fig. 77, D); *Aspidiotus perniciosus*, the San Jose Scale; *Icerya purchasi*, the Fluted Scale; *Pseudococcus citri*, the Citrus Mealy Bug, and many others. On the other hand, *Coccus cacti* yields cochineal, and *Laccifer lacca* of India produces a resinous exudation or lac providing commercial shellac. In the early instars the two sexes of coccids are indistinguishable and the young insects are active with well-developed antennae, legs and mouth-parts. Those producing females pass through one or two instars fewer than the males. In the more primitive types, or mealy bugs, including *Monophlebus*, *Pseudococcus*, &c., the females continue active (Fig. 77, C), but in most forms they become sedentary after the 1st or 2nd instar and various degrees of reduction of the appendages supervene (Fig. 77, F). Culmination is reached in *Physokermes* and other genera wherein the antennae and legs have totally atrophied. In the males the 3rd or 4th instar is a prepupa and the succeeding instar is a pupa : during these phases the original appendages disappear and the imaginal organs that replace them are external growths. In the male imago anterior wings only are present, the hind pair being represented by slender halteres that are linked to the wing-bases by hooklets (Fig. 77, E): mouth-parts are absent.

APPENDIX

Fecundity and Biological Equilibrium. Insects abundantly exemplify the rule that every organism when freed from environmental resistance and allowed unrestricted multiplication sooner or later attains a supernormal ascendancy. Thus, the progeny of a single aphid, at the end of 300 days—if all the members survived—would be somewhere in the order of the 15th power of 210. Reproductive rate, however, is not a criterion of the relative abundance of a species. As Darwin pointed out many years ago, the Fulmar petrel lays only a single egg, yet it is believed to be one of the most abundant birds in the world. A parallel example is afforded by the Tsetse flies (*Glossina*) that are so abundant and pestilential in tropical Africa. Each fly, however, produces but a single larva at a time and only a few in its whole life. The greatest fecundity is met with in those species that suffer the heaviest destruction and particularly where, as is usual among insects, the parent has no means for protecting the eggs or young. Thus, among Tachinid flies (p. 163) the smallest number of eggs are produced by those species that deposit them, or the resulting larvae, on or within their hosts: in such examples fewer than 100 up to about 200 eggs are produced. At the other extreme are those Tachinidae that lay from 2,000 to about 6,000 eggs: these are deposited on or about the food of their hosts. The continuance of the species depends upon some of the eggs being swallowed, otherwise they do not hatch. To revert to the Tsetse-flies and with them must be included the Forest-flies or Hippoboscidae. In these insects only a single egg matures at a time in the ovary and the resulting larva is nourished within the parental body until ready for pupation. It will be evident that the perils besetting the eggs after deposition, and the subsequent larvae, are eliminated: also, the swiftly flying inconspicuous Tsetse is well endowed for taking care of itself and its contained progeny.

The ability of a species to multiply in a given time when freed from all environmental resistance is its *biotic potential.* It depends upon the rate of multiplication and the sex ratio, while the rate of multiplication itself is dependent upon fecundity and the length of the developmental cycle. If p represent the original population; z be the product of the number of eggs per female and the sex factor, and n the number of generations passed through in a given time, then pz^n represents the biotic potential. Thus, if a female lays 800 eggs and $p = 2$, the sex ratio[1] is 0·5 and there is a single generation per annum, the biotic potential would be 800. In the House-fly (*Musca domestica*) numerous batches of eggs are laid, with about 120 eggs to a batch; $p = 2$ (one male and one female) and the sex ratio is 0·5. Allowing 7 generations a year, and 10 batches of eggs laid by each female, the biotic potential is given by $2\ (120 \times 10 \times 0{\cdot}5)^7$.

A little reflection will make it clear that in a state of nature there are many forces that reduce the biotic potential. Under normal circumstances the actual number of descendants that survive at the end of a season keep the population of a given species in a steady state or condition of *biological equilibrium,* i.e. in a condition involving relatively small fluctuations within narrow limits. The forces that operate in reducing the biotic potential of a species are termed collectively *environmental resistance.* The percentage of the progeny that must normally be eliminated by the action of these forces, in order to maintain the numbers of a given species in a state of equilibrium, is expressed by the *coefficient of destruction* and, using Bremer's formula, where $q_c = 1 - \frac{1}{a^c b^c}$ the coefficient is q, a is the progeny per female, b is the

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[1] i.e., the ratio of females to individuals of both sexes: where the numbers are equal the ratio is $\frac{50}{100} = 0{\cdot}5$.

sex ratio, and the number of generations in a year is represented by c. In the case of the Mangold-fly (*Pegomyia hyoscyami*), for example, $a = 50$, $b = 0{\cdot}5$ and $c = 3$. The normal coefficient of destruction would be 96 per cent for one generation and 99·9 per cent for 3 generations. In other words, the survival of only 0·01 per cent of the individuals produced during a year will keep the number of flies in a state of biological equilibrium. The factors constituting environmental resistance are physical and biological. Physical factors are mainly climate, while biological factors include parasites, predators, food, disease, and competition with other species. Climatic factors operate as a rule independently of the density of the population of a given species, whereas biological factors are density-dependent, or, in other words, they have very little effect where the population density is low. In the case of parasites and predators their capacity for discovering their hosts, in relation to the density of the latter, largely determines their efficacy as controlling agents. It will be evident that the greater the host density the easier it will be for natural enemies to discover them. The contention that the density of a given species is controlled by biological factors needs amplification. Let it be supposed that climate destroys 65 per cent of the individuals of the species, it is clear that its numbers would rapidly increase if no other factors operated. This progressive multiplication will remain unchecked by climate, which will continue to destroy 65 per cent as before. If there is some other factor, such as a natural enemy, or a disease, whose action is governed by the density of its hosts, the destruction of the remaining per centage of the individuals would be accomplished. It will be evident that although climate may destroy 65 per cent of the insects, actual control to a state of biological equilibrium is the resultant activity of the biological agency. Convincing evidence of the controlling influence of such agencies as parasites and predators is afforded in the case of insects that have assumed the status of major pests when accidentally introduced into lands they did not previously inhabit. In the new environment biological factors that were operating in the original habitat are wanting. In a number of instances of this kind *biological control* has been achieved by the introduction of specific natural enemies whose activities have reduced the density of the population of the introduced insect to a degree in which the economic damage caused is negligible.

ORDER XVI. NEUROPTERA (*neuron*, a nerve ; *pteron*, a wing)

SMALL TO LARGE SOFT-BODIED INSECTS WITH TWO PAIRS OF MEMBRANOUS WINGS WITHOUT ANAL LOBES : VENATION GENERALLY WITH MANY ACCESSORY BRANCHES AND NUMEROUS COSTAL VEINLETS : RS USUALLY PECTINATELY BRANCHED. MOUTH-PARTS FOR BITING, ANTENNAE WELL DEVELOPED, CERCI ABSENT. LARVAE CAMPODEIFORM WITH BITING OR SUCTORIAL MOUTH-PARTS : PREDACEOUS AND AQUATIC OR TERRESTRIAL. *Alder-flies, Lacewings, Ant-lion flies, Mealy-wings, &c.*

This rather heterogenous order (Fig. 78) is divided into the sub-orders Megaloptera and Planipennia. The **Megaloptera** have the more primitive venation with fewer accessory veins and the pectination of Rs is usually undeveloped : their larvae have biting mouth-parts. The Alder-flies (*Sialis*) and allies have aquatic larvae with seven or eight pairs of hair-fringed abdominal appendages. *Corydalis*, which occurs in North and South America and Northern India, attains a wing expanse of 15 cm., with gigantic mandibles in the male. The Snake-flies (*Raphidia*) have a long neck-like prothorax and an elongated ovipositor: their larvae live under bark of conifers, &c.

The **Planipennia** include the majority of Neuroptera. The venation shows a pectinate Rs and a great development of secondary branching, especially as bifurcations along the wing margins. The larvae occur on vegetation, or in the earth, or are aquatic. All have exserted, piercing mouth-parts of similar basic design. The mandibles and maxillae (Fig. 78, C, D) are co-ordinated and enclose a groove-like suction canal through which the body fluids of the prey are imbibed : also, six out of the eight Malpighian tubes become silk glands and they weave their cocoons through an anal spinneret. As in the Megaloptera the pupae are primitive and capable of walking, or climbing, before the eclosion of the imago. Of the main families the *Hemerobiidae* (Brown Lacewings) and *Chrysopidae* (Green Lacewings) are notably beneficial since their larvae destroy large numbers of Homoptera and other small insects. The *Sisyridae* and *Osmylidae* have aquatic larvae : those of the first-named live in association with fresh-water sponges, piercing the tissues with their mouth-parts. The *Nemopteridae* have very elongate filiform hind-wings : their larvae have very long necks, sometimes exceeding the whole of the rest of their bodies. The *Myrmeleonidae* are large insects with knobbed antennae : their larvae, or ant-lions, commonly make pit-like snares for capturing their prey. The *Ascalaphidae* are closely related, but the antennae are longer and filiform : their larvae lurk under stones, on leaves or on trees. The *Mantispidae* are predators and resemble the Mantids in the formation of their raptorial legs : the life-cycle involves hypermetamorphosis and the larvae become external parasites on the egg cocoons of certain spiders. The *Coniopterygidae*, or Mealy-wings, seldom exceed 8 mm. in wing-expanse and have greatly simplified venation. Their claim for inclusion in the order is based on the morphological characters of their larvae. They occur on trees and shrubs, the larvae preying upon minute insects, mites, &c. ; the adults are covered with a powdery exudation from epidermal glands and resemble small aphides. About 4,000 species of Neuroptera are known, and of these 60 occur in Britain.

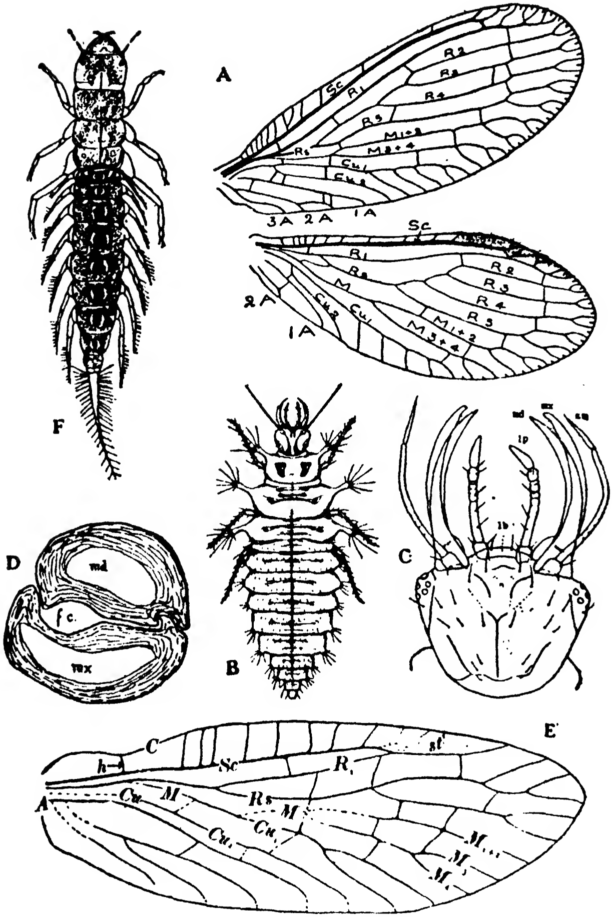

FIG. 78.—NEUROPTERA

A, right wings of a Neuropteron (*Sisyra*) (*after* Comstock). B, Larva of *Chrysopa alba* (*after* Withycombe). C, do., head (*after* Withycombe): *an*, antenna; *lb*, labrum; *md*, mandible; *mx*, maxilla. D, transverse section showing interlocking of mandible and maxilla of *Chrysopa* larva forming a food-channel (*f.c*). E, venation of forewing of *Sialis* (*after* Needham). F, larva of *Sialis* (*after* Needham)

ORDER XVII. MECOPTERA (*mekos*, length; *pteron*, a wing)

SOFT-BODIED INSECTS WITH TWO PAIRS OF ELONGATE SIMILAR WINGS: VENATION PRIMITIVE, COSTAL VEINLETS FEW. HEAD PROLONGED INTO A BEAK: MOUTH-PARTS FOR BITING: SHORT CERCI PRESENT. LARVAE OLIGOPOD OR POLYPOD: PUPAE IN EARTHEN CELLS. *Scorpion-flies.*

A small order of fewer than 500 species but with a world-wide range. Its members are usually recognizable by the beak-like head, maculated wings and the prominent external genitalia of the male. They are separable from Neuroptera by the small number of costal veinlets, the dichotomously branched Rs and by the undivided Cu_1. The habit of the males carrying the end of the abdomen upturned has given the name of Scorpion-flies to species of *Panorpa* and their allies. The imagines prefer shaded places and both they and the larvae are mainly carnivorous. The larvae are chiefly subterranean : those of *Panorpa* bear three pairs of thoracic and eight pairs of abdominal limbs, while in *Boreus* only thoracic legs are present. There are only four British species which belong to *Panorpa* and *Boreus*. The last-named has vestigial wings and its larva is exceptional in feeding upon mosses. Six genera and about 50 species occur in North America. Numerous fossilized wings from Permian rocks are referred to the Mecoptera, and the order is claimed to be closely related to forms that are ancestral to most of the Holometabola.

