PRESENT STATUS OF THE CLASSIFICATION OF IMMATURE INSECTS[1]

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INTRODUCTION

The present day knowledge of immature insects is incomplete and fragmentary as compared to the information that is available concerning adult insects. The study of immature insects has been neglected, but is of great biological interest because a knowledge of the preparatory stages of insects is essential to an understanding of the many adaptations of insects, whose significance can only be recognized when light is thrown on the immature stages. Comparative studies of immature forms will yield light on the significance of metamorphosis, especially as to the origin and development of this phenomenon which appears in its greatest development in the specialized insects. Certain adaptations of immature insects when fully understood should aid in the application of the biogenetic law to insects and all attempts to correlate insect ontogeny with phylogeny must give careful consideration to the characteristics and peculiarities of postembryonic development. It seems hardly necessary to stress the importance of the study of immature insects. They afford numerous aids in the study of phylogeny and classification when study of the adults fails to furnish the necessary evidence. Moreover, larvae are of great interest because of their habits which furnish abundant material for the study of insect ecology, a much neglected field.

Not only have the structural and functional modifications of immature insects been neglected but the taxonomic aspect is in a deplorable state and there is at present a crying need among the economic investigators for a way out of the present chaos. There is scarcely an economic entomologist but what has dire need for a system of classification of immature insects. To be sure, some work has been accomplished but what little has been done is scattered widely in the ever increasing flood of entomological literature. No attempt has ever been

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made to bring together the known facts of larval and nymphal development and not even a bibliography on the whole subject is available.

The present paper is an attempt to bring together some of the materials for the classification of immature insects; the important facts of metamorphosis and some structural characteristics are considered, and some available keys to the immature stages of insects are listed in the hope that others will strive for a further advancement in the classification of immature insects.

Present Status of Classification

Most of the earlier students of entomology devoted their efforts to the study of adult insects, stressing at first the classification, and later, the morphology of mature insects. A few workers such as Swammerdam and Reaumur devoted their attention to the metamorphosis and habits of insects. Led by the great Linneaus, the vast majority of the students of taxonomy, even up to the present day, have confined their attention to the classification of adult insects. Through their efforts new species are being defined and a limited number of descriptions of the egg, larval, and pupal stages are being compiled. These descriptions have been augmented in recent years by the increased interest in economic entomology which is especially evidenced in the United States, as well as some foreign countries, and by the establishment and development of numerous federal and state agencies for the study of insect life. These laboratories have expended a large share of their efforts in making known a vast number of our economically important insects and fortunately the work is still progressing. In spite of the fact that our knowledge of the immature stages of insects is rapidly increasing, it has by no means kept pace with the advance made in the study of adult forms. The available information is scattered widely in the literature and until some effort is made to assemble the present known facts, progress will be slow.

Perhaps the best known groups of immature insects are the Lepidoptera and certain members of several insect orders which are generally referred to under the group term "aquatic insects". The students of Lepidoptera have been among the foremost in advancing the study from the systematic standpoint. This can be explained, in part at least, by the unexcelled beauty of the adults which has led many collectors to rear and study the immature stages, in many cases merely to obtain more adult specimens. It must not be forgotten, however, that many students have been impelled by a desire to know more about the immature insects.

The early stages of aquatic insects are better known because of the ease with which many of the insects can be reared. There are some groups in which only the immature stages are aquatic, others in which both the young and the adult spend most of their life in the water, and only rare instances, as in the case of some aquatic Hymenoptera, in which only the adult is aquatic. The study of fresh-water biology has developed rapidly with the aid of many investigators who are not strictly entomologists, but who have, nevertheless, given some time to the study of aquatic insects. In Europe, Rosseau and others have done an immense amount of work on the classification of water-inhabiting forms. Other entomologists, and they are rare, have been interested and have given some attention to various groups of immature forms. Such workers as Schiödte, Dufour, Perris, Böving, Dyar, Fracker, Yuasa, and Mosher may be considered as initiators of the systematic study of immature groups.

Phases of Insect Development

Insects, as well as other Arthropoda, undergo three distinct periods during their life-history, an embryonic period, a postembryonic period, and an adult period. In the first or embryonic period are comprised the processes of maturation, fertilization, egg cleavage, the formation of the germ layers and the growth of organs and appendages. Naturally, these occur while the insect is still within the egg and the animal is known as the embryo.

Omitting, for the moment, the second or postembryonic period, brief mention is made of the final stage. In the adult stage the insect exhibits all or most of the structures of the body (excepting provisional organs) as evidenced by completely developed appendages and internal organs. In some species the newly transformed adult requires some time for the complete development of the organs of reproduction. In others, for example the ants, a period just after transformation is undergone in which the individuals are not fully colored and, in a still helpless condition, must be nourished and cared for by other members of the colony. Such individuals are termed callows. The insect in this last phase of its life is known as the adult whose chief function is the perpetuation of its kind. This is accomplished by the act of copulation when the female is supplied with spermatozoa for the fertilization of the eggs. The male, however, is not always required for this purpose. As is well known many insects may reproduce parthenogenetically and the males may be entirely lacking, few in number, or appearing only at certain intervals during the seasonal life-cycle of the species.

