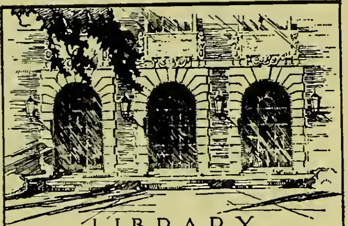

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THE EXTERNAL MORPHOLOGY AND POSTEMBRYOLOGY OF NOCTUID LARVAE

WITH EIGHT PLATES

BY

LEWIS BRADFORD RIPLEY

Contribution from the
Entomological Laboratories of the University of Illinois

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THESIS

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INTRODUCTION

The principal object sought in this work is to investigate the value of certain more or less neglected lines of evidence as a source of phylogenetic information. Such evidence has been applied to the Noctuidae for the purpose of throwing light upon our knowledge of the structural and biological relationships within the family. It has also been our aim to perform the necessary studies preliminary to the making of natural tables for the identification of noctuid larvae.

There are four kinds of evidence contributing to our knowledge of the phylogeny of animals: comparative anatomical, recapitulative, paleontological, and biological. Heretofore the systematic entomologist has concerned himself almost entirely with the first of these, the second remaining either uninvestigated or uninterpreted, the third presenting a relatively scant amount of material, and the last offering a virtually untouched field of somewhat uncertain possibility. Not only has the worker on the taxonomy of insects practically confined himself to anatomical evidence, but he has, until quite recently, based his classification solely on the structure of adult insects. Within the last decade a few excellent researches on the classification of immature insects, such as Fracker's upon lepidopterous larvae, Howard, Dyar, and Knab's upon mosquito larvae, Edna Mosher's upon the taxonomy of lepidopterous pupae, and Malloch's studies upon immature Diptera, have demonstrated beyond a doubt the value of a morphological study of immature insects as a source of phylogenetic information.

The study of the ontogeny of insects may be conveniently divided into embryology and postembryology. The latter deals with development after hatching from the egg. It regards the larva as a free-living embryo, and the pupa as representing a highly specialized stage corresponding to a larval stadium. We may, then, speak of larval or pupal postembryology.

Since the earlier embryonic stages of insects must recapitulate, so far as the law is manifested, conditions in phylogeny prior to the appearance of insects, the taxonomist must look to the older embryonic stages, which have usually not been studied, and to the postembryonic development for recapitulative evidence. As might be expected from their highly adaptive nature, pupae reveal the working of recapitulation to a less marked extent than do larvae. Comstock, however, based his hypothetical ancestral wing venation upon the pupal wing of Hepialus, and Dr. Edna Mosher found that certain wingless female moths have pupal wing-pads. In general, larval postembryology may reasonably be regarded as the principal source of recapitulative evidence to be applied within families or smaller groups. A study of the later embryonic stages may, on the other hand, be expected to throw light upon the relationships between families and orders.

Biology, although never serving as a basis for classification, under our present system, quite frequently furnishes evidence of a corroborative nature. For example, the peculiar scattered distribution of Peripatus is regarded as an indication of great phylogenetic antiquity. Physiological life-history in relation to taxonomy has been studied but little. Since various types of life-history are often found within closely related groups, no marked correlation is generally evident; however, when the evolution of life-history becomes better understood, it seems quite possible that our sources of phylogenetic knowledge will be further supplemented by a study of physiological life-history.

This consideration of the sources of our taxonomic knowledge with reference to their development in entomology may be summarized thus: the comparative morphology of the immature stages presents a relatively new field of well established systematic value; recapitulation offers a practically unexplored source of information of considerable promise, and biology may yield valuable evidence from the taxonomic point of view.

In a systematic treatment of an unsatisfactorily classified group all evidence available should be sought. It is to be expected that neglected sources of information will first be called into use in those difficult groups where the morphology of the adults alone has not been sufficient to bring about a satisfactory understanding of relationships. The Noctuidae represent such a group. With its 3500 North American species, its many ill-defined genera, its striking structural uniformity, and its large number of extremely variable species, we are not surprised to find that systematists have had considerable difficulty with this family. A large proportion of the misnamed and unnamed Lepidoptera in collections belong to the Noctuidae. Its general importance is probably not surpassed by that of any other family of insects, containing, as it does, about one-half of the described Lepidoptera of North America. The great economic importance of the Noctuidae needs only to be mentioned.

It is hoped that the following contribution to the larval postembryology, larval morphology, and general biology of the Noctuidae may not only demonstrate the general value of these more or less neglected sources of phylogenetic evidence, but may also present, in a preliminary manner, their application to the solving of some of the many problems of the evolution of structure and habit within the family.

LARVAL MORPHOLOGY

Noctuid larvae, with the exception of a few genera, are characterized by their marked uniformity of structure. Of these the genus Acronycta and its allies, whose larvae resemble those of the arctiids, with their characteristic tufts of setae, has been treated by Dyar to the number of about fifty species. The larvae of certain other genera look like those of the Geometridae, lacking one or two pairs of larvapods. For the greater part, however, noctuid larvae are uniform with regard to most of the characters used by Fracker in his key to lepidopterous larvae. The position of body-setae, for instance, the taxonomic value of which was early pointed out by Dyar and which plays an important rôle in Fracker's work, is very nearly uniform thruout the family. The same may be said of the arrangement of the crochets. Certain head-structures, however, first emphasized by Forbes, are variable within the Noctuidae. Crumb, in his key to cutworms injurious to tobacco, used various types of skin-sculpture, the microscopic structure of the cuticle of the body. The conspicuous variation in the number of larvapods has, of course, long been known. With the exception of Dyar's monograph of Acronycta and its allies, and Crumb's artificial key for the identification of fourteen species of tobacco cut-worms, we have no works dealing with the classification of noctuid larvae. Fracker, however, gives characters for separating the family from all others but the Agaristidae. He divides it into four groups, all of which are listed in different places in his table. The following morphological study has been made to determine the taxonomic value of the structural variation which this family exhibits in its larvae, as well as to provide the basis for a post-embryological study of the group.

FIXED PARTS OF THE HEAD

Since the structure of the head (Figs. 1–17) of noctuid larvae does not differ fundamentally from that typical of the entire order, the morphological treatment which follows applies for the most part to lepidopterous larvae in general. The epicranial suture assumes the form of an inverted Y (Fig. 2) with the stem following the dorsal portion of the meson and the two arms extending ventrolaterad on either side. Since the epicranial stem represents the median line of dorsal closure in the embryo, the arms being derived from the closure on either side of the so-called unpaired appendage, the homology of this suture with that of the larvae of all other orders is unquestionable. In nymphs or adults of the Orthoptera the antacoriae divide each epicranial arm into two portions, the ventral being known as the fronto-genal suture. These are homologous, therefore, with the ventral portions of the epicranial arms of larvae. The two large sclerites which are separated by the epicranial stem, lie dorsad of the arms, comprise the greater part of the head-capsule, and make up the vertex. Its apparent large size in larvae is due to the absence of compound eyes. Since the occipital sutures are undeveloped, the caudal extent of the vertex is indefinite. It has been customary to refer to the fused vertex, occiput and postgenae as the epicranium. The vertex of lepidopterous larvae does not differ from larval vertices generally in bearing the ocellarae, and antennarae. The antennarae, which bear the antennae, are distinct in the noctuid larvae, a generalized condition found typically in the adults of the more primitive orders.

There is but one marked indication of fundamental structural specialization visible externally on the vertex of lepidopterous larvae. The adfrontal sutures, which have developed solely in the larvae of this order, run subparallel to the epicranial arms, dividing the vertex on each side into two portions, the mesal one being the well known adfrontal area. Heretofore, these secondary adfrontal sutures have been generally regarded as the epicranial arms and vice versa. Heinrich agrees with Dampf in his assertion that the adfrontal sclerites are a part of the front, regarding the sutures between the front and adfrontals as secondary infoldings. Both of these investigators were aware that the pretentoria invaginate at the bottoms of these infoldings, a point demonstrated by Berlese one year previous to the publication of Dampf's paper on case-bearing larvae. The interpretation of these authors necessitates the supposition that the pretentorinae were originally located on the front some distance mesad of the epicranial arms and that they were subsequently involved by this supposedly secondary infolding, which resulted in their present position. We shall present evidence which appears to show conclusively that the mesal sutures are the epicranial arms and that the lateral ones are secondarily developed.