ORDER XVIII. TRICHOPTERA (*thrix*, gen. *trichos*, a hair ; *pteron*, a wing)

MOTH-LIKE INSECTS WITH TWO PAIRS OF DENSELY HAIR-COVERED WINGS SHOWING PREDOMINANTLY LONGITUDINAL VENATION WITH FEW CROSS VEINS. MOUTH-PARTS REDUCED : MANDIBLES RARELY FUNCTIONAL. LARVAE AQUATIC, GENERALLY IN PORTABLE CASES : THORACIC LEGS AND PAIRED CAUDAL APPENDAGES ENDING IN HOOKS PRESENT. PUPAE AQUATIC, WITH STRONG MANDIBLES. *Caddis-flies.*

Trichoptera (Fig. 79) are weakly flying and mostly nocturnal insects, found usually in the vicinity of water. They are obscurely coloured, generally of some shades of brown or grey, and the wings are closed roof-like over the back when at rest. They are closely allied to the Lepidoptera-Homoneura (p. 138), the venation of the family Rhyacophilidae closely resembling that of *Micropteryx* and allied moths. Caddis-flies only take liquid food, which is licked up by the broad ligula and traverses the channel formed by the labrum and hypopharynx. The maxillary lobes are galeae only, thus prefiguring the condition found in Lepidoptera. The eggs are laid in masses in or near water and are commonly protected by mucilage. The larvae all have the head well sclerotized with very small antennae and the 1st pair of legs shortest and stoutest ; the abdomen is formed of nine segments, the last bearing a pair of jointed appendages ending in hooks. Caddis larvae present two main types : in the first type the head is inclined at an angle with the body and there are dorsal, lateral and ventral tufts of abdominal tracheal gills. Such larvae make portable cases of extraneous material bound together and lined with silk produced by the modified salivary (labial) glands. These cases may be constructed of leaf- or stem-fragments, sand grains, empty shells of molluscs, &c., and are very constant in character for different genera. Dorsal and lateral papillae on the 1st abdominal segment maintain the larva in position within its case and allow of an even flow of water through the latter. When walking, the head and the sclerotized 1st, or 1st and 2nd, thoracic segments are protruded through the case, which is gripped by the caudal hooks and dragged along at the same time. In the second type the larvae are usually more active, with elongated body and the head prognathous. They seldom make cases and in many instances live in silken retreats. There are no papillae on the 1st abdominal segment and gills are usually wanting. The anal appendages are often well developed and are used to grip the silken tunnels or to hold on to rocks when they leave their retreats. Trichopterous pupae breathe cutaneously or by means of the persistent larval gills. They are protected either by the original but adapted larval cases, or by special shelters constructed for the purpose. Strong mandibles are present which enable them to

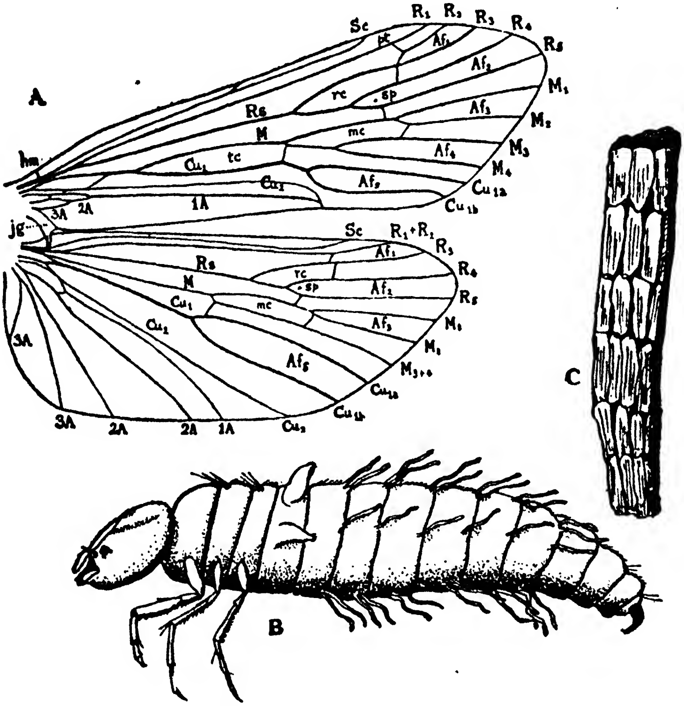

FIG. 79.—TRICHOPTERA

A, right wings of *Stenopsychodes* (Rhyacophilidae) (*after* Tillyard). B, *Phryganea*, larva, and C, its case cut their way out for the eclosion of the imago. In many species the pupae are able to swim in order to reach the surface of the water. For this purpose they use the long middle legs that are fringed with swimming hairs. Fewer than 3,000 species of Trichoptera have been described and, of these, 180 species inhabit Britain.

ORDER XIX. LEPIDOPTERA (*lepis*, gen. *lepidos*, a scale ; *pteron*, a wing)

SMALL TO VERY LARGE INSECTS CLOTHED WITH SCALES. MOUTH-PARTS WITH GALEAE MODIFIED INTO A SPIRALLY COILED SUCTORIAL PROBOSCIS : MANDIBLES RARELY PRESENT. LARVAE PHYTOPHAGOUS, POLYPODOUS : PUPAE OBTECTED OR PARTIALLY FREE, USUALLY IN COCOONS. *Butterflies* and *Moths*.

An immense order with over 140,000 species which have the wings, and usually the body and appendages, more or less covered with pigmented scales (p. 7) : over the wing-surfaces the scales give rise to characteristic colour patterns. The structural similarity of these insects has led to great uniformity of behaviour. The imagines live

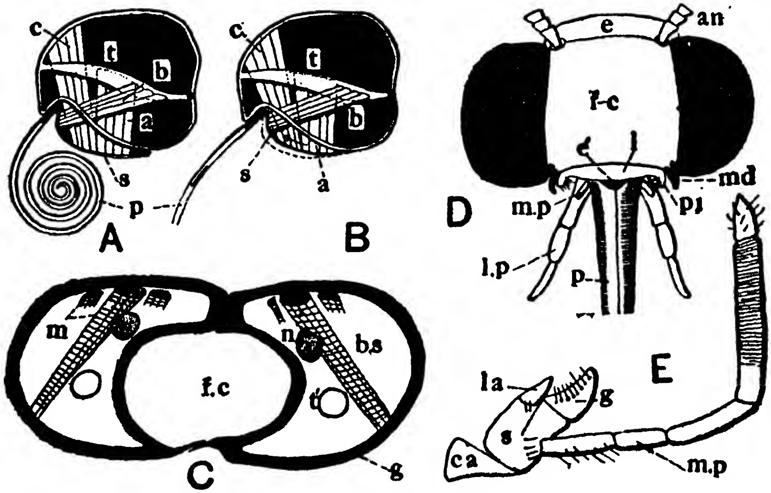

FIG. 80.—LEPIDOPTERA

A, diagram of action of proboscis : right half of head in section with proboscis retracted and coiled. B, the same with proboscis extended by contraction of extensor muscles, *a*, *b*, and *c*, which compresses the stipes and forces blood through a valve into the proboscis. C, transverse section of proboscis. D, frontal view of head and mouth-parts of a moth. E, right maxilla of *Micropteryx*. (A and B *adapted from* J. B. Schmitt). *an*, base of antenna ; *b.s*, blood space of proboscis ; *ca*, cardo ; *e*, epicranium ; *e'*, epipharynx ; *f.c*, food channel ; *f-c*, fronto-clypeus ; *g*, galea ; *l*, labrum ; *la*, lacinia ; *m*, retractor muscles ; *md*, mandible (vestigial) ; *mp*, maxillary palp ; *n*, nerve ; *p*, proboscis ; *pi*, pilifer ; *t*, tentorium ; *t'*, trachea upon nectar, over-ripe fruit, honeydew, &c., while their larvae with few exceptions feed entirely upon phanerogamic plants—leaves, roots, seeds, wood. In *Micropteryx* and its allies, which are pollen feeders, functional and complete mandibles and maxillae (Fig. 80, E) are present. In *Eriocrania* mandibles are reduced, the maxillae have lost the laciniae, while the galea of either side is grooved and functions with its fellow as a suctorial proboscis. In the rest of the Lepidoptera mandibles are vestigial or wanting and the proboscis (Fig. 80, D) may attain a length greater than that of the insect. Each galea is a tube whose cavity is continuous with that of the head: its flexibility is caused by a series of rings separated by membrane. The two components of the proboscis interlock and thus enclose a median food canal (Fig. 80, C). The actual intake of food is affected by the action of a buccopharyngeal pump.

Extension of the proboscis is caused by the contraction of three pairs of extensor muscles which exert pressure on the blood by reducing the cranial cavity. This results in blood being forced through a valve in the cavity of the stipes and so into the interior of each half of the proboscis, thus extending the organ as a whole. As R. E. Snodgrass has stated, the extension of the proboscis by blood-pressure has its analogy in the unrolling of a toy paper ‘ snake ’ by inflating it. Relaxation of the extensor muscles results in a backward flow of blood from the proboscis and the coiling of the latter is brought about by the contraction of the numerous oblique muscles that cross the cavity of each component (Fig. 80, A, B). A reduced labrum, bearing lateral lobes or pilifers, overlies the base of the proboscis. Except in some primitive families maxillary palpi are much reduced or absent. The labium is represented by a simple plate bearing 3-segmented palpi that project conspicuously on either side. Numerous moths take no food and their mouth-parts consequently display varying degrees of atrophy. The prothorax bears a pair of erectile lobes or *patagia*, well displayed in many Noctuidae, &c.; tegulae (p. 16) are well developed and characteristic. The venation (Fig. 81) of the most primitive families is of a generalized type with very few cross-veins. Specialization involves the ultimate disappearance of Cu_2 from both pairs of wings, the reduction of Rs to a single branch in the hind wing and the formation of a large *discal cell* in each wing by the absorption of intervening veins and cells. The prevalent wing-coupling apparatus shows sexual difference. In the male the *frenulum* (p 16.) is single and a hook-like *retinaculum* is usually near the base of Sc (Fig. 81, B); in the female the frenulum is commonly formed of several bristles and the retinaculum is on Cu_1. In the Hepialidae (Fig. 81, A) and some other primitive moths a process or *jugum* arises from the base of the fore-wing: the base of the hind-wing engages in the notch thus formed with the jugum above. In butterflies and certain moths, that have lost the frenulum, *amplexiform coupling* obtains: the enlarged humeral lobe of the hind-wing is maintained against the stiffened base of the fore-wing, thus insuring synchronous action of the two wings. It may be added that wings are vestigial or absent in the females of certain families, notably the Psychidae and a few Geometridae. On either side of the metathorax, or the base of the abdomen, in many moths there is a complex *tympanum* (p. 88), its presence or absence being constant for large groups of families.

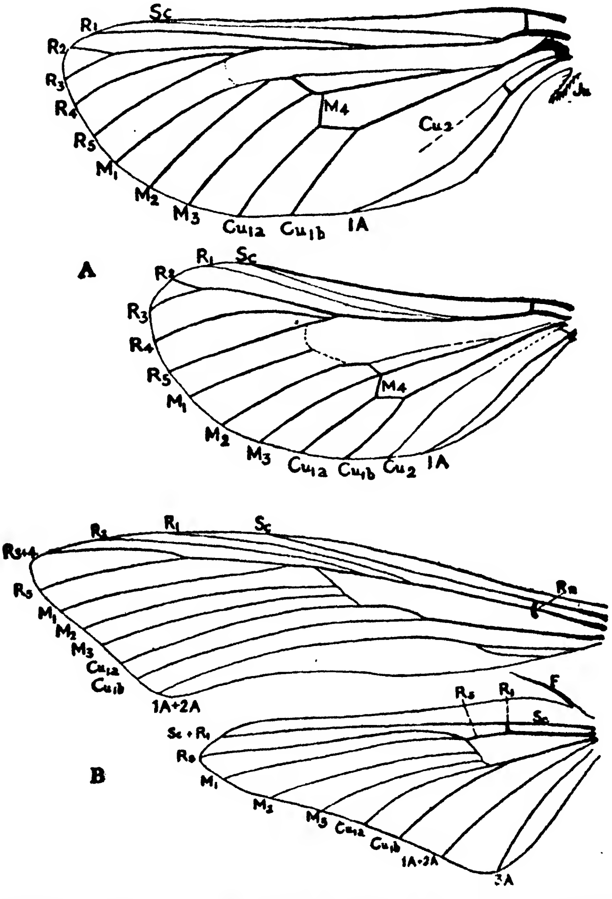

FIG. 81.—VENATION OF, A, HOMONEURA (Hepialidae) AND, B, HETERONEURA (Sphingidae)

Ju, jugum ; F, frenulum ; Rn, retinaculum

The larvae or caterpillars have a well-developed head, 3 thoracic and 10 abdominal segments (Fig. 54, B). Spiracles are present on the prothoracic and first 8 abdominal segments. The mouth-parts are masticatory and highly modified: the antennae are small 3-segmented organs, and behind them is a group of 6 ocelli on either side. Each thoracic segment bears single-clawed legs and a pair of abdominal feet is present on segments 3 to 6 and 10. These organs are fleshy projections whose grasping surface is armed with hooks or crochets that are arranged in circles in the lower families but restricted to an arc or band in the more specialized groups.

In the Geometridae abdominal feet are present only on segments 6 and 10, their caterpillars being known as 'loopers' from their method of crawling. Most caterpillars are protected either by their cryptic form and colour, or by the display of warning patterns, or by the adoption of concealed habits. The salivary glands (p. 65) are modified into silk glands whose secretion is emitted through a median spinneret associated with the hypopharynx. Silk glands may be several times longer than the body in species that form dense cocoons: in all cases the salivary function is performed by mandibular glands.

The pupa in the lower Lepidoptera has the appendages free and most of the abdominal segments movable: aided by a spiny armature, such a pupa usually issues partially from the cocoon to allow of the emergence of the imago. In the higher forms the pupa is obtected (p. 93) with only three free abdominal segments and remains attached to the cocoon by means of a terminal hooking device or *cremaster*. Many butterflies have naked and protectively coloured pupae with the cocoon reduced to a pad of silk to which the cremaster is hooked.

Economically the order is of great importance owing to the damage incurred by the feeding activities of the caterpillars. Only a few examples will be quoted. Species of *Pieris* or the 'White' butterflies, are major pests of cruciferous and other crops. The Gipsy Moth (*Porthetria dispar*) and the Nun Moth (*Liparis monacha*) are great defoliators of forest trees: the European Corn Borer (*Pyrausta nubilalis*) is destructive to maize, &c., in North America: the Codling Moth (*Cydia pomonella*) is a widespread enemy of the apple, and the Mediterranean Flour Moth (*Ephestia kuehniella*) is an almost universally distributed pest in flour mills, &c. Two other pests of very wide range are the Pink Bollworm (*Platyedra gossypiella*) of the cotton plant and the Angoumois Grain Moth (*Sitotroga cerealella*) which infests wheat, maize, &c. Mention also needs to be made of the Clothes Moths (*Tinea pellionella*, *T. bisselliella* and *Trichophaga tapetzella*) which attack woollen clothing, rugs, furs, &c. As an offset, the Silk Moths *Bombyx mori* and certain Saturniidae are beneficial in that they provide commercial silks.