The second or postembryonic period is that between the hatching of the embryo and the attainment of the adult condition. In some groups of insects the changes during this period are very slight and may be only an increase in size, whereas in other groups very striking and remarkable changes may occur. Also, the groups are not all in the same stage of development when hatched and consequently the greater the difference between the newly hatched insect and the adults, the greater will be the postembryonic changes. When only minor changes occur the development is said to be direct and the type of change is sometimes called direct metamorphosis. If the course of development is devious and each successive change is different, with complicated processes occurring, the development is said to be indirect and is frequently known as indirect metamorphosis. In direct metamorphosis the young and adults are quite similar. This type of development occurs in the Apterygota as represented by the orders Thysanura and Collembola. A somewhat more complicated type of direct metamorphosis is found among these Pterygota in which the wing development is external, as found in Orthoptera, Dermaptera, and some other ten orders. The remaining orders, belonging to the Pterygota such as Coleoptera, Lepidoptera and others, present a complicated change from the larval to the pupal stage and likewise a pronounced change from the pupa to the adult. They are consequently said to have indirect metamorphosis. These two types of development occur in varying degrees among many animals other than insects, but to a less pronounced degree. Entomologists as a rule apply the term metamorphosis to both direct and indirect types of development, whereas some zoölogists consider only the changes occurring in indirect development as metamorphosis.

Provisional Organs

During the postembryonic period, in many insects, certain structures are developed which are for use only during the period of growth and are lost or absorbed before or at the time of the emergence of the adult. Such temporary organs are *provisional organs* and their presence tends to increase the differences between the organization of the immature and adult stages. Some of the provisional structures are the *prolegs* of caterpillars, digging *fore-legs* of the cicada nymph and the *pseudopods* of dipterous larvae. As these organs are essentially structures of the immature stages and not of the adult, the young insects possessing provisional organs may differ from their parents in at least one of the following types of provisional organs:

1. In the form of body segmentation.
2. In the degree of development or number of organs of locomotion.
3. In the degree of color, chitinization or armature such as setae, bristles or spines.
4. In the location or number of glands.
5. In the degree of development of antennae or mouthparts.
6. In the presence or absence of certain external structural characters.
7. In the degree of development of internal structures.

Deegener (1909) has classed provisional organs into "provisional organs of the first order" and "provisional organs of the second order". Those of the first order are those which are characteristic only of the immature stages, such as prolegs, exuvial glands, and osmateria. Organs of the second order are represented by the mandibles of sucking neuropterous larvae, which are also present in the adults.

Escherich has classified immature insects on the basis of provisional organs as follows:

CLASSIFICATION OF LARVAE ON BASIS OF PROVISIONAL ORGANS
(After Escherich from Lochhead, Economic Entomology, p. 343)

Primary Larvae.
Larvae like adult, without provisional larval organs.
Thysanura, Collembola, Mallophaga, Pediculidae, Orthoptera, Isoptera, Corredentia.

Secondary Larvae.
Unlike adults and with a few provisional larval organs.
Ephemeridae, Plecoptera, Cicadidae, Odonata, Coccidae.

Tertiary Larvae.
Unlike adult with numerous provisional larval organs.

Classification of Tertiary Larvae.

A. Larvae without prolegs
  B. Larvae with a well formed sternum
    C. Larvae more or less chitinized, thorax or at least the prothorax differing from the other segments quite noticeably, large or more strongly chitinized, or otherwise sculptured; head generally with lateral eye points. EXAMPLES: Rhaphidians, Ant-lions, Carabidae, Dytiscidae, Silphidae, Coccinellidae, Elateridae, Chrysomelidae.
    CC. Larvae weakly chitinized, soft-skinned and mostly whitish, but with chitinized dark head; thorax differing but little from the other segments. EXAMPLES: White Grubs, Stag Beetles and Dung Beetles.
  BB. Larvae with poorly developed or rudimentary sternum. EXAMPLES Many Cerambycids, Sirex.
  BBB. Larvae with sternum wholly atrophied or undeveloped.
    C. Larvae with a head capsule and typically formed mouthparts. EXAMPLE: Bark-beetles, Snout Beetles, Bees, Wasps, Ants, Ichneumons, Midges.
    CC. Larvae without a head capsule or well-formed mouth parts. EXAMPLES: Most diptera.

AA. Larvae with prolegs.

B. Larvae usually with five pairs of prolegs. EXAMPLES: Butterflies and Moths.

BB. Larvae with more than five pairs of prolegs. EXAMPLE: Sawflies.[1]

MOLTING

The fundamental processes of metamorphosis are *growth, development of wings* and, in rare paedogenetic insects, *reproduction.* Growth can only be accomplished by the shedding of the cuticula, or *molting.* The body, as well as its appendages, is covered by the cuticula in which there is a substance called chitin, the amount of which determines the rigidity or flexibility of the body wall and this is dependent to some extent on the age of the insect. Soon after the deposition of chitin the body wall hardens and becomes inflexible and inelastic so that it becomes difficult for the insect to expand its body during growth. In order to permit expansion, the insect periodically casts off or sheds this hardened layer of cuticula. This process is known as *molting* or *ecdysis,* and the molted or cast skin is the *exuviae.* When the growing insect is ready to shed this hardened, outer, body wall it becomes quiescent for a short period during which the primary or outer cuticula becomes separated from the inner or secondary cuticula. This separation is aided by a fluid secreted from certain *exuvial* glands which is said to act corrosively on the structures beneath the primary cuticula. Finally, the old cuticula splits on the dorso-mesal surface of the head and thorax and after forcing the edges of the rent apart, the insect slowly forces its body out of the old cuticula. The new cuticula is soft and often colorless and some time must elapse to allow for the hardening of the new chitin and for deposition of pigment before coloration is completed. It should be recalled, that not only the body wall and the appendages lose their cuticula, but also the cuticular lining of the alimentary canal, tracheae, and parts of the reproductive organs are molted.