In the first place, the pretentorinae of the larvae of other orders, so far as we know, are associated with the epicranial arms. They are rarely situated on the front removed from primary sutures. Moreover, the epicranial stem in lepidopterous larvae, unquestionably a primary structure, is followed internally (Fig. 1) by a deep infolding, which is continuous with and exactly like those of the mesal sutures which bear the pretentorinae. It seems highly improbable that the former suture should be primary and the latter secondary, when their infoldings are continuous. The fronto-clypeal suture, also a primary suture beyond a doubt, is expressed internally by a similar infolding. This suture extends between the mesal sutures and does not traverse the adfrontal sclerites terminating at the lateral sutures, as it should if the lateral sutures were the epicranial arms. Postembryological evidence offers still stronger support to this interpretation. The lateral sutures are not distinct in noctuid larvae in instars earlier than the penultimate. So far as we have been able to ascertain the earlier instars of all lepidopterous larvae lack the adfrontal area, although this point appears to have been generally overlooked. It is not always distinctly separated from the vertex even in full grown larvae. The accurate morphologist, Berlese, shows no trace of it in his figures of the ectal and ental aspects of the larval head of *Acherontia.* These are secondary structures appearing relatively late in their postembryonic development. Therefore, they cannot be homologous with the epicranial arms, which represent the lines of dorsal closure on each side of the so-called unpaired appendage in the embryonic development.

The triangular front between the epicranial arms is separated from the postclypeus by a more or less distinct frontoclypeal suture. This suture in the more primitive insects terminates near the precoilae. In lepidopterous larvae this suture has migrated dorsad, its ends joining the epicranial arms at points considerably removed from the articulations of the mandibles, a condition frequently found in specialized insects. Whereas the position of this suture probably denotes specialization, its well developed condition, on the other hand, is to be regarded as a generalization, since it is frequently lost in both larvae and adults of various orders. It is sometimes not traceable externally in noctuid larvae and is rarely as prominent as the clypeal suture, which marks the division between the preclypeus and the postclypeus. This division also denotes a primitive condition, as is evident from a general study of insect morphology. The labrum of the noctuid larva always presents the bilobed shape characteristic of lepidopterous larvae.

The caudal aspect of the lepidopterous larval head shows pronounced and varied specialization. It seems odd that this region, which perhaps offers points of greater morphological interest than any other part of the head, should have been so utterly neglected. Prominent secondary sutures extend dorsad from the mesal edge of the postcoilae, marking the location of deep infoldings. The position of these sutures with reference to the postcoilae precludes their being homologous with the occipital sutures, which are always situated laterad of the postcoilae and are universally borne by the postgenae. It is convenient to refer to the region mesad of these sutures as postgenae, although it should be remembered that the lateral extent of the true postgenae is undefined, the occipital sutures being undeveloped. In all but certain of the more specialized orders the postgenae in both larval and adult insects are widely separated by the cervix. In lepidopterous larvae there has been a tendency toward the extension mesad and an ultimate fusion of the postgenae, resulting in a separation of the labium from the cervix. Consequently, this appendage is finally borne by the postgenae instead of by the cervix, which represents the segment to which the labium morphologically belongs. A parallel specialization is exhibited by the adults of certain aculeate Hymenoptera.

In the more generalized lepidopterous larvae of the Cossidae, Pyralididae, and Tortricidae examined, a few species of each, we find the postgenae quite widely separated (Figs. 3, 4, 5). Young larvae of *Thyridopteryx ephemeraeformis* from the first to the fourth instars (Fig. 6) also reveal this condition, although these sclerites meet on the meson in the full-grown larvae (Fig. 7), a recapitulation to be treated later in the section on postembryology. Secondary sclerites are sometimes formed by a chitinization of this membrane (Fig. 4). Frequently each postgena (Fig. 5) is divided by an oblique secondary suture. In hesperiid larvae the postgenae are exceptionally widely separated, the area (Fig. 8) between them being uniformly and heavily chitinized, resembling the gula of the Coleoptera. Larvae of several families have retained but a narrow strip of cervacoria between the postgenae. In representatives of the Sphingidae, Saturniidae, Lymantriidae, and Pieridae examined, they are separated only by a suture. The Noctuidae (Figs. 9-12) present the same condition most frequently, although a narrow strip of coria often persists.

In certain of the more specialized families, notably the Saturniidae and Noctuidae, the cervix caudad of the postgenae has developed a varying number of folds, some of which have become flattened one onto the other, chitinized, and cemented to the postgenae, where they now resemble sclerites. This peculiar condition appears to reach its height in the former family, some of whose larvae have several such folds superimposed upon one another and apparently fused into a thick, heavily chitinized sclerite, which lies flat upon the postgenae. In the Noctuidae the most cephalic fold only is chitinized and fastened down in this manner, where it assumes a bilobed form. The dorsal portion of this cervical fold is covered by the membranous one which follows it, exposing the brown, flat, crescent-shaped ends of the bilobed first fold, so that they appear as divisions of the postgenae, one on each side of the meson.

In the Noctuidae part of the secondary infolding which extends around the dorsal portion of the margin of the foramen separates on each side a crescent-shaped secondary sclerite (Fig. 9) from the remainder of the vertex. The pleural portion of the neck-membrane is fastened to this sclerite.

ENDOSKELETON

The tentorium of lepidopterous larvae (Figs. 3, 13, 14) is very greatly reduced. It is unfit for the function of support generally performed by this structure. In correlation with this reduction a large number of large, heavily chitinized infoldings have developed along certain primary and secondary sutures, comprising the sole endoskeleton functioning as such, the tentorium being not only very vestigeal but to a large extent membranous and flimsy. These secondary infoldings will be referred to as parademes, a term used to designate secondary infoldings in general.

In the order Orthoptera the pretentorinae are always found at the ends of the fronto-clypeal suture, this being probably the most generalized condition. These invaginations have migrated dorsad along the fronto-clypeal suture for a considerable distance in the aculeate Hymenoptera. A similar specialization has developed in the lepidopterous larva in a parallel manner, the pretentorinae being located on the epicranial arms (Fig. 13) usually nearer to the dorsal end of the front than to the clypeus. It is of interest to recall that the condition of the postgenae in these larvae is also parallelled in important respects by that of adult Hymenoptera. The position of the pretentorinae is not externally marked, since they invaginate at the bottoms of the epicranial parademes, large infoldings, which extend throughout the entire length of the epicranial suture. Each ribbon-like pretentorium extends caudad to a metatentorium, which it joins near the dorsal end of each secondary postgenal suture. The pretentoria are usually chitinized for the greater portion of their length. The metatentorina is also located at the bottom of a deep parademe, one of which arises on each side of the ventral portion of the margin of the foramen. These invaginations are always to be found just mesad of a large tendon which is supported by the parademe. The metatentoria are short and membranous and are located near the dorsal ends of the secondary postgenal sutures. The corpotentorium persists as a fine thread originating just caudo-mesad of the point where the pretentorium and metatentorium of each side join and extend across the ventral portion of the foramen between the metatentoria. In the more generalized families it is often thicker and sometimes heavily chitinized. It assumes the appearance of a delicate white thread in the Noctuidae. We are thus amply justified in concluding that the tentorium of lepidopterous larvae is very highly specialized, being not only vestigial, but also unusual in position and form.

Heavily chitinized parademes extend the entire length of the epicranial, fronto-clypeal and secondary postgenal sutures and along the dorsal and lateral portions of the margin of the foramen. The latter parademe is divided on each side by a short suture into a ventral and a dorsal occipital parademe. The ventral ones are the deepest of all of these infoldings, bearing the metatentorinae and the tendons already mentioned. They are the only ones not heavily chitinized. The fronto-clypeal parademe is not so well developed as the others. These secondary structures serve for support and for the attachment of muscles. They have been developed in correlation with the specialization by reduction which is characteristic of the tentorium of lepidopterous larvae.