Lepidoptera are closely related to the Trichoptera, the two orders being derived from a common ancestor. The complete M_4 in the

The Coleoptera with over 250,000 described species rank as the largest order in the animal kingdom. While their habits are very varied they are more especially ground insects that live either in the soil, or in decaying matter associated with it. Several families are aquatic and great numbers of species are phytophagous both as larvae and adults. In addition, various species live in timber and dry stored products. Beetles are very uniform in external structure. The head (Fig. 82) is characterized by the very general presence of a *gula* (p. 10) and the legs are well adapted for running or often for burrowing also. The hind wings are the functional organs of flight and, when the insect is in the air, the elytra play no active part in propulsion and are held at an acute angle with the body. The wings

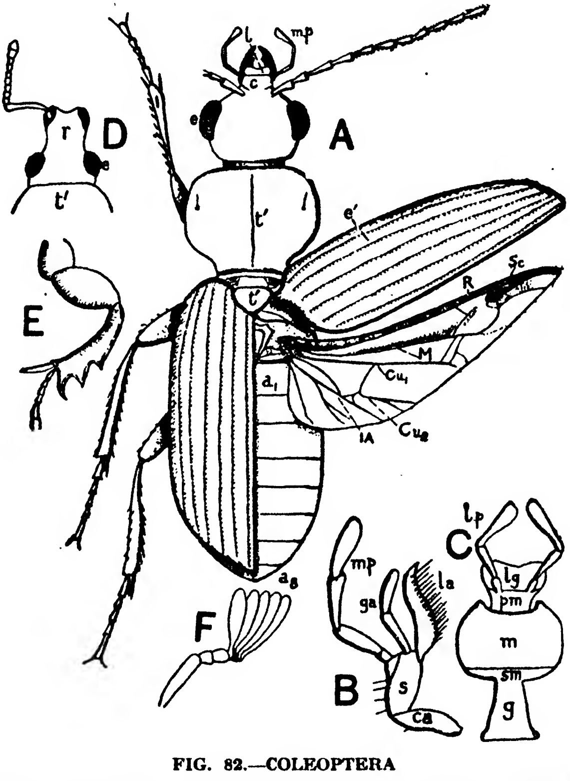

FIG. 82.—COLEOPTERA

A, a beetle, fam. Carabidae. B and C, maxilla and labium of same. D, head of weevil, showing rostrum, *r*. E, leg of a Scarabaeid beetle. F, antenna of a cockchafer. *a*, 1st abdominal segment; a_8, 8th do.; *c*, clypeus; *ca*, cardo; *e*, compound eye; *e'*, elytron; *g*, gula; *ga*, galea; *l*, labrum; *la*, lacinia; *l.p*, labial palp; *lg*, ligula; *m*, mentum; *m.p*, maxillary palp; *pm*, prementum; *s*, stipes; *sm*, submentum; *t'*, prothorax; *t''*, scutellum are often long and are complexly folded beneath the elytra; sometimes they are much reduced or wanting and, in such cases, the elytra are often soldered together. In the Staphylinidae and related families the elytra are much shortened, while in the Oil Beetles (*Melöe*) they are vestigial. The wing-venation is difficult to homologize with that of other insects: there is a predominance of longitudinal veins and, except in Adephaga, cross-veins are either absent or very few.

Coleopterous larvae (Fig. 83) afford excellent examples of adaptation to particular modes of life. Thus, in the Adephaga and the Staphylinidae the campodeiform type prevails. Such larvae have the antennae, legs and sensoria well developed, thereby fitting them for an active predatory life. Elongated simple, or jointed, processes are borne on the 9th abdominal segment: these are apparently cerci that have moved forward from their original segment—the 10th—which usually functions as a pseudopod. Less active larvae, which have no need to seek far for sustenance, are characteristic of a large number of families. They are of a modified campodeiform type with the appendages and sensory organs reduced. Examples are larvae of the Coccinellidae (lady-birds), Elateridae (wire-worms) and Chrysomelidae (leaf-beetles). The scarabaeoid type of larva is subterranean in habit and prevails in cockchafers, dorbeetles and

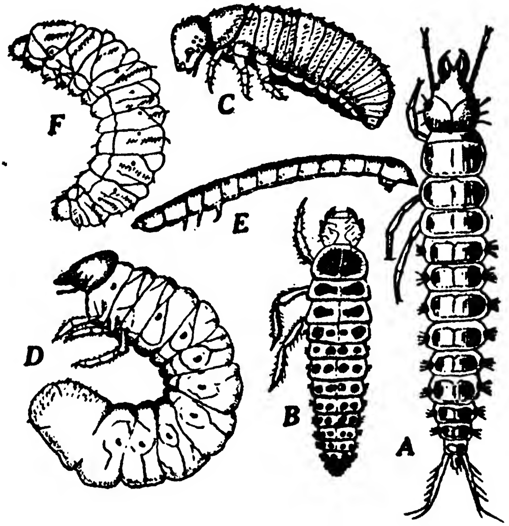

FIG. 83.—TYPES OF COLEOPTEROUS LARVAE

A, Ground beetle (Carabidae). B, Lady Bird (Coccinellidae). C, Leaf beetle (Chysomelidae). D, Chafer (Scarabaeidae). E, Wireworm (Elateridae). F, Weevil (Curculionidae) their allies. Crescentic in form, it has a large sclerotized head, well-developed legs, a soft inflated abdomen and conspicuous cribriform spiracles. Among wood-boring larvae the body is usually fleshy and unpigmented with stout jaws and a small sclerotized head partly withdrawn into the broadly transverse thorax. Legs are greatly reduced and sometimes atrophied. The extreme type of larval modification is in weevils, where life occurs amidst immediately available food. Usually crescentic in form and entirely apodous, these larvae are mostly eyeless, with the antennae reduced to small papillae and there are no cerci.

Coleoptera are divided into two suborders, Adephaga and Polyphaga. The **Adephaga** usually have filiform antennae and the basal abdominal sternum is divided longitudinally by the hind coxal cavities: the hind wing has a short rectangular cell or oblongum. The larvae (Fig. 83, A) are campodeiform with definite tarsi and usually paired claws. Included in this suborder is the single superfamily CARABOIDEA whose members are mainly predators both as adults and larvae. Most of the terrestrial forms belong to the large families Carabidae (Ground Beetles) and Cicindelidae (Tiger Beetles). Many aquatic Caraboids are included in the Dytiscidae while the more anomalous forms, or Whirligig Beetles, comprise the family Gyrinidae. The **Polyphaga** include the greater part of the order. The antennae are varied in character and the hind coxal cavities do not completely divide the basal abdominal sternum : the hind wing has a general absence of cross-veins and the oblongum is undeveloped. The larvae pertain to diverse types but are devoid of tarsi and have single claws. The superfamily STAPHYLINOIDEA includes the Staphylinidae (Rove Beetles), the Silphidae (Carrion Beetles) and their allies. The DIVERSICORNIA are an ill-defined group of over 40 families. In the clavicorn series are the Coccinellidae (Ladybirds) that are mostly beneficial since their larvae (Fig. 83, B) and adults prey largely upon Aphides : other families are the Dermestidae or Larder Beetles with densely hairy larvae and the Hydrophilidae with greatly elongated maxillary palpi. The last-named include aquatic or subaquatic beetles as well as terrestrial forms. Among the serricorn series are the Elateridae and the Buprestidae. The first-named include the tropical 'fire-flies' and the more numerous Click Beetles whose larvae or 'wire-worms' (Fig. 83, E) are destructive root-feeders of crops. The Buprestidae are metallic green or blue creatures ; their larvae are legless borers living beneath the bark of trees and notable for their greatly widened prothorax. The superfamily HETEROMERA includes a great variety of forms whose only common feature is the 4-jointed hind tarsi—the other pairs being 5-jointed. The most important families are the Tenebrionidae, which includes the Mealworms (*Tenebrio*) and Flour Beetles (*Tri-*

bolium), and the Meloidae. To the last-named family belong the Blister Beetles, whose blood usually contains a caustic or blistering agent termed cantharidin. This product is chiefly prepared from the dried elytra of the 'Spanish Fly' *Lytta* (*Cantharis*) *vesicatoria. Melöe* and its allies undergo hypermetamorphosis (p. 95) and their larvae are parasitic within nests of solitary bees or in the egg-masses of grasshoppers: the adults are known as Oil Beetles. The extensive superfamily PHYTOPHAGA is characterized by the 3rd tarsal joint being either bilobed or dorsally grooved and receives the minute 4th joint at its base. The largest family is the Chrysomelidae or Leaf Beetles with over 30,000 species. Some, such as the Asparagus Beetle (*Crioceris asparagi*), the Flea Beetles (*Phyllotreta*, &c.) and the Colorado Potato Beetle (*Leptinotarsa decemlineata*), are destructive to crops. The last-named was accidentally introduced into France in 1922 and has since greatly extended its range in Western Europe. The *Cerambycidae* or 'longicorns' comprising most other Phytophaga: they are forest insects whose larvae tunnel into the wood of trees. In the superfamily RHYNCHOPHORA the head is usually produced into a rostrum (Fig. 82, D) and the tarsi are apparently 4-jointed. Their most important family are the Curculionidae or weevils with about 70,000 known species. The rostrum enables the female to bore holes in the medium in which the eggs are deposited. Included here are many injurious kinds such as grain weevils (*Calandra*), the Cotton Boll Weevil (*Anthonomus grandis*), the Pine Weevil (*Hylobius abietis*), and others. The closely related Scolytidae or Bark Beetles has many species which rank as major forest pests. The superfamily LAMELLICORNIA is an easily recognized group since its members have fossorial fore-legs (E) and an antennal club formed of plate-like components (F): their larvae are of the scarabaeiform type (Fig. 83, D). Included here are the *Lucanidae* or Stag Beetles and the *Scarabaeidae* or Chafers and Dung Beetles.

APPENDIX

Aquatic Insects. Some of the best examples of adaptation to a particular mode of life are afforded by aquatic insects. Such insects have, in all cases, secondarily acquired this mode of life and their degree of adaptation varies within wide limits.. The vast majority of aquatic insects inhabit fresh water: a much smaller number occur in brackish waters, while very few have colonized the sea.

Adaptations to an aquatic life have arisen independently in the most diverse orders of insects. Thus, among beetles and water-bugs many species are aquatic both in their immature and adult stages: the Trichoptera and many Diptera are aquatic only as larvae and pupae, while the Plecoptera, Odonata, and Ephemeroptera invariably live in the water during their nymphal instars. The main adaptive features affect the form, relations with the surface film, methods of feeding and locomotion and, most important of all, respiration.

The highly polished, smooth, elliptical contour of many water beetles serves to reduce resistance to the water during swimming. The nymphs of may-flies, and the larvae of certain Diptera and Coleoptera, that inhabit torrential streams assume a greatly flattened form. This feature, coupled with the provision of special anchoring devices (spines, suckers), helps to prevent such creatures from being swept away by the current.

Many aquatic insects have to pierce the surface film in order to maintain their posterior spiracles in contact with the atmosphere and, at the same time, prevent water from entering the tracheae. In some cases (e.g. mosquito larvae) perispiracular glands provide an oily secretion that imparts hydrophobe properties to the surrounding cuticle, i.e., the water retreats from such areas, leaving the surface dry. In other cases special devices of hairs achieve the same object. Thus, when the larva of *Dytiscus* is supported at the tail extremity by the surface film the entry of water into the tracheal trunks is precluded owing to the presence of a circlet of hydrofuge hairs around the posterior spiracles. These hairs are so closely set that water is unable to penetrate between them when they pierce the surface film. They function in such a manner that their outer surfaces show strong hydrophile properties, while the inner surfaces of these hairs are hydrophobe in character. In the Collembolan *Podura aquatica* and in the water skaters (*Gerris*) a coating of fine hydrophobe hairs covers the body and holds the water at a distance so that these insects are incapable of being wetted. When submerged they carry a surrounding air film that has special properties in connexion with respiration (p. 55).

Special adaptations concerned with feeding are evident among predators. These are discussed on p. 118 and include prehensile fore-legs, sharply toothed projecting jaws as in the *Dytiscus* larva and the labial ' mask ' of the Odonata. Larvae of *Simulium* and of mosquitoes are provided with vibratile mouth-brushes that set up water currents and thereby waft their microscopic food into the gullet.

In many aquatic insects the 3rd pair of legs, or the 2nd and 3rd pairs, are specially modified for swimming. Thus, in *Dytiscus* the hind legs are elongated and much flattened from side to side so as to function as oars. The tibia and tarsus bear closely-set fringes of swimming hairs along their upper and lower edges. These hairs become spread during the swimming stroke and fall back when the leg is drawn forward. The tarsus rotates on its axis in a way which allows the swimming stroke to be made by its broad surface, while its edge cuts through the water in reaching the return position; in other words the rotation is comparable with a sculler ' feathering ' his oars. *Notonecta* (Fig. 75, F) and its allies, like *Dytiscus*, swim by means of their oar-like hind legs which operate simultaneously. *Hydrophilus*, on the other hand, uses its hind legs alternately while swimming in much the same sequence as a walking insect. The Dytiscidae consequently swim a long straight course, whereas *Hydrophilus* pursues a somewhat wobbling and less efficient mode of progression. Whirligig Beetles (*Gyrinus*) perform their rapid gyrations on the surface of slowly-moving streams and swim by means of their greatly modified 2nd and 3rd pairs of legs. Some fly larvae, notably those of *Chironomus* and mosquitoes, swim by vigorous muscular action of the abdomen that results in side-to-side wriggling movements through the water. Certain minute Chalcids (*Polynema*, &c.), that parasitize the eggs of various aquatic insects, swim beneath the water by means of their wings.