There is a wide range of variation in the number of molts through which insects pass. There is said to be a single partial molt in Campodea and Japyx, and Lubbock has observed the May-fly *Chloen* to molt 23 times. Any number may occur between these extremes and the number may not be constant for the same species. White grubs as a rule molt twice, but some species may molt three times. Certain dipterous larvae (Cyclorrhapha) and some Neuroptera have two molts as a constant number. The number of ecdyses is also variable in caterpillars. May-flies may molt after wings are acquired and Collembola

[1]This group would also include the larvae of Mecoptera.

may molt after reaching sexual maturity. Frequently molts occur soon after hatching. The causal factors of such lack of uniformity may be physiological and are thought by some to be due to food relations.

Most of the stages through which growing insects pass are limited or separated from each other by molts. The intervals occurring between the molts are called *stadia* (single, stadium). The term *instar* applied by Sharp and now widely accepted is used to designate the form assumed by the insect during the various stadia and is used to replace such expressions as "the form assumed at the first molt", or, "the appearance when hatched". The form at the time of hatching is the first instar, that after the first molt is the second instar, and so forth.

Characters Used in the Classification of Immature Insects

As there are marked differences in the body form between the immature stages and the adult, especially in the Holometabola, we find young insects in possession of certain structures which are characteristic only of the developmental period. These have been considered as "provisional organs." It was shown that certain structures like the sucking mandibles of Neuroptera may be carried over into the imago. The presence or absence of some of these organs is now considered. A complete discussion of the countless numbers of larval structures is beyond the scope of this paper and only such generalizations will be made as serve to elucidate the points under discussion.

In the nymphal stages a closer correspondence with the adult stage is to be found than in the larval stage. The three body regions are more marked, the legs are more highly developed, and especially in older nymphs the structures more closely approach the adult form except in the degree of wing development. The body segmentation in nymphs is *heteronymous* or specialized in contrast to the *homonymous* or generalized condition of larvae, in which are recognized varying degrees of specialization. In apodous or footless larvae the metameres of the thorax and abdomen are nearly similar, the animal exhibiting only a head and trunk; frequently, as in some Diptera, the head may be only slightly differentiated. Larvae with well developed legs show more specialization but not to the degree found in nymphs where wing pads are found in addition to the legs, and when the thorax is more specialized. The various degrees of larval specialization are discussed below.

The Body Wall of Nymphs and Larvae

The structure of the body wall in immature insects differs very little from that of the adult except for differences in degree of chitinization, but the appendages of the cuticula, hairs, spines, setae, tubercles, etc. vary in some orders to such an extent that they are useless for purposes of taxonomy whereas in other orders, especially the Lepidoptera, their form and arrangement are sufficiently constant to use in the classification of species. The arrangement of setae is useful in the classification of mosquito larvae and may prove of value in beetle larvae and sawfly larvae. Garman has made use of the various color markings and finer texture of the cuticula to distinguish certain species of cutworms and a deeper study of the shape and structure of the spiracles may prove of importance in other orders, as they have in Diptera where extensive taxonomic use has been made of the minute structure of the peritreme and the shape of the apertures of the spiracles.

The Head of Nymphs and Larvae

The functions of the head of immature insects are practically the same as those of adult insects and consist of the three important physiological processes of *ingestion, sensation,* and *coordination.* The process of ingestion is perhaps of greater importance in young growing insects than in adults, whereas sensation may be less developed, and coordination, brought about by the degree of development of the nervous system, may also be not so well marked. For performing these functions, and chiefly, because the law of cephalization tends to localize a number of structures in the head capsule, the head may be said to contain two rather distinct groups of organs, those which may be classed as essential organs, such as the brain, optic ganglia, cranium, pharynx, and aorta, and those which may be considered as accessory structures, aiding in ingestion, sensation, and coordination. These accessory organs consist of such parts as the muscles, glands, antennae, mouthparts, tentorium, hypopharynx, and the sympathetic nervous system.

In general the head is distinct from the rest of the body and when well developed is known as the *eucephalous type* of head which occurs in both nymphs and larvae. In such heads the integument is generally more heavily chitinized and more resistent to external forces than are the remaining segments of the body. It is ordinarily broadly joined to the thorax but may be separated by a well marked constriction as in the nymphs of the horse louse, *Haematopinus asini* or in earwig nymphs. Sometimes, as in dobson-fly larvae, the occiput may form a distinct collar at the base of the head. In certain insects, the cephalic region is heavily chitinized while the caudal area, more or less protected by the overlapping of the prothorax, is less heavily chitinized and is capable of being invaginated into the foramen of the prothorax.

In many dipterous larvae the head is indistinct, when it is classified as an *acephalous* or *pseudocephalous* type of head. In such larvae the head is greatly reduced and is retracted within the prothorax, if developed at all. Frequently the anterior margin of the prothorax is so modified that it resembles and is frequently mistaken for the head. An intermediate condition between these two extremes is the *hemicephalous* type of head, which is often found in hymenopterous larvae.

The Antennae

The antennae are two in number as in adult insects. They are inserted near the latero-ventral margin of the head capsule in larvae and near the mesad of the compound eyes in nymphs. The number of segments is usually constant in larvae both for the species and for the instar. They apparently do not increase in number of segments following the various molts as Criddle has found to be the case in nymphs of Locustidae (Acridiidae) and as others have observed in other nymphal forms. In most immature forms the first or proximal segment is the *scape,* the second is the *pedicle,* and those which follow constitute the *flagellum* or *clavola.* When only one or two segments are present the divisions cannot be definitely determined. In white grub larvae, a rounded segment-like protuberance of the body wall on which the antennae articulate has frequently been mistaken for a basal segment. Many coleopterous larvae possess a small supplementary segment on the distal end of the penultimate segment, giving the appearance of a forked or split antenna. Larvae of the Dryopidae and some of the coprophagous Scarabaeidae exhibit such a splitting. However, in the Dryopidae, according to Rosseau, the supplementary segment is on the antepenultimate segment instead of the penultimate, which is narrow and constricted like the distal segment.