The relative length of the epicranial stem presents more conspicuous variation than any other character in these larvae, except, of course, the number of uropods. In the majority of noctuid larvae the length of this suture is not strikingly different from that of the front. In certain Agrotinae, however, it is reduced to its adfrontal portion and in *Chamyris cerintha*, Erastrinae, it is markedly longer than the front, all gradations (Figs. 2, 15-17) between these extremes being found. The shortening of this suture, where it occurs, has been brought about apparently by a splitting apart of its two sides at the caudal end, the area between these separated sides being taken up by the coria continuous with the cervanotum. The triangular area thus formed is known as the vertical triangle, although morphologically it is composed of cervacoria and a part of the epicranial suture greatly widened. The apex of this triangle is usually heavily chitinized. The shortening of the epicranial stem is correlated with a general shortening of the cephalic aspect of the head, which has probably been induced by a change in the position of the head from the typical vertical one with the mouth-parts directed ventrad to a somewhat horizontal one with the mandibles directed cephalo-ventrad or cephalad in extreme cases.

The shape of the clypeus (Fig. 2) presents some variation, the frontoclypeal suture being either straight or curved upward in the middle more or less prominently. The relative widths of the preclypeus and postclypeus also vary to some extent. These characters appear to be of generic value. The width of the labrum relative to that of the clypeus and the depth of the labral cleft present characters applying to smaller groups. This sclerite is rarely nearly divided into two parts as in an undetermined species of Catocala.

The position of the ocellarae, although presenting no striking differences within the family, offers some convenient characters evidently applying chiefly to groups of species, although constant specific differences have been noticed in certain genera. In the majority of cases the distance between ocellarae 1 and 2 is distinctly less than that between 2 and 3, the line 1-2 often equalling one-half of the line 2-3. Sometimes 1 and 2 are nearly contiguous.

The coloration of the head is principally cuticular and, therefore, practically permanent in alcohol. Such markings offer much variation within the family, often providing easily recognizable specific characters. The general scheme of coloration is usually constant within a genus. In some species it differs markedly according to the instar. Individual variation is sometimes considerable. The entire head capsule is uniformly colored in but relatively few species. In these it ranges from light brown to nearly black according to the species. Often the vertex is darker than the rest of the head, the preclypeus especially being lightly pigmented. This condition is widely distributed throughout the family. A peculiar reticulate fuscous marking is frequently found on the vertex, where it usually stands out prominently against the light brown background.

In 1896 Dyar introduced the first system for designating the setae of the lepidopterous larval head. He numbered those of each sclerite with Roman numerals from dorsal to ventral margin, departing from this scheme slightly on the ventral portion of the vertex. More recently Dampf has emphasized the taxonomic importance of the head setae in the Psychidae and their allies. He divided the head-setae into groups on the basis of the tendency exhibited to vary their position in the larvae of different species by groups rather than individually. This interpretation led him to refer to them according to these groups. In his study of microlepidopterous larvae Heinrich followed the system of Dampf, which he supplemented by numbering the setae, pointing out the fact that these group migrations are due to the contracting or expanding of the parts of the head-capsule. Fracker and Forbes designated the setae of the head by the Roman numerals of Dyar. Forbes also numbered the labral setae.

In devising a system which may be applicable to the study of the homologies of larval setae throughout the order, and very possibly throughout the larvae of different orders, it seems preferable to name them after the sclerites on which they occur rather than according to certain groupings which are not well understood, except perhaps in the few families studied by Dampf and Heinrich. The latter author disagrees with the former as to the group in which a certain seta should be included. It seems likely that in various families in which the trend of specialization has been divergent this grouping relation may be altogether different. We find in the Noctuidae, for example, certain setae within one of Dampf's groups exhibiting wide variation in position with reference to each other. The system of Dyar and Forbes, with minor changes, has, therefore, been followed in this paper.

These setae may be conveniently designated by the abbreviation for the sclerite bearing them followed by an Arabic numeral. Thus VI refers to the seta typically located furthest dorsad on the epicranium. The abbreviations, *o*, *v*, *a*, *f*, *c*, and *l* stand respectively for occiput, vertex, adfrontal, front, clypeus and labrum. A few minute setae hitherto disregarded, although of general occurrence, have been named. This same system of naming has been applied to the ocellarae, *oc* being the abbreviation used.

MOVABLE PARTS OF THE HEAD

The antennae of lepidopterous larvae appear to be generally uniform in structure and primary setal armature. That of *Cirphis unipuncta* (Figs. 19-21) may be regarded as typical for the order. The antennaria bears a wide antacoria, which may be infolded or extended, permitting the antenna to be either protruded for its full length or retracted into the head so that only the distal portion is exposed. The first two segments are large, the third much smaller and the fourth very minute. These are separated by well developed coriae allowing free movement at the joints. The distal end of the second segment bears five primary setae of characteristic form, which may be named by combining Roman and Arabic numerals, the former referring to the segment, the latter to the seta. The seta III is the only one of these with a normal form; II 2 is extremely long and attenuate, being longer than the entire antenna; II 3, II 4, and II 5 are conical, II 4 being very minute. The distal end of the small third segment bears three conical setae, III 2 being midway in size between III 1 and III 3. A single attenuate seta is carried by the minute fourth segment.

Forbes has shown that the first three segments vary in relative size and that the proximal one sometimes bears secondary setae. The figures of Dampf and Tragardh are the only detailed ones of the antennae of caterpillars known to the author. The former investigator directs attention to the difference in the relative size of the conical setae in the Psychidae, where the condition is normal, and in the Talaeporiidae and the tineid *Adela degeerella,* where these setae are unusually large. Tragardh figures a most interesting series, representing the reduction of the antennae of leaf-miners. The minute size of the distal segment together with the great development of the third and its setae is apparently responsible for his failure to recognize this last segment as such, although it is distinctly shown in his figures. Most of the primary setae named can be identified even in these aberrant antennae. Packard's figures of the larval mouthparts of Eriocephala appear to show four well developed segments, a unique condition for the order.

Within the Noctuidae there appears to be no variation in the antennae of taxonomic value, except perhaps the amount of chitinization. This varies from very slight to very heavy, the heavier chitinization being correlated with a darker color. The habit seems to bear no relation to the amount of chitinization, which varies according to the genus or sometimes within a genus.

The mandibles of caterpillars have been but little studied, accurate figures of them being scarce in literature. They are joined to the head immediately mesad of the antennae by a narrow mandacoria and to the lateral margin of the maxillae by a wide maxacoria. A large socket, the preartis, on the cephalo-dorsal corner serves for the articulation with the precoila and a large globose condyle, the postartis, on the opposite corner fits into the socket of the postcoila. A small caudal extensotendon and a large cephalic rectotendon provide attachment for the abductor and adductor muscles respectively. The left and right mandibles are usually unlike, being formed so that the dentes of one fit into the emarginations of the other. Each mandible bears two large primary setae on its lateral aspect.

The great majority of caterpillars present no striking variation in the maxillae, although a few exceptional conditions have been recorded. Tragardh has discussed certain modifications found in those of the leaf-miners. Packard's figures of the larval mouth-parts of Eriocephala represent three free segments of the maxillary palpus instead of the two found in all families other than the Micropterygidae. Differences exist in the relative size of the segments in various families, as shown by the figures of Forbes. The noctuid larval maxilla (Figs. 24-25) is typical for the order, presenting the highly specialized condition found in that of all caterpillars.

The labium of lepidopterous larvae exhibits a degree of specialization unequalled even by the maxillae. The homologizing of its parts consequently presents a difficult problem. Its condition in the Noctuidae appears to be fairly typical for the order, although certain types of spinneret frequently occur within the family which are not generally found in caterpillars. The labium lies between the two maxillae, its proximal two-thirds being joined on each side to the cardo and stipes by a labacoria, which has been reduced in width to a mere suture. The submentum is large, as it is in the larvae of other orders, and is for the most part usually membranous or slightly chitinized. It is broadly attached to the ventral margin of the postgenae for the entire width of its proximal end by a narrow strip of membrane. This specialized condition has been brought about by the extension mesad of the postgenae, so that they separate the labium from the cervix, which typically bears this appendage in insects. The narrow strip of membrane which connects the postgenae and the submentum is evidently a portion of the cervacoria, which has become separated from the rest by the unusual development of these sclerites. The mesal portion of the submentum is occasionally not borne by the postgenae, since in many species they do not extend to the meson. A subtriangular sclerite located in each latero-proximal corner of the labium is of very frequent occurrence throughout the order and is apparently always present in the Noctuidae. Berlese does not figure these in his drawing of the mouth-parts of Acherontia, evidently considering them as secondary, if they occur in this species. Dampf refers to them as *postmentalstücke*, a term previously employed by Verhoeff, also regarding them as secondary, while Forbes, on the other hand, believed them to constitute the submentum, although they are not represented in several of his figures of the labia of caterpillars. The interpretation of the latter investigator leads him to consider as mentum the large membranous region regarded as submentum by Berlese, Dampf, and the author. The corresponding region in the coccinellid larvae is referred to as submentum by Gage and that of the saw-fly larva figured by Berlese and Yuasa is so labeled. The absence of these sclerites in many lepidopterous larvae together with the fact that they are generally widely separated by the membrane and never constitute a single piece indicates that they represent merely two strongly chitinized areas of the submentum. They seem to have developed in correlation with the arms of the subcardines, whose chitinized portions lie adjacent to these plates of the submentum. The arms extend beneath the chitinized areas of the submentum and serve for the attachment of muscles, hence the advantage of these chitinous plates in the membrane adjacent to them. The membranous portion of the submentum always bears a pair of large setae.