The transparent or phantom larva of *Chaoborus* (*Corethra*), which is a close ally of mosquitoes, has its tracheal system mainly represented by two pairs of bean-shaped sacs that act as hydrostatic organs (Fig. 84). This larva is able, by some unknown means, to vary the size of the sacs so that its specific gravity can be adjusted to that of the water at different depths.

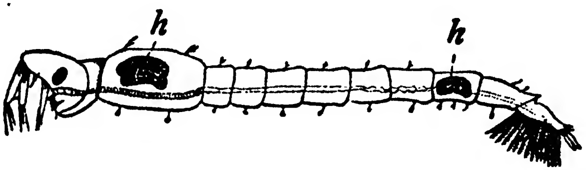

FIG. 84.—LARVA OF *CHAOBORUS* (*CORETHRA*), SHOWING HYDROSTATIC ORGANS, *h*

The respiratory adaptations of aquatic insects are discussed in the chapter dealing with the general subject of respiration (p. 54).

ORDER XXI. STREPSIPTERA (*strepsis*, a twisting; *pteron*, a wing)

MINUTE INSECTS: MALES WITH BRANCHED ANTENNAE AND DEGENERATE BITING MOUTH-PARTS: FORE-WINGS MODIFIED INTO SMALL CLUB-LIKE PROCESSES: HIND-WINGS VERY LARGE, PLICATELY FOLDED. FEMALES ALMOST ALWAYS DEGENERATE PARASITES WITHIN THE BODIES OF OTHER INSECTS. *Stylops.*

In their larval stages Strepsiptera are endoparasites of certain aculeate Hymenoptera and Hemiptera-Homoptera. The 1st instar larvae are active creatures termed triungulins: on meeting a host they bore within and undergo hypermetamorphosis (p. 95). The females remain permanently as parasites with the fused head and thorax protruding between adjacent abdominal segments of the hosts. In a very few cases the females are active and free-living. The males are short-lived and they fly on to the host to mate with the females. Parasitized hosts are said to be ‘ stylopized ’, the term being derived from the generic name *Stylops*. Bees of the genus *Andrena* are often affected and the parasitization tends to cause the hosts concerned to acquire altered sexual and other characters. Similarities in the structure of the triungulin larvae of Strepsiptera, and those of parasitic beetles allied to *Melöe* (p. 143), appear to indicate an affinity of the order with heteromerous Coleoptera.

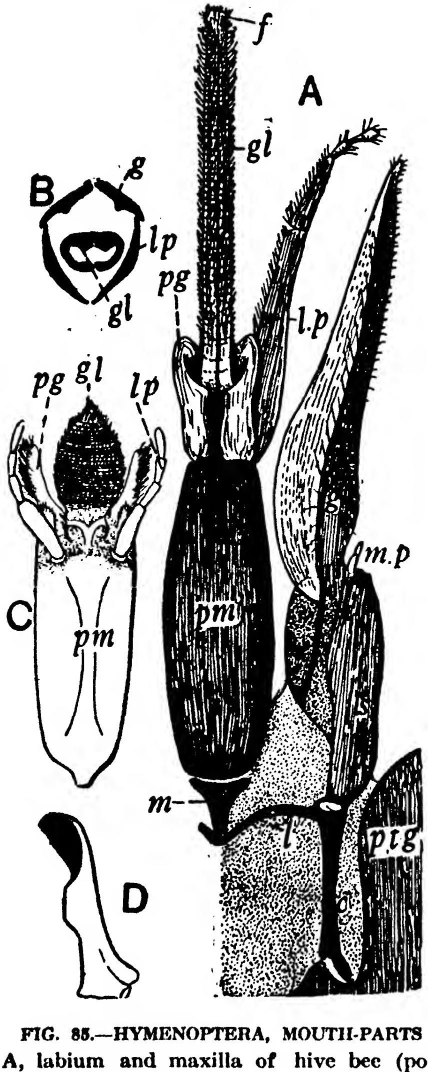

FIG. 85.—HYMENOPTERA, MOUTH-PARTS

A, labium and maxilla of hive bee (posterior or ventral view). B, section across same in feeding position. C, labium of a primitive short-tongued bee (*Sphecodes*). D, hive bee, right mandible. *f*, flabellum; *g*, galea; *gl*, glossa; *l*, lorum; *l.p*, labial palp; *m*, postmentum; *m.p*, maxillary palp; *pg*, paraglossa; *pm*, prementum; *ptg*, postgena; *s*, stipes

ORDER XXII. HYMENOPTERA (*hymen*, a membrane; *pteron*, a wing)

MINUTE TO MODERATE-SIZED INSECTS WITH MEMBRANOUS WINGS: THE HIND PAIR THE SMALLER AND CONNECTED WITH FORE PAIR BY HOOKLETS: VENATION SPECIALIZED BY REDUCTION. MOUTH-PARTS FOR BITING AND LICKING. ABDOMEN WITH 1ST SEGMENT FUSED WITH THORAX: A SAWING OR PIERCING OVIPOSITOR PRESENT. LARVAE USUALLY POLYPOD OR APODOUS: PUPAE GENERALLY IN COCOONS. *Saw-flies*, *Ants*, *Bees*, *Wasps*, *Ichneumon flies* and their allies.

The most constant distinctive feature of Hymenoptera is the fusion of the 1st abdominal segment or *propodeum* (Fig. 9, C) with the metathorax, which occurs in the prepupa. The propodeum, it will be noted, bears the 1st pair of abdominal spiracles. The mouth-parts show the most generalized condition among saw-flies. Mandibles are always present, while the maxillae and labium have all the usual components: the glossae are always fused and form a broad tongue. Only small differences occur in the majority of adult Hymenoptera. In bees (Fig. 85), however, there is a progressive lengthening, in different genera, of the glossa and associated parts to form, in the higher types, a proboscis adapted to extract deeply-seated nectar from flowers. In the hive bee the mandibles are smooth-edged and used for manipulating wax and other purposes (Fig. 85, D). The maxillae are greatly elongated with rod-like cardines and the galeae are large thin blades much longer than the stipites: a pair of small membranous lobes probably represents the laciniae and the palpi are reduced to papillae. In the labium there is a long prementum articulating with a small postmentum whose apex fits into the angle of a V-shaped suspensory sclerite or *lorum* that articulates with the distal ends of the cardines. The glossa is greatly elongated and ends in a spoon-like lobe or *flabellum*: at the base of the glossa there are scale-like paraglossae. The labial palpi have the two basal segments flat and blade-like, leaving the distal segments unmodified. When the

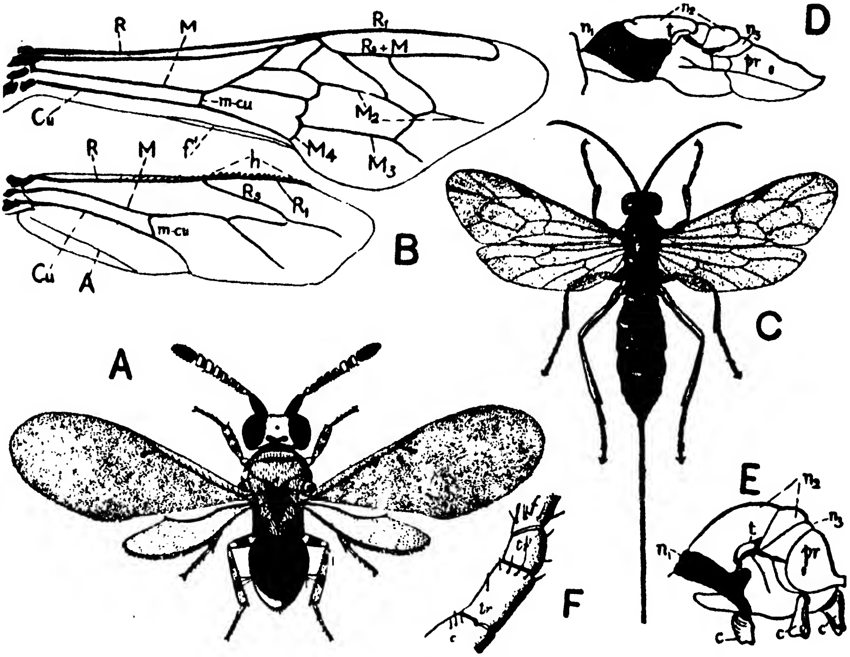

FIG. 86.—HYMENOPTERA

A, a Chalcid (*Aphycus*). B, right wings of worker bee. C, an Ichneumon (*Exeristes*), female (*from Tech. Bull.* 460 *U.S. Dep. Agric.*). D, thorax of an ant, side view. E, do. of a worker bee. F, base of the leg of an Ichneumon. *c*, coxa; *f*, femur; *f'*, flange to hind margin of fore wing; *h*, hooks or hamuli; n_1–n_3, pro-, meso-, and metanota; *pr*, propodeum; *t*, tegula; *tr*, *tr'*, trochanters bee feeds on any easily accessible liquid the maxillary galeae and the labial palpi form an improvised tube along with the glossa (Fig. 85, B). The flabellum is immersed in the food and, by a rapid backward and forward motion of the glossa the liquid is drawn up the tube : it is then sucked up into the digestive canal by the action of the stomodaeal pump. Where the food is more inaccessible the glossa may be projected far beyond the ends of the maxillae. The ventral or posterior surface of the glossa bears a deep channel which reaches to the flabellum : the saliva traverses this channel and becomes mixed with the food during ingestion.

The venation (Fig. 86) deviates widely from the primitive type and during development the veins are demarcated before the tracheae develop. This fact, along with the frequent anastomosis of the veins, forming numerous cells, makes the homologies of the veins hard to ascertain. The most generalized condition occurs in the Symphyta and various stages in reduction prevail in other groups of the order. Bees and wasps show an intermediate condition of reduction while the extreme phases occur in the Parasitica where the veins may be restricted to the costal margin or be totally atrophied. Wing-coupling by means of costal hooklets of the hind-wing engaging the reflected hind margin of the fore-wing prevails throughout the order (Fig. 86, B).

An ovipositor is always present. Its lateral valves are represented by a pair of sensory palpi, the posterior valves are fused to form a sheath and the anterior valves form a pair of stylets which have tongue and groove articulations with the sheath. In the Symphyta the ovipositor functions as a saw, both the stylets and the sheath being prominently toothed. Among the Apocrita, the ovipositor is a piercing organ in many of the Parasitica, while in the Aculeata it is a sting (Fig. 10). In most Hymenoptera the eggs pass down the ovipositor channel and may become greatly compressed and stretched to allow of their free transit : in the stinging forms, on the other hand, the eggs are discharged from the genital pore at the base of the ovipositor and the latter organ acts as a poison-injecting instrument.

A hymenopterous larva has a well-developed head, 3 thoracic and 9 or 10 abdominal segments. In the saw-flies there are three pairs of thoracic legs and abdominal feet are present either on all the segments (*Xyelus*) or, more usually, on segments 2 to 8 and 10. In other Hymenoptera the larvae are apodous (Fig. 54, E) but evanescent appendages may appear in the early instars of some Parasitica. There are usually 9 or 10 pairs of spiracles, except in endoparasitic larvae where the number is variable. A somewhat weak cocoon commonly encloses the pupa, but is wanting in the Chalcidoidea. Hymenoptera rank among the largest and most highly developed orders of insects and are of special interest from the wide range of biological features they display. In the great development of their instincts they stand in the forefront of all invertebrates, and their behaviour has been the subject of studies by some of the most famous naturalists. About 90,000 species are known, and although the vast proportion of these are solitary in habit like other insects, individuals of some groups live together in great societies, as is the case with ants and certain bees and wasps. Hymenoptera are also remarkable for the highly evolved state parasitism has reached in the order: tens of thousands of species betray this habit and their larvae present special respiratory and other adaptions in accord with their modes of life. Associated with parasitism is the phenomenon of polyembryony (p. 77) which attains unique developments. Parthenogenesis is more frequent among Hymenoptera than in any other order of animals: besides being an important factor in social life, it may also be associated with alternations of generations.

From the economic standpoint the Hymenoptera confer many benefits upon man. Bees are important pollinators of fruit trees and other plants, while the hive bee is well known to yield honey and wax. The important part played by the parasitic Hymenoptera in destroying myriads of injurious insects is a recognized feature in the biological control of pests. Among noxious members of the order the majority are defoliating larvae of saw-flies and the boring larvae of wood-wasps or Siricidae. Of lesser importance are the phytophagous larvae of certain Chalcids (p. 151).

Hymenoptera are divided into two suborders, Symphyta and Apocrita. In the **Symphyta** the abdomen is broad with no basal constriction or petiole and the propodeum is only partially amalgamated with the thorax (Fig. 87, B). The larvae are phytophagous and possess thoracic and usually abdominal feet (Fig. 87, C). Most of the species are included in the superfamily Tenthredinoidea, which comprises 6 families.

The Cephidae or Stem Saw-flies are a small group whose larvae tunnel within the stems of graminaceous and other plants, while those of the Siricidae or Wood Wasps bore into the wood of trees. The remaining families comprise the true saw-flies (Fig. 87, A), whose ovipositor acts as a saw in cutting shallow notches or deep incisions in plant tissues for placing their eggs. Their larvae are caterpillars which differ from those of Lepidoptera in the single ocellus on each side of the head; in the segmental positions of the abdominal feet and in the absence of crochets. The only other Symphyta are *Orussus* and its allies which form the small superfamily Orussoidea. Their specialized venation, slender curved ovipositor and the unusual insertion of the antennae—below the clypeus and eyes—separate them from other Hymenoptera. Their larvae are legless ectoparasites of wood-boring beetle larvae. Some writers regard the Orussoidea as a suborder,—the *Idiogastra*, that is intermediate in many features between the Symphyta and Apocrita.