Acephalous dipterous larvae have two, sessile, papillae-like structures beneath the mouth which are known as the *"antennal organs".* They occupy the position of the antennae and probably have a sensory function. On the sides of the antennae of certain aquatic Diptera, for example in *Simulium* (black fly larvae) and *Culex* (mosquito larvae,) are appendages bearing cilia or tufts of setae which help to maintain a current of water toward the mouth, thus providing aquatic organisms for food.

Organs of Sight

Compound eyes are usually found in nymphs of those species in which they are present in the adult form. If the adult lacks eyes, which is frequently the case in degenerate forms, the nymph also lacks them. Well developed eyes are present in nymphs of Hemiptera, most Homoptera, Orthoptera and Odonata. In older nymphs *primary ocelli* are also found but there is some doubt as to their ability to function. Frequently, they may be only the simple eyes of the adult showing through the nymphal cuticle.

Compound eyes are never present in larvae which, as a rule, are provided with groups of simple eyes known as *adaptive ocelli.* This type of ocellus is thought to have been brought about by a change in the habits of individuals as we regard larvae as being secondarily developed by adapting themselves to their particular mode of life. Adaptive ocelli usually occur on the sides of the head. In the Perlidae (Plecoptera) and the Ephemerida ocelli are on the dorsal aspect, although these may be adult ocelli showing through the cuticula. Such eyes are distinctly different from the primary ocelli of adults.

Primary ocelli are usually three in number, but maybe only two. It is believed by some workers that the median ocellus represents a fusion of two ocelli, there having been, primitively, two pairs of simple eyes. Because of the marked differences in structure between the two kinds of simple eyes, MacGillivray[2] has proposed the term *ocella* (pl. ocellae) for all simple eyes of larvae to distinguish them from *ocelli* of adults. The number of adaptive ocelli is variable in different insects and may differ in the same species. *Corydalus* larvae may have six or seven on each side. Henneguy (p. 450) cites the following groups which have from one to twenty ocelli on each side of the head.

One ocellus—Lampyridae, Drillidae, Lycidae, Telephoridae, some Cryptophagidae, Cerambycidae and Curculionidae, phytophagous Hymenoptera (Tenthredinoidea) and Trichoptera.

Two ocelli—Byrrhidae, Melandryidae, Oedemeridae, Tenebrionidae, Nitulidae, Elateridae and some Scarabaeidae (Trox).

Three ocelli—Many Cereambycidae, Tenebrionidae and Coccinellidae.

Four ocelli—Cicindellidae, most Staphylinidae, Pyrochroidae, some Chrysomelidae *(Cassida)* and Coccinellidae.

Five ocelli—Cleridae, Ciodidae, Colydiidae, Mycetophagidae, Heteroceridae, Parnidae, Lagriidae, many Byrrhidae, some Cerambycidae, and many lepidopterous larvae.

Six ocelli—All Carabidae, Dytiscidae, Gyrinidae, Cyphonidae, Erotylidae, most Hydrophilidae, Dermestidae, and many Chrysomelidae, *Sialis* and most Lepidoptera.

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[2]MacGillivray, A. D., The Eyes of Insects. *In* Ent. News, Vol. 31, pp. 97-100, 1920.

Seven ocelli—*Raphidia* and *Bittacus*.
Twenty ocelli or more—*Panorpa* and *Boreus*.

Larvae living in the soil, in wood, or other concealed places have no use for eyes and consequently are blind. Examples of such species can be found in the Scarabaeidae, some Curculionidae, many Cerambycidae, Tenebrionidae and many others. Most hymenopterous larvae, excepting those of the sawflies and their close relatives as well as many Diptera, are without adaptive ocelli. Many aquatic Diptera with well developed heads (*Culex, Corethra,* etc.) are provided with ocelli. In certain Cecidomyidae, scattered pigment spots over the body have been found to be provided with nerve endings which have led certain workers in the past to suggest a visual function similar to that found in many of the lower organisms.

Mouthparts of Immature Insects

Young insects that exhibit gradual metamorphosis ordinarily have the same type of mouthparts as the adult and as a rule they are of the mandibulate (chewing) type; examples are the nymphs of Orthoptera, Isoptera, and others. Those having suctorial mouthparts in the nymphs have the corresponding type in the adults, the Hemiptera, Homoptera and Anoplura.

The common type of immature insect mouthparts in the Holometabola is the mandibulate type which in some groups is carried over to the adult stage. Others in the larval stage possess the chewing type which in the adult is transformed to the sucking or lapping type. The usual biting structures are found in these larvae—a labrum, two mandibles, two maxillae, and a labium which become greatly modified in the adult stage. Henneguy (p. 451) has classified the various types of immature mouthparts as follows:

1. *Insectes menorhynques.* Sucking type in both the immature and adult stages: Homoptera, Hemiptera, and Anoplura.
2. *Insectes menognathes.* Chewing type in both the immature and adult stages: Orthoptera, Odonata, Neuroptera, Mecoptera, Ephemerida, Trichoptera, Coleoptera and some Hymenoptera.
3. *Insectes metagnathes.* Chewing type in the larval stage and sucking or lapping in the adult stage: Diptera, Siphonaptera, Lepidoptera, and some Hymenoptera.

The biting type is the most common but in certain groups it presents striking modifications in which the parts no longer function in a chewing capacity. Some of the parts, especially the mandibles, become organs of piercing and suction. An example of such is found among dytiscid larvae in which the mouth is closed and the mandibles are penetrated by a hollow canal which connects with the esophagus.

The insects are predaceous and their nourishment is the body fluids of their prey, although rarely they can take in solid material. Other examples of this condition are found among the Myrmelionidae, Chrysopidae, and the Hemerobiidae. In these, the mandibles are not penetrated by a canal, but are grooved on the under surface to form a canal with the aid of the corresponding maxillae.