The mentum is usually reduced or undifferentiated in specialized labia, the submentum being well developed and the stipulae always present. In caterpillars the mentum is not present as a distinct area, being presumably fused with the stipulae, which is the condition apparently found in all coleopterous, trichopterous, and saw-fly larvae. In those of the Lepidoptera the stipulae usually consist of a proximal chitinized ring and a distal membranous portion, which bears the palpigers and the vestigial glossae on which the spinneret is located. This area is referred to by Forbes but not named, whereas Berlese and Dampf consider it as the mentum. Just proximad of the proximal end of the spinneret on the caudal aspect there is a pair of minute setae.

The chitinized portion of the palpiger is typically an incomplete ring, its mesal and distal portions being membranous. Dampf has suggested that this structure may represent the basal segment of the palpus, in which case the palpiger must be regarded as undifferentiated. It varies much in width and shape throughout the order, resembling in Enocrania and Adela a basal segment of the palpus. In the Noctuidae it is not closely associated with this appendage, assuming the form of a semicircular sclerite lying in the membrane distad of a stipula. The mesal end of the caudal aspect of this semicircular sclerite is provided with two large sensoria. A reduction of the chitinized area mesad of the sensoria, which has frequently taken place throughout the order, has left them on the mesal end of the sclerite, where they remain surrounded partially or entirely by chitinized rings, the remnants of a more general chitinization. In the Noctuidae, where this reduction is usually marked, the distal sensorium is rarely completely surrounded, the ring being typically broken on its mesal side.

The two-segmented palpus has been correctly named by previous workers. The membrane which bears it within the semi-circular palpiger is generally wide, allowing free movement of this appendage. Its proximal segment is cylindrical, varying from stout to slender, the former shape being the most usual in the order and typical for the Noctuidae. It bears a terminal seta usually laterad of the distal segment, a minute cylinder situated on the membranous end of the proximal segment. A terminal seta is also borne by the distal segment. These two setae are apparently of universal occurrence in caterpillars.

SPINNERET

The spinneret is located on the mesal portion of the membrane on the caudal aspect between the palpigers. The cephalic and lateral portions of its proximal end are surrounded by a semi-circular sclerite of varying width and shape, resembling the palpiger, although much smaller. A pair of sensoria are borne on the caudal aspect of this structure usually at its mesal ends. These sensoria are much smaller than those of the palpiger. A fold of membrane often extends distad from this sclerite surrounding the proximal end of the spinning organ, the tube through which the silk is extruded. This fold is usually much wider on the cephalic aspect, where it may assume the form of a long plate reaching nearly to the end of the spinning organ. Occasionally it is entirely chitinized, when it is indistinguishable from the proximal sclerite. The spinning organ varies extensively, presenting a great diversity of size, form, and modification. It ranges from entirely membranous to largely chitinized, from very long and tubular to short and flat. The silk-duct opens at its distal extremity.

Wide differences of opinion have been expressed as to the homology of this peculiar organ. A number of workers, represented by Packard, regard it as a modified hypopharynx, whereas Berlese and Dampf believe it to be formed of the fused glossae and paraglossae, the latter investigator even venturing to homologize the proximal sclerite and fold with the paraglossa and the spinning organ with the fused glossae. It seems very probable to the author, on the other hand, that this structure has developed secondarily. Those who regard it as hypopharynx appear to be misled by insufficient data. The silk-glands of lepidopterous larvae have reasonably been supposed to be the homologues of the salivary glands of the adults. Lucas subscribes to the same homology in the Trichoptera. The salivary glands of adult insects, so far as known to these investigators, opened at the base of the hypopharynx. Therefore, they reasoned, the silk-glands of caterpillars, which they regarded as the homologues of salivary glands generally, would presumably open on the hypopharynx, giving rise to the belief that this structure had been modified into a spinneret. MacGillivray has shown, however, that the salivary ducts of the Entopteraria open on the glossae of the labium, wherever these structures can be identified, and not at the base of the hypopharynx as in the Exopteraria, which was evidently the only condition known to these earlier workers. It seems questionable, therefore, whether these glands are homologous in the two superorders. However this may be, no evidence remains in support of the old view that the spinneret has arisen from the hypopharynx, which, as will be shown later, is otherwise represented in lepidopterous larvae.

The position of the spinneret is that normally occupied by the glossae and paraglossae. It may represent the fusion of either or both of these lobes, altho its mesal position indicates that it is derived only from the glossae. Dampf's homologies, where he regards the paraglossae as represented by the proximal semicircle and the alaglossa by the spinning organ are, therefore, open to no serious objection by those who regard the spinneret as a primary structure.

Certain biological considerations lend weight to the view that the spinneret has developed secondarily, being without homologue in the typical insectean labium. Since the spinning habit appears in insects only in the larvae of Entopteraria, except in the Embiidae, where the glands open on the legs, it is evidently a secondary acquisition, which was not present in ancestral insect. The widespread occurrence of silk-spinning, however, in the larvae of Lepidoptera, Trichoptera, Hymenoptera, and Diptera seems to justify the conclusion that the common ancestral larva of these orders spun silk, although this habit has been lost in certain groups of each order, as Wheeler has shown it to be in certain families of ants. This acquisition has apparently developed furthest in the Lepidoptera, although it is possible that it was at one time equally extensive in the other orders mentioned, having been subsequently reduced. So far as known the spinneret is well developed only in caterpillars, the opening of the silkduct in silk-spinning hymenopterous, dipterous, and trichopterous larvae being without any well developed spinning organ and usually represented by a small aperture located near the distal end of the labium and surrounded by a chitinized ring. The glossae or paraglossae are rarely, if ever, well developed in these larvae. The condition of these structures leads us to suppose that they were probably vestigial in the ancestral larva of these orders, from which we may reasonably conclude that they are not well developed in caterpillars. The spinneret, therefore, is apparently a secondary development which evolved in correlation with the extensive spinning of silk. The proximal semicircular sclerite in lepidopterous larvae appears to correspond to the chitinized ring around the aperture in other orders and was apparently derived from the vestigial glossae. Although these conclusions are by no means certain, they seem to be the most reasonable on the basis of the evidence available.

The variations presented by the labium and their taxonomic value in the Noctuidae will now be considered. This appendage offers more extensive variation in caterpillars than any other structure, both in the form of its sclerites and of its distal lobes, especially of the spinneret, which exhibits the most diverse conditions. As Forbes has shown, the sclerites of the submentum present considerable differences in the extent of their development. In the Noctuidae, however, they do not vary markedly, being typically as represented in *Cirphis unipuncta* (Fig. 24). The chitinized areas which occasionally appear in the membranous portion of the submentum in other families are rarely met with in the noctuids. The width and shape of the chitinized portion (Figs. 24, 28, 31) of the stipulae varies considerably according to the genus. Much generic and some specific variation is also presented by the chitinized portion (Figs. 26, 28, 31, 38, 44) of the palpiger. In the noctuids this sclerite exhibits a comparatively reduced condition and never appears as the basal segment of the palpus as it does in some other families. The long and slender type of palpus occurring in a few groups has not been found in the Noctuidae, this appendage exhibiting the stout form most common in the order. It varies, however, according to the genus or to larger groups in relative width and length and in the proportional size of the two segments. The setae of the palpus present differences within the family in form, size, and position. The one borne on the distal end of the proximal segment is usually located laterad of the minute distal segment throughout the order, although in certain noctuid genera it has migrated around the cephalic side of the distal end of the first segment until it appears mesad of the terminal segment, as in *Lycophotia margaritosa* (Fig. 38), a process revealed by postembryonic development. This is the only instance known to the author where a seta of the head or mouth-parts appears to have migrated by itself uninfluenced by movements of the cuticle. Forbes notes and figures an exceptional condition in an unnamed species of Catocala where there is apparently an extra small basal segment of the palpus. A similar development is often present in the Catocalinae due to the globular shape of the coria proximad of the basal segment. The situation figured by Forbes is evidently due to the secondary chitinization of this coria, the distal portion of the labium of this species exhibiting an unusual amount of chitin generally for a noctuid larva.