The **Apocrita**, which comprise the majority of Hymenoptera,

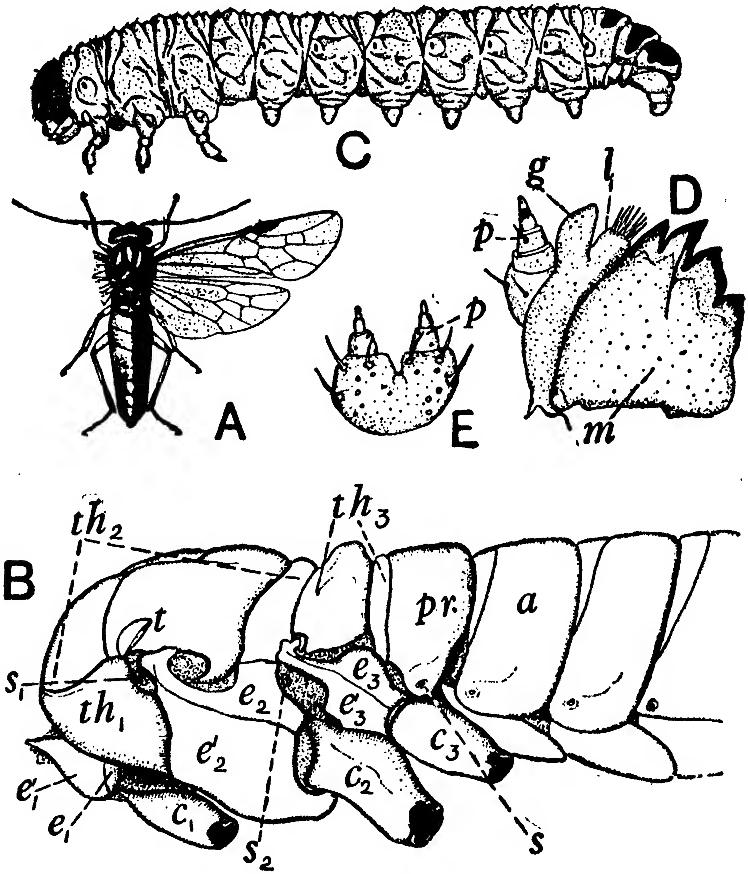

FIG. 87.—HYMENOPTERA SYMPHYTA

A, Larch Sawfly (*Lygaeonematus erichsonii*), female (*after* Washburn). B, side view of thorax and base of abdomen of a Sawfly. C, larva of Plum Sawfly (*Hoplocampa flava*) in 4th instar, × 7. D, left mandible and maxilla of same, × 55. E, labium, × 55. (C, D, and E *adapted from* H. W. Miles.) *a*, basal segment of abdomen; *c*, coxa; *e'*, episternum; *e*, epimeron; *g*, galea; *l*, lacinia; *m*, mandible; *p*, palp; *pr*, propodeum; *s*, spiracle; *t*, tegula; th_1–th_3 thoracic segments. The numerals refer to the respective thoracic segments

have the abdomen stalked or constricted at the base. They are divided into two main groups, the Aculeata and the Parasitica, which, however, intergrade both as regards structure and habit. In the

ORDER XXIII. DIPTERA (*dis*, two; *pteron*, a wing)

MODERATE-SIZED TO VERY SMALL INSECTS WITH A SINGLE PAIR OF MEMBRANOUS WINGS: HIND PAIR MODIFIED INTO HALTERES. MOUTH-PARTS FOR SUCKING OR FOR PIERCING ALSO AND USUALLY FORMING A PROBOSCIS. LARVAE VERMIFORM: TERRESTRIAL, AQUATIC OR PARASITIC: PUPAE EXARATE OR COARCTATE: NO COCOON. *Flies.*

Most flies are diurnal and many visit flowers for nectar, while numerous others feed upon decaying organic matter and diverse fluid substances. There is also a number of flies that are predators on smaller insects or have acquired blood-sucking habits. The single pair of wings is borne on the mesothorax and the metathoracic wings are modified into *halteres*, or balancers (p. 16). The mouth-parts differ greatly in various families but in most cases the elongated labium forms the chief part of the proboscis.

A prevalent type of mouth-parts is seen in the Blow-fly (*Calliphora*). Here the proboscis (Fig. 88) consists of a broad, basal *rostrum*, shaped like an inverted cone, and a distal *haustellum* bearing a pair of oral lobes or *labella*. The *rostrum* is formed by the clypeal region combined with the basal parts of the maxillae and labium. Situated in the rostrum is a cuticular stirrup-shaped framework or *fulcrum*. On the anterior surface of the rostrum the fulcrum presents an inverted V-shaped sclerite (Fig. 88, c), which is probably a derivative of the original *clypeus*. The foot piece of the stirrup strengthens the posterior wall of the pharynx and lateral extensions unite it with the clypeus. The clypeus and adjacent parts give origin to the dilator muscles of the pharynx and to the flexor muscle of the labrum. In front of the fulcrum are the *maxillary palpi*, and on either side is a darkly sclerotized rod-like *apodeme* which articulates with the labrum. The pharynx is closely attached to the posterior wall of the fulcrum and just in front of the latter it becomes enclosed in a small U-shaped *hyoid sclerite* which keeps its cavity distended. The *haustellum* probably represents the prementum and distal parts of the mentum. Its anterior surface is inflexed to form a median *labial groove* or gutter. Posteriorly the haustellum is strengthened by a large concave plate or *theca*. The labial groove is sclerotized and each side is supported by a rod-like *paraphysis* (Fig. 88, A and B). The groove is roofed in anteriorly, to a large extent, by the *labrum*, whose inner lining or *epipharynx* is a channel forming a half tube that is closed by the *hypopharynx*. In front of the labrum the labial groove is closed by folds of the integument and is continued to the *prestomum*.[1] This is an aperture that is bounded and kept open by

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[1] Some authors regard the prestomum as the cleft between the labella and term the opening enclosed by the discal sclerite as the 'oral aperture'. This latter term is confusing since the functional mouth is the opening into the pharynx at the base of the labrum and hypopharynx.

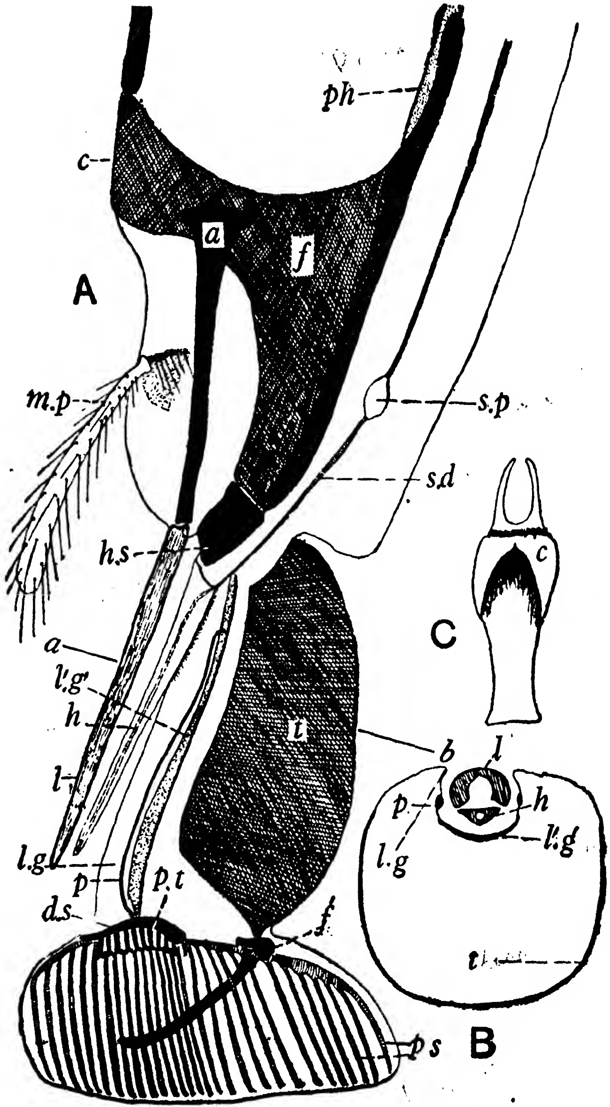

FIG. 88.—*CALLIPHORA* PROBOSCIS

A lateral view, muscles omitted. B, transverse section of haustellum across line *a–b* in A. C, fulcrum, viewed from outer or anterior surface (drawn on smaller scale). *a*, apophysis ; *c*, clypeus ; *d.s*, discal sclerite ; *f*, fulcium ; *f'*, furca ; *h*, hypopharynx ; *h.s*, hyoid sclerite ; *l*, labrum ; *l.g*, side wall of labia groove ; *l'g'*, sclerotized part of labial groove ; *m.p*, maxillary palp ; *p*, paraphysis (left) ; *ps*, pseudo-tracheae ; *p.t*, prestomal teeth ; *s.d*, salivary duct ; *s.p*, salivary pump ; *t*, theca

the arms of the *discal sclerite.* Attached to the latter are the *prestomal teeth.* Proximally the discal sclerite is connected to the paraphyses of the labial groove. The main skeletal support of the labella are the two arms of the *furca,* whose base articulates with paired processes of the theca. The membrane covering the distal surface of the labella contains a series of food-channels or *pseudo-tracheae.* These channels are kept open by a framework of incomplete cuticular rings which give them the appearance of tracheae. Each ring is bifurcated at one end and flattened at the other, the flattened and bifurcated extremities alternating (Fig. 89, D–F). The pseudo tracheae open on the external surface of the labella through the cleft at the forked extremities of the cuticular rings. The pseudotracheae all converge to the prestomum and there are three sets of these channels to each labellum, i.e. those that run into an anterior collecting canal, those that run into a posterior collecting canal and a group between the two whose components open directly between the prestomal teeth which serve as conducting channels. When the proboscis is protruded the rostrum is extended through the expansion of the lateral air-sacs at its base and probably of certain of the cephalic air-sacs also. The haustellum is brought into use by the contraction of its extensor muscles, and finally the labella are extended and rendered turgid by blood-pressure. The retraction of the proboscis is mainly effected by the contraction of its numerous

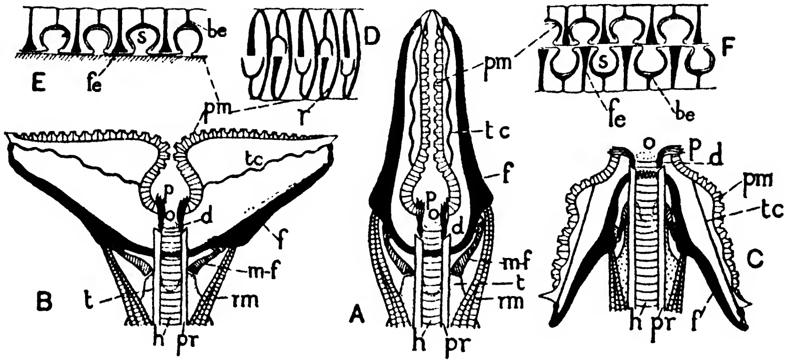

FIG. 89.—DIAGRAMS OF THE POSITIONS ASSUMED BY THE LABELLA OF *CALLIPHORA.* (*Adapted from* Graham-Smith)

A, resting position. B, filtering position. C, direct-feeding position. D, inner or dorsal view of portion of a pseudotrachea showing 5 rings. E, lateral view showing pseudotracheal membrane applied to a feeding surface. F, outer or ventral view of portion of a pseudotrachea. *be*, bifid end of ring ; *d*, discal sclerite ; *f*, arm of furca ; *f.e*, flattened end of ring ; *h*, sclerotised floor of labial groove ; *m.-f*, bar connecting theca *t* with *f* ; *o*, prestomum (' oral aperture ' of authors) ; *p*, prestomal teeth ; *pr*, paraphysis ; *p.m*, pseudotracheal membrane ; *r.m*, retractor muscle of furca ; *s*, interbifid space ; *t*, theca ; *t.c*, tendonous cord muscles. In the *resting position* the labella are flaccid and the two labella are in apposition (Fig. 89, A). When the fly is feeding on fluids the labella assume a phase termed by Graham-Smith the *filtering position* (B) and are pulled apart by the retractor muscles of the furca. The simultaneous injection of blood into the cavity of the labella converts the pseudotracheal surface into a pad which accommodates itself to unevenness of any surface to which it is applied. By means of the pumping action of the pharyngeal muscles suction is set up and liquid food is filtered in through the interbifid spaces of the pseudotracheae to the prestomum. From here it passes along the channel formed by labrum—hypopharynx and so into the alimentary canal. In the *direct feeding position* (C) the lateral arms of the furca and the labella are pulled upward against the sides of the haustellum, thus completely exposing the prestomum. In a slightly less reflected condition the prestomal teeth project vertically downward, but the prestomum is not exposed. This phase is the *scraping position* of Graham-Smith, which enables the insect to rasp particles of sugar and other substances. Whereas in position B only fluids, and particles of a diameter not exceeding 0·006 mm., can enter the pseudotracheae, in position C particles of much larger size can be taken in directly along with fluids.