A unique specialization of the mandibulate type of mouthparts is found in the Odonata. The mandibles and maxillae show no special modifications, but the labium is a curious structure, varying in degree of development among the various genera. The labium is normal in the adult stage. It is usually longer than the head in the nymph and possesses a double articulation which allows it to be protruded or retracted. It is thus an extensile and prehensile organ used to grasp food. When retracted it covers the mouthparts, in whole or in part, and it is then called the *mask,* a name applied to it by Reaumur. The submentum of the mask is very long and, when retracted, is usually under the prothorax. The mentum, likewise, is elongated and bears on its distal end a pair of labial palpi which terminate in a *movable hook.* The setae of the mentum *(mental setae)* and other characters of the labium are used to a large extent in taxonomic keys to the nymphs (or naiads) of this order. The movable hooks are used, when the labium is extended, to aid in grasping the prey which is then brought back to the mouth.

In the Lepidoptera there is a marked transformation from the biting type of larval mouthparts to a siphoning structure of the adult. The structures are normal in the larva but during its period of growth a large, invaginated histoblast is developing which produces the elongated maxillae, or more properly speaking, the galea of the maxilla of the adult. This becomes evaginated at the end of the larval period but does not assume its final form until the adult stage is reached. Observers have noted that no adult mandibles are developing within or behind the larval mandibles, so that in the adult the mandibles are either absent or are vestigial.

The mouthparts are fairly well developed among the larvae of eucephalous Diptera, but extreme modification occurs in the acephalous and legless dipterous larvae; in these insects the mouthparts do not appear externally until the pupal stage and do not function until the adult stage is reached. The larval mouthparts are greatly reduced and usually consist of two chitinous hooks which can be extended and retracted, used to lacerate food, and in some insects (Oestridae) serving as organs of attachment or fixation. The hooks, which may be bifurcated, work in a vertical plane and some species use them as claspers during locomotion. Larval mouthparts of this sort are in no way homologous to the mandibles, maxillae, and labium of other larvae.

The most common examples of insects having sucking mouthparts in both the young and adult stages are found in the orders Homoptera, Hemiptera, and Anoplura. The nymphal mouth organs consist of a labrum, epipharynx (or possibly a combined labrum-epipharynx), two mandibular stylets, two maxillary stylets, and a sheath, or scabbard-like labium, with palpi usually lacking. They are essentially like the corresponding adult structures and further description is not necessary here. The sucking types occurring among holometabolous larvae have been mentioned above as specialized mandibulate types (Dytiscidae, Myrmelionidae, Chrysopidae and Hemerobiidae). These modified, sucking mandibles are usually projected cephalad and not folded under the body as are the mouthparts of the Hemiptera and Homoptera.

Other Appendages of the Head

Except for the antennae and mouthparts, the head is generally devoid of other appendages, but the non-functional tracheal gills found on the heads of some Plecoptera should be called to mind. The hypopharynx in nymphs of *Perla* of the order Plecoptera is elongated and extends beyond the glossae and may thus appear as a non-movable appendage of the head.

The Thorax of Nymphs and Larvae

The thorax is the second division of the body and is not as specialized in either nymphs or larvae as it is in most adult forms. Usually the segments are quite similar to the remaining segments of the body and are designated, as are the adults, by the terms *pro- meso-* and *metathorax*. In the aculeate Hymenoptera the basal or first abdominal segment is transferred to the thorax during the change from the larval to the pupal stage. This first abdominal segment is the *median segment or propodeum* and the thorax as thus constituted is the *alitrunk* in both pupae and adults.

Thoracic Appendages

The developing wings or wing pads of nymphs are conspicuous appendages of the thorax. The *tracheal gills* of aquatic forms are non-articulating appendages of both the thorax and abdomen. Other appendages are *osmateria,* eversible glands, on the dorsal aspect of the prothorax in *Papilio* and the ventral eversible glands in Notodontidae, Noctuidae, and other lepidopterous larvae. The clothing hairs or setae and the chitinous tubercles of many caterpillars are also less conspicuous appendages. There may be *setiferous tubercles,* or, if the tubercles are larger and with many hairs, *verrucae,* as found in the Arctiidae. If the tubercle is spinose as found in the Saturnioidea it is known as a *scolus.* Setae that are not constant are known as *secondary setae.* If they are constant and have a definite position and usually a definite number, they are called *primary setae.* In some groups there are certain setae present in all the instars except the first which are distinguished from those present in the first instar by the appellation *subprimary setae.* In the classification of the lepidopterous larvae each of these setae is given a distinguishing name.

The locomotor, thoracic appendages are usually called the "true legs" in contrast to the abdominal legs when they are present. When thoracic legs are present they are, as with the adult, six in number. In a few cases, for example, the larvae of *Passalus cornutus,* the metathoracic pair is much reduced. In this instance, the reduction is due to a modification in which this leg is used as a scraper to stridulate with the mesothoracic leg for the production of sound.

As a rule the same divisions of the leg occur in the immature insect as are found in the adult insect although the segments are usually shorter and the tarsi have fewer segments which sometimes increase in number with the later molts. The tarsus is provided with a single claw in most Coleoptera, Neuroptera and Lepidoptera. The Carabidae, Dytiscidae and Gyrinidae are exceptions to the Coleoptera in the possession of two tarsal claws and some Neuroptera likewise have two claws. *Meloe, Mylabris* and other triungulin larvae are so-called because they possess three tarsal claws of which the median claw is enlarged for piercing whereas the lateral claws are sharp and curved. Riley and others have shown that the lateral claws are two large setae.