In spite of the very extensive variety of form offered by the spinneret, the amount of investigation which has been performed upon this interesting structure is surprisingly meager. Beyond Lyonet's figures showing the spinneret of *Cossus cossus*, those by Forbes of a species of Catocala and of *Thyridopteryx ephemeraeformis*, two by Dampf showing the mouth-parts of case-bearing larvae, and a short series of the labia of leaf-miners by Tragardh, there are no detailed representations of the spinneret known to the author. Yet this organ probably presents a greater range of variation than any other structure of lepidopterous larvae. The proximal semicircular sclerite varies much in width and shape, as Forbes has shown. It is typically broken on the caudal aspect, although its mesal ends (Fig. 31) are often joined by secondary chitinization, as in *Polia renigera*. This condition may exist in some groups as a primary one, since postembryological evidence indicates that the semicircular sclerite was originally a complete ring, its reduction having begun on the meson and proceeded laterad. Its shape varies much within the family affording generic and specific characters. The proximal fold, which assumes a great variety of forms within the order, also exhibits marked differences within the family, ranging from membranous and rounded, the more usual condition, to chitinized, long and pointed, when it serves as a support (Fig. 32) for the spinning organ, which lies caudad of its caudal surface. This is the situation found by Dampf in the psychid genus Eumeta, which presumably led him to believe that this structure represents the paraglossae.

In three European species of Hepialus examined the spinneret is exceptionally long, tubular, and tapering, almost filiform, extending several times the length of the labial palpi. According to Packard it is well developed in Micropteryx, but his figures of the larval heads of Eriocephala, drawn from a few poorly mounted specimens, fail to show any spinneret. Most commonly throughout the order it is tubular, slightly tapering, truncate, and distinctly longer that the palpi. It is often supported (Fig. 32) by longitudinal chitinized areas, as in *Polia renigera.* In certain groups, notably the Sphingidae, Noctuidae, and Nepticulidae, it is short, flat, and stubby, frequently exhibiting a peculiar fringe (Figs. 26, 38, 39, 45, 46) in the two former families. When of this type in the Noctuidae the spinneret is often emarginate on the sides so that an upper and lower lip is formed, the latter usually being the longer. The lower lip may be deeply emarginate, as in *Cirphis unipuncta* (Fig. 27) or bilobed, as in many Agrotinae. Both lips or the upper one only may be fringed. All stages in the development of the fringe are represented by various species of noctuid larvae. It appears to have developed on the upper lip earliest in phylogeny (Figs. 45, 46) appearing later (Figs. 26, 39) on both surfaces.

With the exception of the subfiliform type of Hepialus, all forms of spinning organ observed in other families are represented within the Noctuidae, this family probably presenting a greater range of variation in its spinneret than any other. In the Agrotinae it is often much shorter than the palpi, flat, with upper and lower lips, and frequently bilobed or fringed, or it may be long and pointed, as in Chloridea. It ranges from long and slender to fairly stout and about equal to the palpi in length in the Hadeninae, being either truncate and fringed, as in *Cirphis unipuncta,* or pointed, as in *Moliana albilinea.* Most commonly it is distinctly longer than the palpi in this subfamily and is apparently never markedly shorter, as it is in the Agrotinae. In the species of Cucullinae, Phytometrinae, and Hypeninae examined it is much longer than the palpi and usually tapering. It distinctly exceeds the palpi in length in the Catocalinae, where it ranges from stout to slender. The spinneret of the Acronyctinae varies from slightly to greatly longer than the palpi, presenting an extensive variety of form. Larger groups of genera or even single genera may be often separated by characters based on the length and form of the spinneret more readily than by any other means. The general type of this organ is usually the same for large groups. Some of the most fundamental and valuable characters for the taxonomic treatment of noctuid larvae are provided by the spinneret. The failure of previous workers to appreciate the phylogenetic significance of its variations has probably been due to its small size, which often necessitates the removal of the labium to allow careful examination. This operation, however, is performed with the utmost readiness by means of a single stroke of a needle.

The types of spinneret within the Noctuidae, unlike those of the mandibles, can be largely correlated with biological characteristics. The amount of silk employed as a protective covering for the pupa varies extensively according to the situation in which pupation takes place, the type of location selected being generally characteristic for the taxonomic group. Noctuid larvae usually pupate either within a cocoon or a subterranean cell. The cocoon may be fairly dense, as in many Acronyctinae and Phytometrinae, to very slight, as in the genus Polia of the Hadeninae. It never approaches those of the Saturniidae in density or in the amount of silk employed, being usually very slight, although often supplemented by foreign matter such as leaves or grass or by setae from the verrucae in Acronycta, where these structures are present. Those which pupate beneath the soil, on the other hand, usually spin but a few threads, as in *Cirphis unipuncta*, or no silk whatever, a condition exemplified by most species of Agrotinae which have been reared by the author.

This reduction in the amount of silk used for a pupal covering is also met with in certain other families, notably in the butterflies, where only a button of silk is spun for the attachment of the cremaster, in the Sphingidae, which usually enter the soil to pupate, spinning little or no silk, and in certain leaf-miners, which, according to Trägardh, have lost this habit in correlation with their protected habitat. The accompaniment of pupation beneath the soil or in similarly protected situations by a marked reduction in the amount of silken covering, appears to be of general if not of universal occurrence. It should be noted, however, that the converse is not true, the naked pupae of butterflies having developed other means of protection than subterranean pupation.

An interesting instance of individual variation in the amount of silk spun is furnished by four larvae of *Polia lorea*. Two were taken on the floor of typical Illinois forest, the other two being collected on the following day on the prairie, about six miles from the nearest woodland. The latter were feeding upon sweet clover, the former upon some plant not definitely known, probably *Geranium maculatum*, but not upon any species of Trifolium, since none was present in the vicinity. The two larvae of the prairie spun fairly dense cocoons, while a mere network of threads covered the pupae of the individuals collected in the forest. All four pupated on the surface of the ground among grass on the same day under approximately the same external conditions. Since both sexes were represented by those of the prairie, the difference in the amount of silk spun was not a sexual one. A question of considerable interest arises as to whether this striking biological variation is to be explained by the direct effect of different food upon the activity of the silk-glands or upon the basis of physiological adjustment to environment, the pupae of the prairie requiring more protection from the sun than those of the forest. Instances of much less pronounced individual variation in this respect have been frequently noted with various species reared.

Contrary to what would perhaps be the natural supposition, the subterranean mode of life frequently exhibited by noctuid larvae, exemplified by the cut-worms, appears to bear no definite relation to the habit of pupation beneath the soil. Larvae which never enter the earth during the feeding period often pupate in earthen cells, while some species showing pronounced subterranean tendencies as larvae always spin slight cocoons among the debris on the surface of the ground. Similarly the Sphingidae, which usually undergo pupation in the earth, are never subterranean as larvae so far as known. The habit of pupation in the soil is a fundamental one which remains constant throughout large groups, whereas the degree of development of the subterranean mode of life in larvae is variable in closely related species.

Caterpillars which spin much silk are generally provided with a long, slender, tubular, tapering spinneret. The short depressed type is apparently found only in those groups whose larvae spin little or no pupal covering. The Sphingidae and Noctuidae which pupate in earthen cells and certain leaf-miners which undergo this process in their mines without spinning silk present this reduced type of spinneret. It has not been found to occur where the spinning habit is well developed. The general accompaniment in the Noctuidae of the short flat spinning organ by the marked reduction or entire loss of silk-spinning is unquestionable. Some species with the long type of spinneret, however, pupate in the soil, as instanced by *Chloridea armigera.* This condition is to be expected in those species whose last instars spin silk during the feeding period. *Sidemia devastatrix* has been observed by the author to spin a cocoon in which to undergo ecdysis, a peculiar habit, which, so far as known, has not been recorded for any other caterpillar, except for certain leaf-miners studied by Trägardh.