The mouth-parts of *Calliphora* are highly specialized, and to determine the homologies of their components it is necessary to examine those of the lower Diptera. Mandibles are only present in blood-sucking Nematocera and Brachycera and are usually confined to the female. The maxillae in these suborders exhibit almost all the usual parts and comparisons indicate that the apodemes of *Calliphora* are probably derivatives of the stipes. The labella are regarded as modified labial palpi and, in this connection, it may be noted that in some forms they are 2-segmented. In mosquitoes (*Anopheles*, *Culex*, &c.) the mouth-parts in the female are very slender organs lodged in the labial groove (Fig. 90). The mandibles and the galeae of the maxillae are modified into piercing stylets ; the maxillae, being the stronger organs, are used for piercing. During feeding the labium becomes looped backward to allow of the maxillae perforating the skin of the host. The labrum is then inserted into the puncture and its tubular epipharynx forms the food canal. The hypopharynx is concerned with the ejection of saliva which apparently acts as an anticoagulin on the blood. The part played by the mandibles seems to be of secondary importance. In the males both mandibles and maxillae are much reduced in *Anopheles* and are even more so in *Culex* : in feeding habits they are non-piercing, the apex of the labrum being merely dipped below the surface of liquid food so that the nutriment can be imbibed through the tubular epipharynx. Some of the Cyclorrhapha have also acquired blood-sucking habits which prevails in individuals of both sexes, notably in the Biting House-fly (*Stomoxys*), the Tsetse-flies (*Glossina*), the Forest-fly (*Hippobosca*), &c. The haustellum (Fig. 90) in such cases is a rigid, horny, piercing organ devoid of pseudotracheae and there

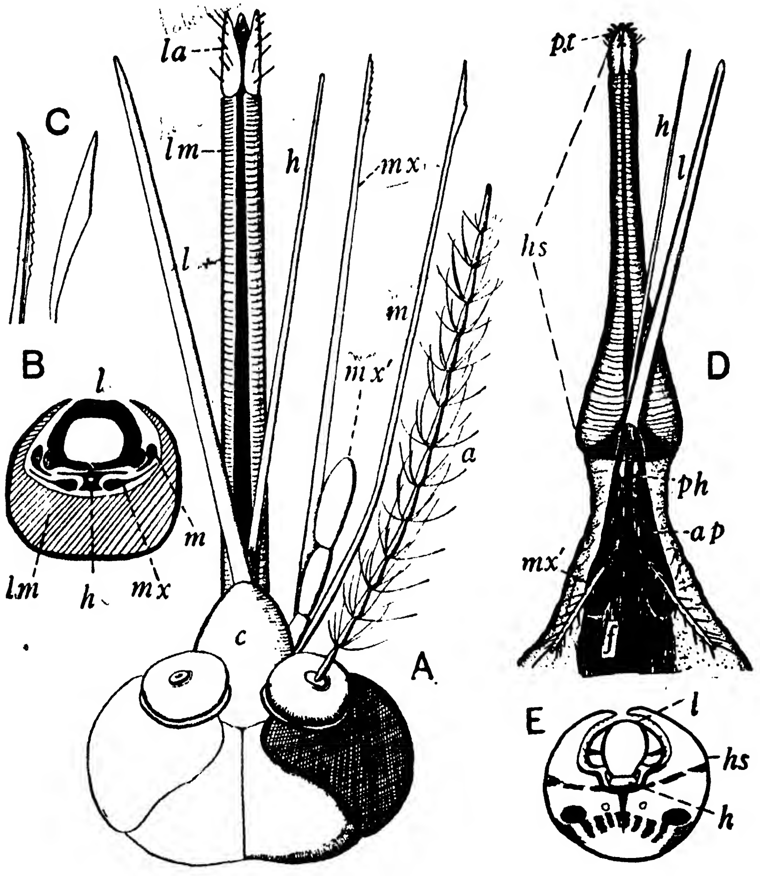

FIG. 90.—MOUTH-PARTS OF DIPTERA

A, mouth-parts of *Culex* (female). B, transverse section of same. C, apices of maxilla and mandible respectively. D, *Stomoxys* mouth-parts. E, transverse section of same. *a*, antenna ; *ap*, apophysis ; *c*, clypeus ; *f*, fulcrum ; *h*, hypopharynx ; *hs*, haustellum ; *l*, labrum ; *la*, labellum ; *lm*, labium ; *m*, mandible ; *mx*, maxilla ; *mx′*, maxillary palp ; *ph*, pharynx ; *p.t*, prestomal teeth

are no mandibular or maxillary stylets. The puncture is made by the strong prestomal teeth and the blood-meal is drawn in through the prestomum into the food canal formed by the combined labrum and hypopharynx.

The Horse-flies (*Tabanidae*) combine the filter feeding method of the blow-fly with the piercing method of mosquitoes. Pseudotracheae are present on the labella and, in the females, the mandibles and maxillae are broad stylets used for piercing in order to obtain blood.

The *ptilinum* or frontal sac is a cephalic organ found in the most highly specialized flies. Its presence is shown externally by the U-shaped *ptilinal suture* embracing the insertions of the antennae (Fig. 91, I). The suture is an extremely narrow slit along the

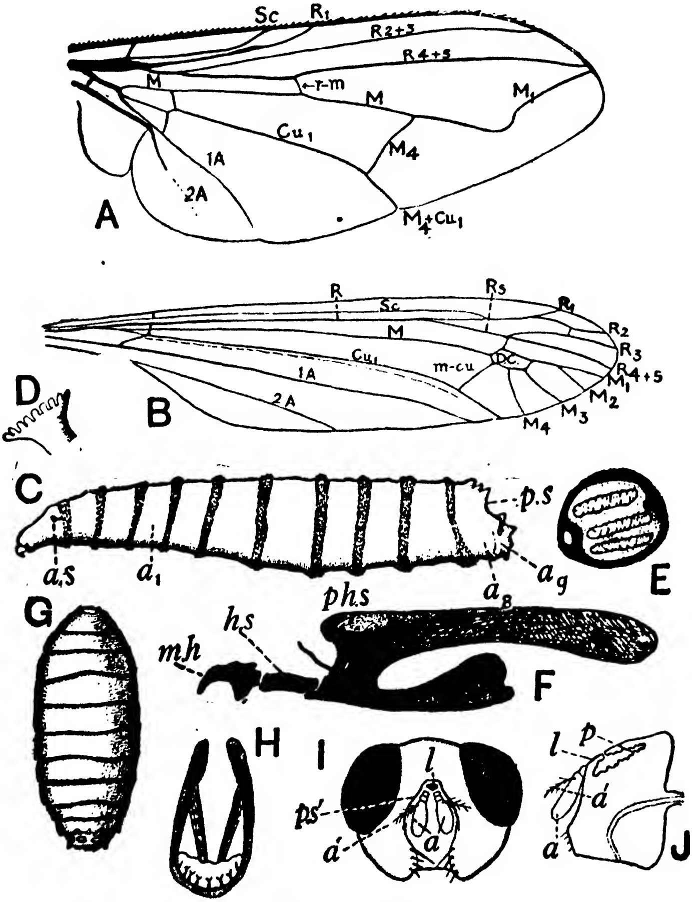

FIG. 91.—DIPTERA

A, *Musca domestica*, right wing. B, *Tipula*, right wing. C-G, *Calliphora*. C, larva. D, anterior spiracle and, E, posterior spiracle of same. F, cephalopharyngeal skeleton. G, puparium. H, transverse section of pharynx of larva of *Sarcophaga*. I, frontal view of head of fly of suborder Cyclorrhapha. J, lateral and sectional view of the same. *a_1*, *a_8*, *a_9*, abdominal segments; *a*, antenna; *a′*, arista; *a.s*, anterior spiracle; *d.c*, discal-cell; *h.s*, hypostomal sclerite; *l*, lunule; *m.h*, mouth-hook; *p*, ptilinum (retracted); *p.s*, posterior spiracle; *p.s′*, ptilinal suture; *ph.s*, pharyngeal sclerite margins of which the integument is invaginated as a sac or ptilinum. The latter is everted through the suture prior to the eclosion of the fly. With the aid of the ptilinum the insect ruptures the puparium. The ptilinum is everted by blood pressure and muscular action and, having served its purpose, it becomes withdrawn into the head cavity, where it remains (Fig. 91, J). It can, however, be everted again by squeezing the thorax of a newly-killed fly with forceps so as to force the blood forward.

The thorax of Diptera is characterized by the great size of the middle segment bearing the wings and the correlated reduction of the segments in front and behind. The most primitive venation occurs in Crane-flies and some other Nematocera, the veins being predominantly longitudinal with but few cross-veins (Fig. 91, B). The narrow wing-bases have led to a great reduction of the anal veins and Cu_2 is absent or vestigial. Specialization is by reduction and is most pronounced in Cyclorrhapha (Fig. 91, A). An ovipositor is never developed, but in *Musca*, and many other flies, the end-segments of the abdomen form a telescopic tube serving the same purpose.

Dipterous larvae are always apodous and are typically amphipneustic or often metapneustic: propneustic or apneustic forms occur more rarely. Three thoracic and nine abdominal segments are present, and in Nematocera the head is fully developed (*holocephalous*). The mouth-parts are less modified than in other groups and the paired components work horizontally. In the Brachycera the head is incomplete posteriorly and partly embedded in the prothorax (*hemicephalous*): the mouth-parts are highly modified and work in the vertical plane. Among Cyclorrhapha (Fig. 91) the larvae are *acephalous* and this condition results from the whole head being invaginated into the thorax. During this process the mouth becomes carried far inward and communication with the exterior is by means of a secondary passage or *atrium*. The apparent head-rudiment is in reality a circular papilla-like fold of the neck. True mouth-parts are atrophied and their place is taken by adaptive structures that form the *cephalo-pharyngeal skeleton* (Fig. 91, F). Of these the paired *mouth-hooks* are alone freely movable and work in the vertical plane: they articulate with a *hypostomal sclerite* whose two components are joined by a crossbar. This sclerite articulates in turn with the *pharyngeal sclerite* that is composed of two vertical lamellae united below to form a trough for the support of the pharynx (Fig. 91, H). The pharyngeal sclerite is the homologue of the fulcrum of the imago. The mode of life of cyclorrhaphous larvae can be ascertained from the mouth-parts. In carnivorous forms the mouth-parts are sharply hooked, whereas in phytophagous forms they are toothed. Also, the pharyngeal floor is ridged in saprophagous forms, less so or smooth in phytophagous forms and wholly without ridges in carnivores.

Dipterous larvae commonly pass through three instars and the pupae are either free, or *coarctate* as in all Cyclorrhapha. In the latter case the larval skin, instead of being moulted, hardens and forms a shell or *puparium* (Fig. 91, G), enclosing the pupa. The puparium ruptures along special lines of fracture owing to pressure exerted from within. In the higher Cyclorrhapha the inflated ptilinum forces open the puparium and so liberates the imago.

About 85,000 species of flies are known, and of these more than 5,200 kinds inhabit the British Isles. The order is one of very great economic importance either as larvae or as adults. The pathogenic organisms of some of the most virulent diseases such as malaria, sleeping sickness, elephantiasis and yellow fever are transmitted to man through the agency of blood-sucking flies. The house-fly and its allies act as mechanical carriers of disease germs, and in this way contaminate human foods. Various dipterous larvae induce diseased conditions in the bodies of man and domestic animals, and such infections are included under the term *myiasis*. Larvae of other species are injurious to the agriculturist and their activities result in great financial losses. The depredations of members of this order are offset, to a considerable degree, by those species of carnivorous habit that destroy large numbers of noxious insects. Some of these are predators, either as larvae or adults, while many others are endoparasites in their larval stages.

Diptera are classified into three suborders viz.: **Nematocera, Brachycera** and **Cyclorrhapha.** The **Nematocera** have many-jointed antennae, usually longer than the head and thorax, and the maxillary palpi are 4- or 5-jointed. The larvae are usually holocephalous, with horizontally biting mandibles. The slender, long-legged Crane-flies or *Tipulidae* are familiar creatures. The larvae are metapneustic and those of some species of *Tipula*, known as 'leather jackets', are injurious to the roots of pasture grasses and crops. The *Chironomidae* or midges have mostly aquatic larvae that are apneustic. In some species the larvae are known as blood worms owing to the presence of haemoglobin in the blood plasma. The *Culicidae* or mosquitoes are very slender insects with long piercing mouth-parts and the wing margins, together with the veins, are clothed with scales. All the immature stages are aquatic (p. 54), the larvae being metapneustic. With few exceptions, female mosquitoes are able to pierce the skin of vertebrates and feed upon the blood: they also feed upon various plant-juices and some kinds may never taste blood at all. The larval habits are varied: some inhabit shady pools, others are found in streams, dykes, tree holes, salt marshes, &c. Some 29 species of mosquitoes occur in Britain, and of these the commonest is *Culex pipiens*. Among other families of Nematocera are the *Simuliidae* or Buffalo Gnats, the *Mycetophilidae* or Fungus Gnats and the *Cecidomyidae* (*Itonididae*) or Gall Midges. Included in **Brachycera** are 14 families of stout-bodied flies with short antennae, generally 3-jointed and often with the last joint prolonged into a style. The maxillary palpi are 1- or 2-segmented and the larvae are hemicephalous with vertically biting mandibles. Mention may be made of the *Tabanidae* or Horse-flies, the females of which are blood-sucking in habit, and the *Asilidae* or Robber-flies, which are predators on other insects.

The **Cyclorrhapha** comprise all the higher Diptera. Their antennae are 3-jointed with a dorsal bristle-like *arista* (Fig. 91, I) and the maxillary palpi are 1-segmented. The larvae are acephalous and commonly amphipneustic: their mandibles are replaced by mouth-hooks movable only in the vertical plane and the pupae are coarctate. Among this great assemblage of forms the *Syrphidae* or Hover-flies are without a ptilinum and their larvae include many predators of aphides. Most families possess a ptilinum, but only a few can receive separate mention. The *Trypaneidae* or Fruit-flies include destructive larvae that mine the pulp of economic and other fruits. The *Drosophilidae* or Pomace-flies have saprophagous larvae and the *Oestridae*, which include the Warble-flies and Bot-flies, have larvae that are endoparasites of mammals. The *Muscidae* include the House-fly (*Musca domestica*) and its allies, together with blood-sucking forms such as the Stable-flies (*Stomoxys*) and the Tsetse-flies (*Glossina*). The *Tachinidae* are very bristly flies whose larvae are either saprophagous like those of the Blow-flies (*Calliphora*, *Lucilia*), &c., or are endoparasites of other insects. The *Hippoboscidae* are viviparous and live, as adults, as blood-sucking ectoparasites on birds and mammals: the wingless Sheep Ked (*Melophagus*) and the Forest-fly (*Hippobosca*) are well-known examples.

APPENDIX

Parasitism. A parasite is an organism that lives temporarily or permanently in intimate relationship with some other organism (its host) and at whose expense it obtains its nourishment. Among insects parasites fall into two very different categories, viz. true, or 'non-fatal', parasites, and 'fatal' parasites or 'parasitoids'.

Anoplura are excellent examples of the first kind and included in this same category are the Aphaniptera or fleas, the bed-bugs or Cimicidae, the Hippoboscidae and certain others. Such parasites are insignificant in size compared with their hosts, which are nearly always vertebrates. The hosts have developed a tolerance to their presence and consequently do not suffer fatal effects from their activities. The majority of these parasites are ectoparasites that live on the bodies of their hosts and, since they breathe ordinary atmospheric air, special respiratory adaptations are not required. While the Anoplura spend their whole existence on their hosts, in the other groups metamorphosis takes place elsewhere. Excepting the Mallophaga, these parasites are pre-eminently blood-sucking in habit. In adaptation to their special mode of life the skin of such parasites is tough and leathery. In form they are dorso-ventrally flattened and are thus enabled to lie close to the host's body ; the fleas are exceptional in being laterally compressed. The legs are stout with prominent and often toothed claws which enable them to maintain a firm hold on to their hosts. Eyes are greatly reduced or absent and wings are absent or only rarely present in other than a vestigial condition.