The development of the thoracic legs is frequently correlated with the mode of life of the immature insect. If it must search for its food, as with the carabid larvae, the legs are well developed. If food is close by and abundant the legs are less developed and even entirely atrophied in forms that live in their food material. They may have legs in earlier instars, retaining them until food is found after which they cast them off with the next molt. Such forms are usually considered as having a simple type of hypermetamorphosis, especially if other striking changes such as body form occur. Footless, larval insects are common and the loss of these appendages is usually considered as a secondary adaption. The larvae of all Diptera and Siphonaptera are legless. Some Coleoptera, such as the Rhynchophora, Eucnemidae, Buprestidae and many Cerambycidae are apodous. A few Lepidoptera and all the Hymenoptera except the sawflies are without thoracic legs. All degrees of development between the fully developed leg and the apodous forms can be traced in various groups.

In nymphs there are generally three pairs of well developed legs with the usual divisions. Female Coccidae have none in later instars. The tarsi are from one to five-segmented and in aquatic forms may be greatly flattened and ciliated for swimming. The anterior pair of legs are usually fitted for locomotion but may be modified for prehension in many Hemiptera (*Nepa, Ranatra* and Nabidae). The legs also serve for fixation. A unique structure is the modified leg of the Cicada nymph, which is flattened for digging during nymphal life but normal in the imago.

The Abdomen of Nymphs and Larvae

The abdomen, the largest of the three body regions, comprises all parts behind the thorax. In larvae there is no distinct separation of the terga, pleura, and sterna whereas in nymphs there are usually only terga and sterna present. The pleura are absent and the terga and sterna may or may not be connected by a longitudinal membrane or conjunctiva. Spiracles are usually present and functional in the first eight segments. They may, in some species be present but not functional. The caudal segments gradually become specialized as development proceeds and as a rule differ in the two sexes.

The Cerci

Appendages of the abdomen may serve in the capacity of sensation, locomotion, respiration, or fixation, and for reproduction in the adult stage. The cerci are considered as being sensory in function, serving in a tactile or olfactory capacity. They have been variously regarded as appendages of the ninth, tenth, and eleventh segments. Comstock considers them to belong to the eleventh segment. Their position may vary in different groups. They are always paired and exhibit a great deal of variation in size and shape. They may or may not be segmented and composed of from one to many segments. Many segmented cerci are found in the Thysanura, some Orthoptera (Mantidae, Blattidae and some Gryllidae), the Ephemerida and the Plecoptera. In the Embiidoptera they are two-segmented. Those composed of one segment, and therefore considered as non-segmented, are found in some Orthoptera (Locustidae, Tettigoniidae, Phasmidae and some Gryllidae), Odonata, and the Dermaptera. In the Dermaptera they are strongly curved to form the "pinchers." The cerci in the odd Mayfly genus *Prosopistoma* are retractile.

In some Thysanura (*Machilis, Lepisma et al*) and in the nymphs of the Ephemerida, besides the lateral pair of cerci there is a median appendage called the *median caudal filament* or the *alacercus*. It is quite similar to the many-jointed cerci but is thought to have a different origin in that it is considered a prolongation of the tergum of the last abdominal segment.

Locomotor Appendages of the Abdomen

The so-called "false-feet" of caterpillars, sawfly larvae, and scorpion-fly larvae are usually known as *prolegs*. Objection has been raised to the use of this name by some authors who maintain that a proleg should be an appendage of the prothorax. Accordingly, such other terms as *uropod, larvapod* and *propleg* have been suggested as substitutes. The prolegs are non-articulating appendages of most of the abdominal segments. They are used in locomotion and for fixation. In shape, the prolegs are usually cylindrical or conical and in the Lepidoptera are terminated by a series of hooks or crochets. Embryologists have shown that the evanescent abdominal appendages of the embryo are retained and transformed into functional prolegs in those species in which prolegs are present and that the embryonic appendages disappear in those species without prolegs.

In the Tenthredinidae and Mecoptera the crochets are absent but in Lepidoptera they are important structures in the classification of caterpillars. The arrangement, size, and shape are quite varied. They are said to be absent in *Agriotis* and the European genus *Hepialus*. They are ordinarily arranged in a complete or incomplete circle, in transverse bands or in the shape of an ellipse and may be of the same length or regularly graded in length (uniordinal), alternately composed of two lengths (biordinal) or of three lengths (triordinal). When there are present one or more rows of small, rudimentary crochets at the bases of the functional hooks, the arrangement is known as *multiserial*. In some cases there is a longitudinal band of crochets on the inner side of the proleg and a weaker band of scattered hooks on the outer side. This sort of an arrangement is called a *pseudocircle*. The apex of the proleg is called the *planta*. To the planta is attached a muscle which when contracted may cause the proleg to be completely retracted.

The location and numbers of pairs of prolegs is quite variable. Most of the Lepidoptera have five pairs on the third, fourth, fifth, and sixth segments and a terminal pair on the posterior segment. Imms calls the first four pairs "abdominal feet" and the last pair "claspers." All serve more or less as claspers. Caterpillars as a rule never have prolegs on the first, second, seventh, and eighth segments and they may sometimes be absent on other segments thus having fewer than five pairs. The early instars of many Noctuidae have only three pairs or only rudimentary prolegs on the fifth, sixth, and tenth segments, but after the third molt the prolegs of the third and fourth segments appear. In the subfamily Plusinae of the Noctuidae and in some other subfamilies the prolegs of the third and fourth segments are permanently absent. Other noctuids *(Catacola, et. al)* have only four pairs of prolegs. In the family Geometridae prolegs are present only on the sixth and tenth segments. Other geometers may have prolegs on the fifth segment as well. Caterpillars with fewer than five pairs of prolegs usually have the "looping" habit of locomotion. The anterior part of the body is fixed with the thoracic legs and the prolegs are drawn forward causing the body to become strongly arched, or looped, after which the thoracic legs are released and pushed forward to become attached again during which time the prolegs remain firmly attached. The caterpillars of the genus *Micropteryx* are exceptional in having eight pairs of prolegs while certain leaf-mining Lepidoptera are totally footless and are called "slug caterpillars." Examples of this condition occur in the genera *Eriocraina, Phyllocnistis* and *Limacodes.* In some genera the anal prolegs are extremely elongated and are retractile. They are said to be used as organs of defense against parasitic insects attempting to oviposit on the caterpillars.