The peculiar fringe borne on the distal end of the spinneret has been found only in noctuid and sphingid larvae with subterranean pupae. Although the function of this strange modification has not been definitely determined it seems probable that it is used as a brush to distribute a secretion of the silk-glands over the inner surface of the earthen cell. Examination of the inside of these cells seems to reveal the presence of such a substance. This lining serves perhaps to render the cell waterproof or to prevent it from crumbling. The burrows leading to the pupal cell of *Chloridea armigera* have been observed to be fortified with a similar secretion of unknown origin, although the spinneret of this species bears no fringe. Chapman observed that the thread spun by the flat short spinneret of the earlier instars of the leaf-miner, *Limacodes testudo*, assumed the form, not of a thread but of "a very thin ribbon," indicating that the semifluid silk may issue from the spinneret in different physical states. A microscopic study of the silk of noctuid larvae, as well as an investigation of the comparative morphology of the silk-press promises to throw light upon this question.

Both morphological and biological evidence indicates that the long cylindrical spinneret represents the ancestral condition for the Noctuidae. The development of this type to a very marked degree in Hepialus, the well developed spinneret in Micropteryx, and the general occurrence of the long spinning-organ throughout all caterpillars seem to justify this conclusion. As previously stated, the widespread distribution of the silk-spinning habit throughout trichopterous, hymenopterous, and lepidopterous larvae and its appearance in those of certain dipterous families indicates its development at an early phylogenetic period. Its absence or reduction in members of these orders may reasonably be regarded as a specialization. Since the loss or reduction of this habit in noctuid larvae, which is evidently a biological departure from the ancestral condition, is generally correlated with the short, flat spinneret, we must conclude that this type of spinning-organ is a specialized one derived from the tubular type in correlation with subterranean pupation.

PREPHARYNX

The hypopharynx of caterpillars has been largely neglected, the sole morphological studies of this structure having been performed by Trägardh on the leaf-miners, where it frequently presents a highly modified condition, and by DeGryse, who has written a brief paper on this subject, embracing a number of families. The only detailed figures of the normal hypopharynx of lepidopterous larvae known to the author are those by Dampf of two species of case-bearing caterpillars, and a few by DeGryse. It assumes the form of a large membranous lobe lying cephalad of the labium and continuous with it, and extends dorsad as a rather low mound forming the lower floor of the prepharynx. A narrow sclerite continuous with the chitinized portion of the stipula extends longitudinally on each side of its proximal end, corresponding apparently to the lingula shown by Yuasa. In many noctuid larvae the hypopharynx is distinctly divided into a ventral portion, which follows the general contour of the labium, and a dorsal mound-like part, which resembles the subgusta in the Orthoptera (Fig. 25). Very often this division is not clearly marked, as in Dampf's figure of the psychid Eumeta and in the noctuid *Lycophotia margaritosa.* The question as to whether it is primary or secondary cannot be decided upon the basis of our meager knowledge of the condition, generally found within the order. It is very possible that the dorsal portion may be homologous with the subgusta of the Orthoptera, although the entire structure may represent the hypopharynx, in which case the division must be regarded as secondary.

The hypopharynx typically bears numerous small setae, whose distribution, form, size and number vary greatly within the family, offering excellent generic and specific characters. They are rarely apparently absent, as in Rhodophora and Xylina or may, on the other hand, cover the entire distal portion of the hypopharynx. Frequently the pubescence does not begin immediately cephalad of the labial palpi, leaving a glabrous area in this region, as in Monima, Epizeuxis, and Platyhypena. The setae may be approximately equal in length, as in *Lycophotia margaritosa* or longer toward the postpharynx, as in Nephalodes, or shorter in this region than the setae near the labium, as in *Sidemia devastatrix.* In Phytometra and Chloridea they are longer on the sides of the hypopharynx than in the middle. They may be sparse, as in Platyhypena, but are more often very densely distributed. They vary greatly in length, sometimes attaining that of the palpi, as in *Cirphis unipuncta* (Fig. 26), but are most frequently much shorter, like those of *Lycophotia margaritosa* (Fig. 38), or stout and very minute as in *Agrotis ypsilon* (Fig. 44). In *Lycophotia infecta* they are so short that the surface of the membrane appears granular. No correlation between these various conditions and the feeding habit has been discovered. The function of these setae is probably essentially protective, although they may serve as sensory organs.

The epipharynx of lepidopterous larvae is membranous and continuous with the labium on its ventral and lateral margins and with the postpharynx at its dorsal end (Fig. 13). It bears a pair of narrow longitudinal sclerites, the tormae, which lie entad of the ends of the clypeo-labral suture. Three stout primary setae are borne on each side in the membrane near the ventral margin. A fourth minute seta figured by Dampf in the psychid genus Eumeta has not been found in the Noctuidae. No modifications of the epipharynx, such as those which occur in the leaf-miners, have been encountered in the family. Neither the form of the torma nor the position of the setae is subject to marked variations.

SETAE OF TRUNK

A number of the earlier students of lepidopterous larvae noted the definite arrangement of certain setae throughout large groups, which led them to investigate the taxonomic value of setal position. Müller in 1886 and Dyar in 1894 published important works on this subject, the latter attempting to make a table to the families of Lepidoptera based on the setal pattern of the larvae. The distinction between primary and secondary setae was recognized by Müller, Dyar subsequently introducing the term subprimary, which he applied to setae of general occurrence which are absent from the first instar. The most extensive researches on the setae of the trunk have been performed recently by Fracker in 1914 and by Schierbeek in 1917. The former author has provided us with a most useful and easily workable table for the identification of caterpillars, exclusive of the Noctuidae, in which work the setae play an important part. The latter investigator pursued the subject from the morphological point of view rather than from the systematic one. These two workers disagree on the selection of a primitive type of setal position, Fracker regarding the prothorax as presenting the more generalized position, while Schierbeek gives good reasons for considering the abdominal segments which bear larvapods as the more primitive. They hold different views, moreover, as to the homodynamies between thoracic and abdominal setae. On at least one important point they agree, namely, that verrucae correspond to single primary setae, the former having been developed from the latter, and, in certain groups, having been subsequently reduced again to single setae, this process being a reversible one.

Inasmuch as an investigation purposing to settle the disagreements of these two workers would involve a detailed study of the larvae of the whole order, the disputed questions of homodynamy and primitive segments cannot be decided from researches on the Noctuidae alone. It is consequently not a part of the plan of this work to discuss these points. The treatment of the setae of the trunk here presented will be confined chiefly to a discussion of the variation in the setal pattern of noctuid larvae, exclusive of those which bear verrucae, as in Acronycta. The forms with tufts of setae are confined within the family to this genus and to a few allied ones of little importance. Since they present various stages in the development and reduction of verrucae, these genera promise a rich field for the study of the evolution of setal tufts.

Of the various systems of naming setae which have been proposed that of Fracker is undoubtedly the most satisfactory. As Schierbeek states, the older system of numbering them has resulted in so much confusion that any further schemes employing numerals would only increase our difficulties. He rejects Fracker's Greek letter system, apparently because he disagrees with the homodynamies proposed by this author, and proceeds to apply names descriptive of the location of the setae to which they refer. We fail to understand why a difference of opinion as to homodynamy should render advisable the addition of yet a new system to our already superfluous supply. The fact, moreover, that particular setae may be located in widely different positions according to the segment and to the species opens to objection all names of setae descriptive of position. Schierbeek would change the names of the setae in instances of this sort, maintaining a nomenclature should provide a simple means of describing larvae, rather than of indicating questionable homologies. Inasmuch as the general progress of all morphology and of taxonomy, which should always be based on morphology, depends largely upon the correct homologizing of structures, we can by no means accept this view, even in cases where the homologies indicated by the nomenclature are doubtful. The shortness of the names of Greek letters compared to the very long ones proposed by Schierbeek also favors the use of the former. Furthermore, because of the great utilitarian value of Fracker's tables, this system will probably come into more general use than any other. For these reasons it will be used in this paper so far as possible. Schierbeek's plan of naming the types of setal arrangement of numerals seems very commendable. No occasion arises, however, for using it in this work.