By far the larger number of parasites belong to the category of 'parasitoids', which include the dipterous family Tachinidae, the Hymenoptera Parasitica and several minor groups. They are parasites in the larval condition only and, unlike parasites belonging to the preceding category, the adults into which they transform are active and non parasitic creatures. They are relatively large in comparison with the size of their hosts, which are almost always destroyed as the result of their activities. The vast majority of hosts are other insects, and these may be parasitized while in the egg or later stages, the imagines, however, being seldom attacked. Among the Tachinidae the parasitism is internal but their eggs may be laid on or away from the hosts. In either event the resultant larvae have to bore their way beneath the skin of their victims : or, they may develop from minute eggs that are adapted to be swallowed by the hosts along with their food. Since no ovipositor is present in the Tachinidae, only a small proportion of the species are specially adapted for inserting their eggs internally to their hosts. In the parasitic Hymenoptera an ovipositor is universally present ; it varies greatly in length and is longest in those species that have to penetrate the wood of trees in order to reach their victims. While many of the parasitic Hymenoptera live as ectoparasites, the greater proportion are endoparasites and result from eggs inserted directly beneath the integument of their hosts. In their earlier instars, at least, 'parasitoids' feed upon the blood and fat-body of their victims, thus avoiding injury to the more vital organs. Death of the hosts may result from the nutritive drain thus entailed, or the demands of growth may cause the parasites later to turn to other tissues and so to become, virtually, 'internal predators'. The most important adaptations of 'parasitoids' concern respiration. Whereas ectoparasites breathe the free atmospheric air and retain in consequence an unmodified peripneustic tracheal system, the endoparasitic forms display very evident adaptations. Whereas many forms breathe cutaneously the oxygen held in physical solution in the blood of their hosts, others maintain a more or less direct connection with the atmosphere (see p. 55):

ORDER XXIV. APHANIPTERA (*aphanes*, not apparent ; *pteron*, a wing)

VERY SMALL, APTEROUS, LATERALLY COMPRESSED INSECTS WHOSE ADULTS ARE ECTOPARASITES OF WARM-BLOODED ANIMALS. MOUTH-PARTS FOR PIERCING AND SUCKING. LARVAE VERMIFORM : PUPAE EXARATE IN SILKEN COCOONS. *Fleas.*

The Aphaniptera (or Siphonaptera) are readily separated from other apterous parasitic insects owing to their being laterally, and not dorso-ventrally, flattened. Eyes are present or absent and the antennae are short, 3-jointed organs reposing in grooves. The mouth-parts (Fig. 92) are for piercing and have features in common with those of the lower blood-sucking Diptera. The stylet-like mandibles are finely denticulate and are the actual piercing organs. They are closely apposed to the slender labrum to form the food channel. Ventrally the edge of each mandible is grooved and the apposition of the two grooves forms a salivary canal which receives a small process of the hypopharynx bearing the end of the salivary duct. The maxillae are short triangular blades that play no part in piercing and the palpi are 4-segmented. The labium is a small basal plate bearing elongated palpi composed of a variable number of segments: their concave inner surfaces enable them to ensheath the mandibles. Fleas are covered with a tough cuticle and the legs are adapted for clinging and leaping. The maximum vertical leap of the human flea (*Pulex irritans*) is stated to be 7¾ inches. All fleas are blood-sucking ectoparasites of birds and mammals and rarely exceed 4 mm. in length. Usually each species has its particular host, but many can live, at least temporarily on some other host. Thus the rat-flea, *Xenopsylla cheopis*, (Fig. 93), frequently migrates to man and is the most potent vector in the transmission of the

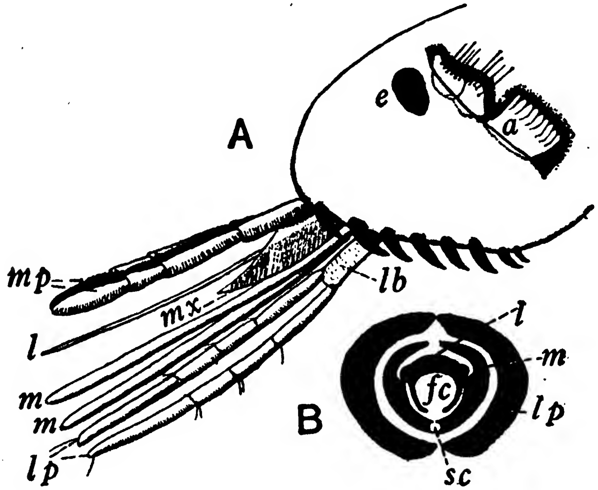

FIG. 92.—APHANIPTERA

A head of flea showing mouth-parts. B, transverse section of mouth-parts. *a*, antenna; *f.c*, food canal; *l*, labrum; *lb*, labium; *l.p*, labial palp; *m*, mandible; *mx*, maxilla; *m.p*, maxillary palp; *s.c*, salivary canal; *e*, eye bacillus of bubonic plague which affects both rodents and man. The eggs of fleas are normally found in the haunts or sleeping-places of the hosts. The larvae are whitish and vermiform, with a well-developed head bearing biting mouth-parts and 13 trunk segments: they feed on particles of organic matter found in the hosts' layer or, in the case of the human flea, upon such matter among the dust and dirt of floors. The pupae are exarate and are enclosed in silken cocoons. Nearly 1,000 species of fleas are known.

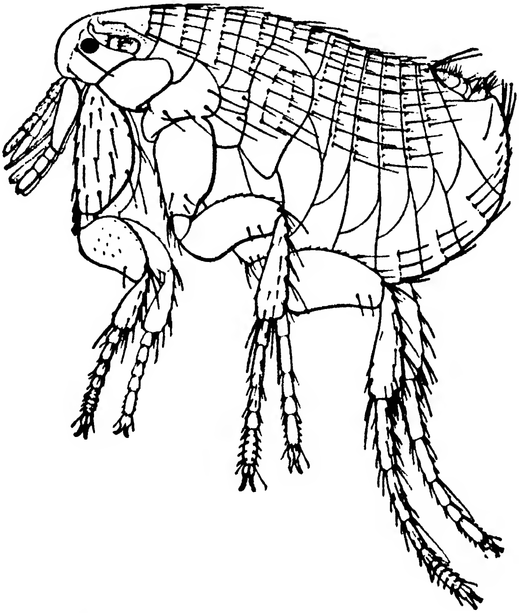

FIG. 93.—*XENOPSYLLA CHEOPIS*, MALE, × 20
(*After* Waterson. Reproduced by permission of the Trustees of the British Museum)

The order is an isolated one, but it shows some affinity with Diptera. This is borne out in (1) the nature of the mouth-parts: (2) the presence of mesothoracic wing-buds in the pupae of certain species: (3) the number of Malpighian tubes being four, as in most Diptera: and (4) the larvae resembling those of Nematocera.

V. RELATIONSHIPS OF INSECTS

INSECTS AND OTHER ARTHROPODS

THE Arthropoda form the largest phylum in the animal kingdom and can be recognized by the following characters. The body is segmented and covered by a chitinous exoskeleton. A variable number of the segments carry paired, jointed appendages that exhibit functional modifications in different regions of the body. The heart is dorsal and is provided with paired ostia, a pericardium is present and the body-cavity is a haemocoele. The central nervous system consists of a supra-oesophageal centre or brain connected with a ganglionated ventral nerve-cord. The muscles are composed almost entirely of striated fibres and there is a general absence of ciliated epithelium. The earliest known arthropods, i.e. the fossil group of the Trilobita, were aquatic, but among living forms it is only the Crustacea that have retained this mode of life to a predominant extent. No other phylum of invertebrate animals has so large a proportion of its members terrestrial in habit.

Arthropoda are divisible into six main classes as follows:

(*a*) Worm-like terrestrial forms bearing a pair of pre-antennae: the body unsegmented externally and with numerous pairs of unjointed legs. Onychophora.

(*b*) Bearing antennae: aquatic in habit and breathing either cutaneously or by means of branchiae. Trilobita, Crustacea.

(*c*) Bearing antennae, primarily terrestrial in habit and breathing by means of tracheae. Myriapoda, Insecta.

(*d*) Without antennae, usually terrestrial in habit and breathing by means of lung-books and tracheae. Arachnida.

The Onychophora are in many ways intermediate between the Annelida or worms and the Arthropoda. They are represented by rather more than 50 species included in the genus *Peripatus* and its allies. Like many declining groups, they have a discontinuous geographical distribution and are found in warm countries in many parts of the world. Their relationships with arthropods is very evident on account of the presence of (1) paired limbs ending in claws: (2) respiration taking place by means of tracheae: (3) the haemocoelic body-cavity: (4) a heart with paired ostia, and (5) the general character of the reproductive system. Annelidan characters include (1) segmentally repeated nephridia; (2) the structure of the eyes; (3) the rudimentary cephalisation, only three head-segments being present, and (4) the muscular body-wall. Onychophora inhabit permanently damp localities and occur more especially beneath the bark of trees and underneath stones. They form a class very remote from all other Arthropoda and appear to have developed as an offshoot from the main line of evolution in that phylum. The antennae, unlike those of other arthropods, are pre-antennae which arise from the first head segment and the second segment bears the jaws. The tracheal system has a non-segmental arrangement since the absence of hard sclerites has allowed of an irregular distribution. The tracheae are very fine tubes, 2–3μ in diameter, which arises in dense bundles from flask-like pits in the integument.

The true arthropods have a thicker and more rigid cuticle and consequently individual sclerites became developed so as to allow of the necessary flexibility. The appendages for the same reason have acquired a jointed structure. The development of this exoskeleton has also resulted in the tracheae becoming segmentally arranged owing to the initial invaginations being mainly confined to the membranes between individual somites.

The Trilobita were marine animals and their remains are numerous in palaeozoic rocks of Cambrian to Silurian date. The body is highly specialized and divided longitudinally into median and lateral or pleural regions. The appendages, on the other hand, are of a very primitive character and consist of a single pair of antennae almost certainly homologous with the crustacean 1st antennae. The remaining appendages are biramous and only slightly differentiated among themselves. The first four pairs belong to the head and are forwardly directed. They have large gnathobases that evidently crushed the food since no jaws are developed.

The Crustacea include lobsters, shrimps, crabs, barnacles, &c., and are predominantly marine animals: a smaller number inhabit fresh water, while a few kinds of crabs and the woodlice have invaded the land. They are characterized by the possession of two pairs of antennae followed by a pair of mandibles and at least five pairs of legs. In the higher forms the body segments are fixed in number and are grouped into two regions—the cephalothorax and abdomen. The appendages are for the most part specialized to perform a number of functions and, like those of the Trilobita, are often of the biramous type. The excretory organs are modified nephridia and are usually represented by green glands or shell glands. The genital apertures are located anteriorly, i.e. on the 9th post-oral segment in some cases, up to the 14th in others.

The Myriapoda have a 6-segmented head bearing a single pair of antennae. The trunk is composed of numerous leg-bearing segments and is without differentiation into thorax and abdomen. The tracheal system is provided with segmentally repeated spiracles and the excretory organs are Malpighian tubes. These animals almost always hatch from the egg with a smaller number of trunk segments and limbs than are present when they are sexually mature. The addition of new segments takes place by subdivision of the penultimate segment. Myriapoda are divided into two chief subclasses—the Chilopoda, or centipedes, and the Diplopoda, or millipedes. The Symphyla constitute a third and much smaller group of very definite phylogenetic importance.

The Chilopoda have long, many-segmented antennae and the mouth-parts comprise three pairs of appendages similar to those found in insects. The first pair of legs is modified into jaw-like poison-claws and the gonopore is on the penultimate segment of the body.

The Diplopoda have short 7-segmented antennae and their mouth-parts are more specialized than those of Chilopoda. The body-segments are mostly grouped in pairs under each apparent tergum and the gonopore is on the 3rd segment.

The Symphyla are small colourless Myriapoda with long, many-segmented antennae and mouth-parts resembling those of Insecta. The trunk consists of 14 segments, each bearing a pair of appendages and usually a pair of styli and protrusible vesicles. The gonopore is on the 4th trunk segment.

The Insecta show characters that ally them more closely with the Myriapoda than with any other arthropods. The division of the body into head, thorax and abdomen, the presence of three pairs of legs and usually two pairs of wings readily differentiate adult insects from other arthropods.

The Arachnida include scorpions, king crabs, spiders, mites, ticks, &c., and have the body divided into cephalothorax and abdomen. There are no antennae, these organs being replaced by prehensile chelicerae. True jaws are wanting and a varying number of the anterior limbs have developed gnathobases for breaking up the food. Four pairs of legs are present.

Reviewing the Arthropoda as a whole, it will be noted that they may be grouped into three series, which probably represent as many evolutionary lines (Fig. 94).

1. The Onychophora are far removed from other Arthropoda since they show a lower degree of development of those special features that characterize the phylum as a whole. They rank more or less as a half-way class between the Arthropoda and their annelidan ancestors.

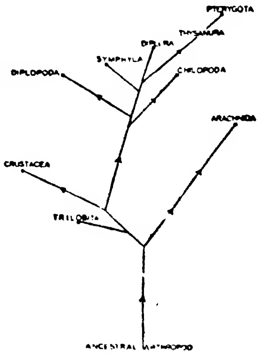

FIG. 94.—RELATIONSHIP OF INSECTS

2. The main evolutionary stem of the arthropods is represented

by the Crustacea-Insecta-Myriapoda series, which is characterized by a 6-segmented head bearing antennae, mandibles, and maxillae. The Trilobita also belong here and they are possibly an offshoot from the original stock that gave rise to the three classes named above.

8. The Arachnida have no differentiated head, the antennae are replaced by chelicerae and neither mandibles nor maxillae are present. It will be evident, therefore, that they represent a separate line of arthropod evolution and are not closely related to any of the other classes named.