The larvae of sawflies (Tenthredinidae) are sometimes called "false-caterpillars." They are usually distinguished from true caterpillars by having more than five pairs of prolegs. The number varies in the various subfamilies. The Xyelinae have prolegs on each abdominal segment. In other groups they are present on segments one to nine but in the Pamphilinae and Oryssinae the prolegs are absent. Scorpion-fly larvae (Mecoptera) have, besides the three pairs of thoracic legs, a pair of prolegs on each of the first eight abdominal segments and none on the last two segments. Others may have no prolegs at all.

Structures serving as abdominal feet are found in a number of other groups of insects. Certain coleopterous larvae have a pair of well-developed prolegs on the anal segment. In certain Elateridae they are more or less retractile. In the beetle family Oedemeridae certain genera *(Asclera* and *Nacerdes)* have on some of the anterior abdominal segments paired outgrowths provided with strong setae which aid in locomotion. Some dipterous larvae belonging to normally footless groups may possess structures on both the thorax and abdomen which serve in locomotion. They are merely cuticular outgrowths in pairs on various segments depending on the individuals and usually terminated with chitinous hooks. These outgrowths are known as *pseudopods.* Some species bear pseudopods on the abdomen whereas others have them on both the thorax and abdomen. In *Dixa* two pairs are located on the first and second abdominal segments. In Dicranota five pairs are formed on the last five segments. In the rat-tailed maggot, *Eristalis,* seven pairs are located on the first and third thoracic and the first five abdominal segments.

Miscellaneous Appendages of the Abdomen

In many larvae appendages occur variously disposed over the abdomen, whose functions are not fully understood. In the larvae of *Lampyris* and certain Carabidae there is a terminal, cylindrical tube which may possibly be used in locomotion. Tiger-beetle larvae (Cicindelidae) have on the back of the abdomen two tubercles with strong hooks which are said to aid in fixing the larva firmly in its burrow when struggling with its prey. Many cerambycid larvae have protuberances on both the dorsal and ventral surfaces which aid in progression. Among the Sphingidae and certain Bombycidae a strong chitinous spine found on the dorsum of the last abdominal segment probably serves as an organ of defense.

Ventral suckers found in the Blepheroceridae are located in a median row on the ventral abdominal segment. They are unpaired, usually six in number, and are thought to have been developed from the embryonic abdominal appendages, representing a fusion of these structures. On the sides of these suckers are digitate processes which have been considered by Kellogg (1907) to function as gills. The suckers themselves serve to fix the larvae to stones in swiftly running water. In the Simulidae a foot-like sucker on the ventral side of the thorax is formed by the fusion of a pair of pseudopods and is provided with hooklets for fixation. The larvae of Trichoptera have two terminal hooks which serve to hold them in their cases and while walking. Gyrinidae have four chitinous terminal hooks.

External Respiratory Structures of Nymphs and Larvae

Adult insects as a rule respire only by means of spiracles. Among immature insects also, normal spiracular respiration is common but many remarkable modifications are found among nymphs and larvae. In general there are four means by which insects breathe, (1) normal *spiracles,* (2) *tracheal gills* which are either external or internal (anal), (3) *blood gills,* and (4) *cuticular respiration,* usually called cutaneous respiration, in which oxygen passes through thinly constructed parts of the body wall. The greatest modifications of the normal condition are found in aquatic forms which present some interesting observations in regard to the methods of respiration.

Modifications of the common spiracles occur principally in variations in the number and location of functional spiracles. When one or more pairs of spiracles are functional the method of respiration is the open or *holopneustic* method of respiration and when closed is the *apneustic*. If all spiracles are functional the system is *peripneustic;* if only the last pair, it is *metapneustic;* and if both the first and last pair is used the system is *amphipneustic*. These types occur most frequently among the Diptera.

From the standpoint of apneustic respiration the immature stages of aquatic insects present many interesting types. Chief among these are *tracheal gills* which are outgrowths of the body wall forming special appendages of the body for obtaining oxygen from the water. Tracheal gills may be external or internal but are more often external. They are penetrated by branches of the main tracheae from which finer tracheoles ramify to all parts of the gills. The form and location of tracheal gills vary considerably. External tracheal gills may be either *filamentous* or *lamelliform* (plate-like). Filamentous gills occur either isolated or in groups. They may be found on the head in some Plecoptera, on each side of the abdomen, on the dorsal and ventral parts of each segment, or they may occur in groups as in the Trichoptera. They occur singly on the sides in *Sialis* or singly on the ventor as in *Sisyra*. Gills may appear to be segmented appendages. In *Cnemidotus* they are dorsal and articulated. Certain gills may be covered with setae and are said to be plumose. These are usually more rigid in structure. Such types are found in the beetle larvae *Gyrinus* and *Hydrophilus*. Other groups may have tracheal gills on both the thorax and abdomen as in *Rhyacophilidae* (Trichoptera), on each side of the anus (*Perla*), at the base of the maxillae (*Chirotonetes*), or at the base of the legs *(Nephelopteryx)*. Plate or lamelliform gills may be plate-like or leaf-like *(foliaceous)*. Like other gills the form and location is variable. The most common lamelliform gills are those found on the end of the abdomen of damsel-fly nymphs, or those on the sides of the abdomen in May-fly nymphs. If gills are external and visible they are termed *nudibranchs*. If they are hidden or partly concealed, they are designated as *cryptobranchs*. An example of hidden or partly concealed gills occur in the Ephemerid genus *Prosopistoma* in which outgrowths of the body wall form a sort of carapace which conceals the abdominal gills.