Except for the marked differences in the development of verrucae exhibited solely within a few genera of the Acronyctinae, the setae of noctuid larvae offer comparatively little variation. Certain minor variations in their number and situation, however, are of great phylogenetic significance because of their fundamental nature. Figures 47, 48, and 49, showing the setal position in *Cirphis unipuncta*, represent the typical condition for the family. The naming of the setae in these figures differs slightly from Fracker's labeling of those of *Feltia gladiaria*. As clearly shown, both by his own figures and by those of the author, his tau on segments 7 and 8 should be omega. The setae on the anal larvapod are not named in his figure of Feltia, where their number and position is quite different from that in Hepialus. Consequently the letters used to designate these setae may not correspond to those in Fracker's figure of Hepialus, which, as he states, do not necessarily indicate homodynamy with setae bearing the same names on other segments. The seta on the anal segment of Feltia which apparently corresponds to his theta on Hepialus is primary in the former, since it occurs in the first instar of this species. Consequently it should not be called theta, which is subprimary according to Fracker. It is referred to as kappa in this paper.

Certain minute setae are omitted from Fracker's figure of Feltia. Omega should be present on segments 1 and 9 and the minute setae labeled x in our figures were either generally overlooked by him or considered as secondary. These seem to have escaped the notice of all workers but Forbes and Dampf in spite of their widespread occurrence in the order. The latter figures them in the psychid, Eumeta, and the former in an unnamed noctuid and in Incurvaria, where he labels them xa, xb, xc and xd. They have been found by the author in nearly all noctuids examined and in the cossid *Zeuzera pyrina*, where they are extremely minute. They are undoubtedly primary, since they have been seen in the first instar of *Cirphis unipuncta* and of *Phytometra brassicae*. They most probably occur in all newly hatched noctuid larvae, if not in those of all caterpillars. Their extreme minuteness renders necessary a most careful search in order to locate them. The ventral two, xc and xd, occur only on the mesothorax and metathorax and apparently correspond to the subprimary gamma of Fracker, which, he states, is primary on the prothorax. These setae perhaps represent a vestigeal verruca, the two together being homologous with one seta. In Hepialus there are three small setae in this region instead of two, as Fracker has shown. On the Noctuidae either one or both of the minute setae xa and xb are present on all segments but the prothorax and the anal one. Xa of the mesothorax has apparently migrated onto the caudal margin of the prothorax. These two setae appear to represent but one primary one just as a verruca corresponds to a single seta.

The homodynamy of these four minute setae cannot be definitely established without involving an extensive study of the setal patterns of caterpillars in general, especially of the first instars. Their position, nevertheless, suggests homodynamy between alpha of the prothorax and xa plus xb of the following segments and between gamma of the former and xc plus xd of the mesothorax and metathorax. If this be true, beta and delta of the prothorax correspond respectively to alpha and beta of the following segments, other homodynamies remaining unchanged. This interpretation reveals a much closer similarity between the prothorax and other segments than that of Fracker, in which the minute setae were disregarded. It seems preferable, however, to retain the names of Forbes for these setae pending more extensive study on this question.

Variations in the setal pattern of the prothorax are clearly discernible and generally fairly constant for genera but they are so slight and grade so continuously that very little taxonomic aid is afforded by them. The location of beta varies longitudinally to some extent, ranging from a position on the transverse line of beta to one distinctly caudad of it. Rho exhibits some transverse variation, being either equidistant from delta and the spiracle, as in *Polia meditata*, or much nearer to the latter, as in *Nephelodes emmedonia*. The situation of epsilon with reference to gamma and to the spiracle offers the best character in setal position on the prothorax. In the Acronyctinae, Cucullinae, and Hadeninae epsilon may be distinctly nearer to either according to the genus. It is apparently always nearer to the spiracle on the Catocalinae and Phytometrinae, but ranges in the

Agrotinae from a point equidistant to one much nearer to gamma. Epsilon also varies in position in the Hypeninae, being equidistant from gamma and the spiracle in some genera and nearer to the spiracle in others. Some longitudinal variation is offered by epsilon, which may be slightly or considerably caudad of kappa according to the genus. Kappa varies slightly but quite constantly in transverse location, ranging from a point distinctly above the spiracle to one a little below it. The relative situation of eta, kappa and the spiracle with reference to one another differs according to the group. Eta is usually distinctly below kappa and slightly caudad of it, being much nearer to kappa than to the spiracle. These setae may, however, be on the same longitudinal line, with kappa so far caudad that it is equidistant from eta and the spiracle.

As in caterpillars generally the mesothorax and metathorax are very similar to each other, although they exhibit a quite different setal pattern than the prothorax, the arrangement on the former segments resembling rather closely that of the abdominal ones. The mesothorax and metathorax differ from those which follow chiefly in the longitudinal position of alpha and beta and in the situation of the setae occupying the region which bears the spiracle in other segments. One or both of the minute setae xa and xb may be present on the mesothorax, this point representing individual variation. Both are usually present on the metathorax. On the mesothorax beta varies from a position on the transverse line through alpha to one distinctly cephalad of it. The location of beta may be the same on the metathorax as on the mesothorax or it may, as is often the case, be a little further caudad on the metathorax (Fig. 48), the amount of variation in this respect remaining the same for both segments. On both mesothorax and metathorax rho varies longitudinally from a point distinctly cephalad to one a little caudad of epsilon, the latter condition being commonly found in the Agrotinae. A greater difference in position is presented by beta, which on the mesothorax may be either equidistant from alpha and epsilon or very much nearer to alpha as in Catocala. On the metathorax beta is usually further ventrad, varying the same amount as on the mesothorax. The position of a line drawn through rho and epsilon with reference to kappa and theta furnishes one of the best characters on these two segments. The condition in this respect is usually the same on these segments, but may be distinctly different as in *Achatodes zeae*, showing that there has been some independent variation in the setal position, notwithstanding their very similar organization. In the Agrotinae and Catocalinae examined this line passes nearer to theta than to kappa. It may be distinctly nearer to either one in the Hadeninae, Acronyctinae and Hypeninae according to the genus. In the Phytometrinae it is usually equidistant from the two setae and ranges from a point equidistant to one much nearer to theta in the Cucullinae. The situation of kappa, theta, and eta relative to one another also varies sufficiently to provide some characters. Kappa may be equidistant from eta and theta or very much nearer to eta. Most commonly it is slightly but distinctly nearer to the latter, being especially close to theta in the Catocalinae, Phytometrinae, and Hypeninae, a group of subfamilies which, as will be shown later, conform as a unit to certain other very fundamental characters. The angle made at kappa by the lines kappa-eta and kappa-theta varies in size from 80 degrees to a very obtuse one according to the genus. The most marked variation in setal position exhibited on the mesothorax and metathorax is furnished by xc and xd. Although closely associated, they vary not only relative to each other but also in transverse position with reference to epsilon and rho, ranging from a point a little above rho to one slightly below epsilon, the latter condition having been found only in *Achatodes zeae.* Their minute size, however, would render impractical their use in tables. The fact that much greater variation occurs in the setal arrangement of these segments than in the prothorax would seem to support Fracker's contention that the condition in this respect is more primitive in the latter. The setal pattern of the mesothorax and metathorax, however, is on the whole very uniform.

The arrangement of the setae of abdominal segments 1 and 2 differs essentially from that of the other segments only in the region where larvapods are borne on the following segments. The setae which are normally borne on the larvapods on segments 3, 4, 5, and 6 are present on this portion of segments 1 and 2. The other setae of these two segments will be considered later in the general treatment of the abdominal setae which follows. On segment 2 tau is apparently always well developed, but it has been found on segment 1 only in the Catocallinae, Phytometrinae and Hypeninae. Fracker figures it in the first abdominal segment of *Feltia gladiaria,* although the author has failed to find it in an abundant supply of material of this species. Omega, on the other hand, which is omitted from his figure, is apparently always present in the family on this segment, although very minute. The presence or absence of tau is the most fundamental character discovered in our entire study of the morphology of the noctuid larvae, making it possible apparently to separate two large groups of subfamilies on this basis. The position of omega varies considerably in a transverse direction according to the genus, its minute size, however, renders it inadvisable to use this variation in tables. Some difference in longitudinal location is offered by sigma, which ranges from a position on the transverse line through pi to one distinctly caudad of it. The Catocalinae apparently differ from other subfamilies in having the line nu-mu longer than the line pi-mu on segments 1 and 2, the opposite condition being distinctly present in all other larvae examined. On both these segments, in those subfamilies where it occurs, tau varies both longitudinally and transversely, furnishing good generic characters throughout the family. It may be nearer to pi or to sigma and varies from a point on the transverse line through nu to one just cephalad of the transverse line through pi.