THE ANCESTRY OF INSECTS

In attempting to trace the ancestry of insects, three sources of evidence are available, viz. embryology, comparative morphology, and palaeontology. It will consequently be necessary to consider whatever data on the subject that those sources may yield.

Embryology. Examination of embryonic development in the lower insects clearly reveals that they all pass through an evanescent stage with a 6-segmented head bearing 5 pairs of appendages followed by 14 trunk segments each with a pair of rudimentary limbs. The general prevalence of this polypod condition with a fixed number of segments is highly suggestive of an ancestral or recapitulatory phase. The adults of two other groups of arthropods display this general type of organization, viz. the higher Crustacea or Malacostraca and the Symphyla. It will be necessary, therefore, to consider these two groups in order to ascertain whether either provides morphological evidence bearing upon insect descent.

Comparative Morphology. The study of comparative morphology and postembryonic development indicates that the most primitive insects are wingless and that the possession of wings is a subsequent acquisition. The largest proportion of archaic characters are to be found in the Diplura. This order includes among its members the familiar genus *Campodea*. The most generalized members, however, are represented by *Anajapyx* and its allies, which display the following significant morphological features:

(*a*) Multisegmented antennae, each segment with intrinsic muscles—a character not present in any other insects.

(*b*) Absence of eyes and ocelli.

(*c*) Legs with 5 segments, the tarsi undivided and bearing paired claws.

(*d*) An abdomen with most of its segments bearing movable styles and protrusible vesicles.

(*e*) A pair of short cerci receiving the openings of posterior glands at their apices.

(*f*) The absence of an amnion and serosa in the developing egg.

The Symphyla inhabit the soil, often in company with Diplura. An examination of their structure shows that all the foregoing characters (*a*) to (*f*) are also present in these creatures. Furthermore, the mouth-parts of the Symphyla have developed along insectan lines with mandibles, superlinguae, maxillae and labium. Additional features, that also prevail among insects, are the labial salivary glands and Malpighian tubes. It will be evident, therefore, that the possession of so many common morphological features by the Diplura and Symphyla is indicative of their close mutual relationship. Furthermore, if it be assumed that the abdominal legs underwent atrophy in the Symphyla, with only the three anterior or thoracic pairs remaining, a typical Dipluran would result as regards most features of its organization.

The position of the gonopore in the Symphyla on the 4th trunk segment, however, precludes this group being the direct ancestors of the Insecta. Considering the immense antiquity of the last-named class it would indeed be remarkable should its actual forerunners be alive to this day.

Any theory that upholds the derivation of insects from Malacostraca regards the Thysanura as being the key order in such a comparison. The identity in number of the head and trunk segments in the two cases is impressive but, as already mentioned, it obtains also in the Symphyla. This feature, together with structural similarities in certain of the appendages and other parts in *Machilis*, on the one hand, and in the Syncarida, on the other, form the basis of the contention. In view of important differences displayed by the internal organs in the two cases, the external similarities referred to are more likely due to convergence rather than to affinity. Furthermore, there is no evidence that any insect appendage reveals a biramous composition that is so prevalent among Malacostracan limbs.

Palaeontology. The oldest known fossil insects are fragmentary remains of Collembola from the Middle Devonian rocks of Scotland. These relics, however, yield no direct evidence bearing upon the ancestry of insects—a conclusion that is by no means unexpected since the Collembola are to be regarded as a side development off the main line of insect evolution. Fossil remains of Diplura and Thysanura are likewise of little significance, since they do not occur before the Tertiary period and are not very different from their living representatives. The oldest Pterygota are found in rocks of Upper Carboniferous date, but, interesting as these remains are, they shed no direct light on the ancestors from which the Insecta were presumably derived.

Conclusions. In the absence of any direct evidence from palaeontology, our conception of the ancestry of insects has to be based upon whatever data can be gleaned from embryology and comparative morphology.

The findings from these sources lead to the conclusion that the Symphyla are nearest related to the primitive insectan stock. The many structural features common to this small class of Myriapoda and to the Diplura can only be interpreted as evidence of close relationship (Fig. 95).

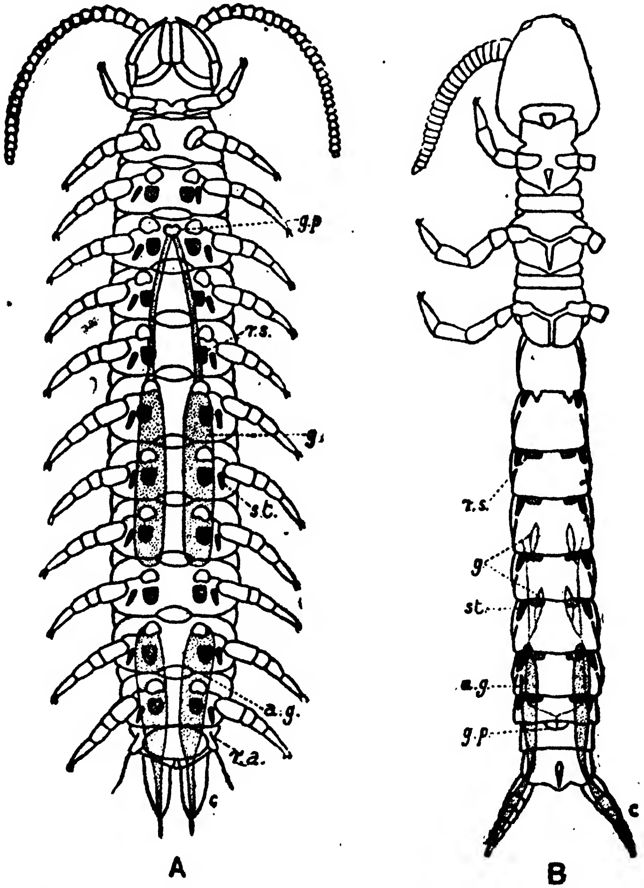

FIG. 95.—STRUCTURAL FEATURES OF, A, SYMPHYLA, AND B, DIPLURA
a.g, posterior gland; *c*, cercus; *g*, gonad; *g.p*, gonopore; *r.a*, rudimentary appendage; *r.s*, protrusible vesicle or sac; *st*, stylus. (B *from* Silvestri)

It is probable that the two groups were evolved from ancestral ‘Protosymphyla’, characterized more especially by their posterior gonopore. Living Symphyla were most likely derived from such ancestors and acquired an anterior gonopore as a secondary development. It is noteworthy that evidence of such a change having taken place has recently been discovered by the Australian embryologist, O. W. Tiegs. The Insecta in their turn were evolved as the result of the atrophy of all except the first three pairs of legs and the last that persist as cerci. The absence of amnion and serosa from both the Diplura and Symphyla is a further important indication of affinity.

MUTUAL RELATIONSHIPS

It is generally conceded that the Diplura and Thysanura are the most primitive insects we know. The Diplura, as already stated, are nearest related, through the Symphyla, with the ancestral stock from which the Insecta were presumably derived. The Thysanura, on the other hand, combine Dipluran features with those of the lower Pterygota. Their ectognathous mouth-parts, annulated antennae, segmented tarsi, together with the possession of compound eyes and ocelli, are characters which are shared with all of the more generalized winged orders. Furthermore, their general body-form prefigures that of the nymphs of those same orders.

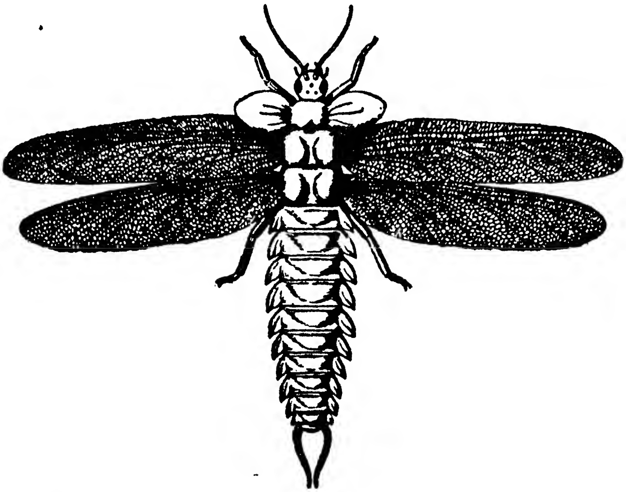

FIG. 96.—*STENODICTYA LOBATA* (*PALAEODICTYOPTERA*). (*After* Handlirsch)

The most primitive winged insects are comprised in the fossil order Palaeodictyoptera (Fig. 96) whose remains are mostly found in rocks of Carboniferous Age. The occurrence of nymphs with prominent wing-buds contemporaneously with the adults in the same strata indicate that the members of this order were Exopterygota. The Palaeodictyoptera were characterized by—

(1) A rounded head bearing annulated antennae, masticatory mouth-parts together with compound eyes and ocelli.

(2) The prothorax bearing lateral expansions resembling wing-buds and by the presence of similar outgrowths at the sides of the abdominal segments. It has been suggested that the ancestral insects had a series of such expansions all along the body that may have functioned as parachutes. Of these, the meso- and metathoracic pairs became greatly enlarged, acquired articulations with the thorax and ultimately developed into wings.

(3) The meso- and metathorax being subequal and bearing wings almost alike in form, size and venation and with broad basal attachments to the thorax. The venation more complete than in any other order and displaying an alternating sequence of convex and concave veins. The wing-membrane strengthened by an irregular meshwork of veinlets or *archidictyon.*

(4) An elongated, 11-segmented abdomen bearing well-developed jointed cerci.

The Palaeodictyoptera represent the nearest approach to a supposed ancestral stock of winged insects that palaeontology has so far disclosed. It is indeed clear that some of the more primitive living orders of insects bear evident indications of palaeodictyopterous descent. The Ephemeroptera, for example, retain the venation of this ancient order, together with the archidictyon, in a less modified condition than is to be found in any other living insects. These features coupled with their primitive body-structure emphasize the great antiquity of may-flies. Certain fossil Ephemeroptera, notably *Proterisma* of the Lower Permian rocks, had fore and hind wings alike in size and venation and, in this way, connect the most primitive living forms with the Upper Carboniferous *Triphlosoba,* which appears to have been a close relative of the Palaeodictyoptera.

The Orthoptera and Plecoptera have diverged widely from the Palaeodictyoptera but, on the other hand, their extinct forerunners, viz. the Protorthoptera and Protoperlaria, show various generalized features that are consistent with derivation from this ancient order.

The Odonata are closely related to the Protodonata that are only known as Palaeozoic fossils. Among the members of this extinct order some attained great size with a wing-expanse exceeding two feet. For the most part the Protodonata show more simplified wing characters than are displayed by the true Odonata and the balance of evidence indicates that the two orders were derivatives of a common ancestral type. Such a type would probably have to be looked for in Devonian rocks and may have arisen from an early branch of the Palaeodictyoptera.

The fossil *Eugereon* from the Lower Permian rocks of Germany represents an insect probably with a wing-spread of 16 cm. It is relegated to the order Protohemiptera, which is characterized by pronotal expansions and a type of venation suggestive of a palaeodictyopterous descent. Its small head and projecting mouth-parts of the piercing and suctorial type suggest hemipterous affinities. No annectant types have been discovered, however, that shed light upon the derivation of such a type of mouth-parts for the mandibulate condition. The oldest known true Hemiptera, it may be noted, are found in rocks of similar date and are evidently members of the suborder Homoptera.

It is outside the scope of an elementary book to consider the affinities of the smaller orders. The Endopterygota, therefore, may now be briefly discussed. Viewed as a whole, they seem to show three lines of descent. The main evolutionary line includes the orders Mecoptera, Neuroptera, Trichoptera, Lepidoptera, and Diptera. These five groups have very possibly been derived from early mecopterous ancestors. The Neuroptera may have been derived from such a stock by acquiring a more profusely branched venation and by the development of a complex series of cross-veins. The other orders have diverged in different ways by reduction in the main veins and in the cross veins. The latter, it will be noted, became very few and developed at points where the greatest mechanical advantage seems to be obtained. The primitive members of the Trichoptera and Lepidoptera show very few differences, but the hairy wings of the lowest Trichoptera are replaced by scale-clad wings in the most primitive Lepidoptera. The balance of evidence points to these two orders having arisen from a common ancestor.

The Diptera are characterized by their narrow wing bases and the consequent reduction of Cu_2 and the anal veins. Their most primitive representatives are found among early Tipulid types that closely resemble some of the living crane-flies. The so-called Protodiptera are 4-winged mecopterous fossil types, whose venation is very like that of existing primitive Nematocera, with characteristic narrow wing bases and correspondingly reduced anal areas. However, no annectant forms have been found linking them with true Diptera, nor do they show any tendency towards reduction of the hind wings.

The Coleoptera, along with the Strepsiptera, represent a second line of evolution. It is possible that they have developed from Protocoleoptera, but so little is known of the last-named that this contention is very hypothetical. The tegmen-like elytron of *Protocoleus*, with its definite venational system, looks very like the antecedent of a true beetle elytron. If this suggestion be correct, it would imply perhaps derivation of the Coleoptera from some early branch of the Protorthoptera.

The third and last branch of the Endopterygota is the Hymenoptera. The saw-flies are generally conceded to include the most primitive members of the order, but they appear to have no close relations with any other insects either living or fossil. The so-called Protohymenoptera, it may be added, are members of the extinct order Megasecoptera and are remote from the line of descent of the Hymenoptera.

In conclusion, it may be said that the most primitive winged insects are those comprised in the palaeozoic order Palaeodictyoptera. While it is probable that the Ephemeroptera, Orthoptera, and Plecoptera have been derived from this ancient group through their extinct forerunners, the links in the chain of evidence are very incomplete. The Endopterygota show three lines of evolutionary development. That which led to the development of the Coleoptera was possibly derived from the Protorthoptera. A second line culminated in the Hymenoptera but no evidence exists regarding its possible origins. The third and most important line was probably derived from mecopterous forerunners and gave rise to existing Mecoptera, Neuroptera, Trichoptera, Lepidoptera, and Diptera.

VI. APPENDIX ON LITERATURE

IN an elementary book of this kind it is only possible to give a small selection from the very voluminous literature on entomology.

(*a*) General Works

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