Internal tracheal gills occur most commonly in the dragon flies (Anisoptera) and the Agrionidae (Zygoptera) where they are found in the rectum. In *Aeschna* they consist of six papillae, in *Libellula* they are formed into transverse plates which are penetrated by tracheae. These gills function when water enters the rectum through a special valvular apparatus and bathes the gills, thus permitting an interchange of respiratory gases. According to Rosseau the larvae of certain Diptera, for example, *Culex, Eristalis* and certain *Psychodidae* have rectal gills as well as some May-fly nymphs, *Baetis and Clöeon.*

Blood gills are usually tubular appendages, very delicate and capable of being evaginated and filled with blood. As a rule they do not contain trachea or at most some unimportant branches. Blood gills occur commonly in the Chironomidae. An intermediate type between the tracheal and blood gills occurs in the Ephemerida in which blood and tracheae are found in the caudal appendages.

Identification of Insect Eggs

The knowledge of the specific identity of a particular insect egg is frequently important, especially, if the species in question is a pest of economic importance. Such a knowledge enables one to predict the possibility of insect outbreaks. Many of our economic species are recognized in the egg stage by the economic entomologist. Other groups are known by specialists. Few attempts have been made to produce keys for the identification of insect eggs. Perhaps the most notable attempt of this sort is that of Scudder (1889) when he presented keys for the identification of butterfly eggs. A few other groups, especially aquatic, have been considered in key form, among which may be cited the key to eggs of Hydrophilidae by Richmond (1920). Mosquito eggs have been keyed by Mitchell (1907) and others, and those of sand flies (Phlebotomus) by Howlett (1916). Heidmann (1911) has considered, in some detail but without keys, the eggs of Hemiptera.

Some Important Keys for the Identification of Larvae

No keys are available and little is known concerning the immature stages of the primitive insect orders Thysanura and Collembola. In those orders having a direct or gradual metamorphosis, of which the young are known as nymphs or naiads, a number of keys are available, especially for aquatic insects. Keys to Holometabolous forms are more numerous but many are still untouched. It is the hope of the writer to publish soon a complete bibliography of these works. Here mention is made only of the most comprehensive keys in each of the principal orders. For a complete citation of the papers listed, the reader is referred to the Zoölogical record of corresponding date.

In the Orthoptera no American keys are available, but the work of Criddle (1926) includes good figures and useful descriptions of grasshopper nymphs. May-flies are difficult to identify when immature. Important keys to special American groups are those of Needham (1905), Clemens (1913 and 1915), Murphy (1922), Walley (1930), Needham and Needham (1927), Ide (1930), and McDonnough (1931).

Many keys to Odonata have been published; the more comprehensive and recent are those of Garman (1917 and 1927), Needham and Needham (1927), Howe (1918, 1922, and 1925), Needham and Haywood (1929). Walker has published separate keys to many genera.

The Plecoptera have not been well worked. Frison (1929) has worked up keys to winter stone-flies and there is to be published soon a comprehensive work by Claassen which will appear as a Thomas Say Memoir of the Entomological Society of America. Needham and Needham (1927) have produced keys to genera.

No American keys to Thysanoptera are available but Priesner (1926) has a key to those of Malayian forms. Hemiptera are worked in many aquatic groups. The only terrestrial species worked up are the Pentatomoidea (Hart, 1919).

Neuroptera are better known in the aquatic species. Smith (1922) has given us a key to Chrysopidae. Comprehensive keys to families of Coleoptera are those of MacGillivray (1903) and Rymer-Roberts (1930). An important work on this order by Böving and Craighead is now in press. Space can not be taken to list the many keys to individual families.

In the Trichoptera important works are those of Betten (1901), Krafka (1915), Lloyd (1921), Sibley (1926), and Iwata (1928), the last citation being a key to Japanese species.

In the Lepidoptera, the most important and comprehensive keys to the order of American species are those of Fracker (1915) and Forbes (1923). Many keys are available for families and genera.

In the order Diptera are to be found many keys to lesser categories. The only comprehensive work is that of Malloch (1917), which treats of the order exclusive of Pupipara. A number of works on aquatic species are known and a few terrestrial families have been keyed.

Immature stages of the Hymenoptera are notably untouched; except for the works of Yuasa (1922), Bird (1927), and Middleton (1922) and a few earlier workers on the Tenthredinoidea, the order is practically untouched.

Keys for the Identification of Pupae

Although there is less need for diagnostic keys to pupae than to larvae, at times they are helpful. Only a few groups have been so worked. Except for Mosher's (1916) key to the pupae of Lepidoptera, no other work deals with the entire order. Other papers by Mosher on lepidopterous pupae were published in 1914, 1917, and 1918. Other keys to Lepidoptera are Heinrich (1919) on European Corn Borer allies, Hutchings (1924) on Cossidae, Packard (1905) on Ceratocampidae, Hart (1896) on Pyralidae, and Forbes (1910 and 1923).

The keys to coleopterous pupae are practically negligible. Satterthwaite has recently published (1931) a key to the genus Calendra. More are available for Diptera, especially the works of Green (1921 and 1925) on Pupipara and the numerous small keys to Culicidae. As far as the writer is aware, no keys to pupal Hymenoptera are known.