Only one of the minute setae xa and xb is usually present on the abdominal segments, altho both are found in *Chloridea armigera* and frequently the persisting seta is associated with a minute spot, which evidently represents the vestige of the other. The transverse variation in the location of xa with reference to alpha and beta affords some phylogenetic indications, altho the minute size of xa precludes the use of its variations in tables. Typically this seta is further dorsad of beta on segment 1 than on segments 2 to 7 inclusive, being most ventrad of all on segment 8. This variation involves the migration of beta as much as that of xa. Two genera examined, Catocala and Xylina, afford exceptions to the rule, xa being further dorsad relative to beta on segment 8 than on 1. In all other groups investigated xa is ventrad of the longitudinal line through beta, whereas in these two genera it is much dorsad of this line, an instance of parallel development.

The difference in the longitudinal position of the spiracle with reference to the surrounding setae on successive segments in the individual follows a certain definite plan throughout the family. On segment 1 the transverse line through rho ranges according to the group from a position distinctly cephalad to one a little caudad of the spiracle. Rho is clearly further cephalad in segments 2 to 6 inclusive than in 1, its transverse line passing cephalad of the spiracle or tangent to the cephalic margin. Segment 7 presents approximately the condition found in segment 1, the seta being further caudad than in segments 2 to 6, and ranging from a situation cephalad of the spiracle to one caudad of it. Two exceptions to this general plan have been noted. In *Sidemia devastatrix* the condition on segments 1 and 7 does not differ clearly from that in the intermediate segments and in *Papaipema nebris* segment 7 exhibits the same location which it occupies on segments 2 to 6, segment 1 differing from the rest as usual. The fact that segments 1 and 7 show much greater variation in this respect than the intermediate segments indicates that the condition found on segments 2 to 6 is the more primitive. Evidently in segments 1 and 7 the spiracle has migrated cephalad of its primitive position. In some cases this process has proceeded further on segment 1 and with other species on segment 7. The condition on segment 8, where the position of rho varies according to the group from a location cephalad to one caudad of the spiracle, reveals no uniform relation to that on other segments. Altho these minor variations in the longitudinal situation of the spiracle offer points of morphological interest they usually do not lend themselves readily to taxonomic application. The Catocalinae, however, apparently differ from all other groups within the family in having rho distinctly cephalad of the spiracle in segment 1.

The spiracle has also migrated in a transverse direction, as indicated by its position with reference to the surrounding setae. In general it is further ventrad on segment 1 and further dorsad on segment 8 than on segments 2 to 7 inclusive. Sometimes segments 7 and 8 present the same condition, as in *Scolecocampa liburna*, which is to be regarded as a specialization, since segment 7 as well as segment 8 has departed from the primitive arrangement. In Sidemia segment 8 does not differ in the transverse position of the spiracle with reference to epsilon from segments 2 to 7, as it does in the other genera examined. This may be reasonably considered as a generalization.

From this consideration of the position of the spiracle it appears that segments 2 to 6 inclusive present the primitive condition, the spiracle having migrated cephalad on segments 1 and 7 and either cephalad or caudad on segment 8 depending on the group. It has, moreover, shifted ventrad on segment 1 and dorsad on segment 8, remaining usually in the same transverse position on segment 7 as on segments 2 to 6.

The taxonomic value of the transverse variation of kappa in caterpillars was early demonstrated by Dyar. Altho the situation of this seta offers no conspicuous differences in this family, it varies sufficiently to provide some generic characters. It is usually much further ventrad of the spiracle on segment 7 than on other segments. *Achatodes zeae* again affords an exception, having kappa further ventrad on segment 8 than on segment 7, the reverse usually being true. Differences in the location of eta and mu afford generic characters, especially on segment 7, where they vary both transversely and longitudinally. The transverse position of omega relative to pi and sigma varies considerably throughout the family, seemingly according to the genus. The very minute size of omega, however, unfortunately precludes the use of this character in a table.

On segment 8 beta is typically much further dorsad than on the segments cephalad of it, presenting a specialized setal arrangement. The longitudinal line through alpha may pass considerably above beta or a little below it, the latter more specialized condition being less frequently encountered. This character promises to be useful in the separation of genera and of larger groups. Pi varies transversely to some extent on segment 8 relative to mu and sigma, affording generic characters.

With the exception of the anal one, segment 9 may reasonably be regarded as the most specialized segment with respect to setal pattern. Here the migration dorsad of beta has proceeded much further than on segment 8. The transverse location of alpha relative to beta and rho varies according to the group, altho presenting considerable individual variation in some species. Rho may be nearer either to alpha or to beta depending on the genus. The transverse line through kappa may pass either caudad or cephalad of pi, both of these setae varying somewhat in their situation according to the group, altho they provide no convenient characters for use in tables.

The setae of the anal segment, which probably represents the fused tenth and eleventh abdominal somites, cannot be definitely homodynamized with those of other segments. Alpha, beta, and kappa vary a little in relative position according to the genus or in some instances within a genus. Kappa is most commonly equidistant from the other two but may be distinctly nearer to beta or less often slightly nearer to alpha. Both extremes have been found within the genus Phytometra. The position of the setae on the lateral aspect of the anal larvapod is perhaps subject to more striking variation than any other group of setae on the trunk of noctuid larvae. An usually conspicuous sensorium, which McIndoo has described, also contributes to the taxonomic value of this region, varying considerably in situation relative to the setae. Eta may be nearer either to epsilon or to omega, furnishing a basis for the separation of genera and larger groups, altho occasionally showing specific variation. *Scolecocampa liburna* presents an exceptional position of the sensorium, which is distad of eta (Fig. 53). In all other species examined it is distinctly proximad of the setae. The sensorium, eta, mu, and tau are frequently arranged so as to form the points of a diamond, which varies considerably in relative length and width, according to larger groups. The line from the sensorium to tau is usually longer than the one from mu to eta, altho the reverse situation is sometimes encountered. Either mu or eta may be nearer to the sensorium, so that the diamond is often out of true. Mu varies in location with reference to the lines epsilon-eta and omega-tau, being nearer to either one. All of these variations appear to apply chiefly to genera.

LARVAPODS

The general form of the larvapods of noctuid larvae (Figs. 50-53) is typical for the entire order. As in a number of related families, the crochets are arranged in a mesoseries and are homoideous and uniordinal (Figs. 51, 58) representing a supposedly specialized type which Dyar considered to have descended from the circular one found in Hepialus. They are operated by muscles which attach entad of a small usually heavily chitinized spot in the center of the distal end of the uropod. As shown in Figure 59 each crochet lies within a membranous invagination whose mesal edge bears a number of pointed membranous projections. These have not been previously described, so far as known. Their function is problematical. The proximal end of each crochet is pointed and curved mesad, serving for the attachment of muscles. Since the larvapods represent embryonic abdominal appendages which have persisted into postembryonic life, the terms proleg and false leg in general use are inappropriate.

Altho the extent of variation in the larvapods of noctuids does not approach that which Goosen's series of these appendages reveals in the entire order, they differ quite markedly in form, number, relative size, number of crochets, and amount of chitinization. The setal arrangement is practically uniform. As previously stated, from two to four pairs of median larvapods may be present, the first one or two pairs, which are located on the third and fourth abdominal segments, being absent in certain groups. In the Phytometrinae the two cephalic pairs are usually wanting, altho Hampson mentions one genus whose larvae have the full number. The Catocalinae exhibit a pronounced tendency toward the reduction of the first two pairs, which reaches its acme in Caenurgia, where they are entirely absent. The first pair only are generally lacking or without crochets in the Hypeninae. According to Hampson, the Erastrinae also bear but three pairs of median larvapods, altho the larva of *Chamyris cerintha*, which was evidently unknown to him, has the full number, the first pair being as well developed as the rest. The larvae of other subfamilies of which material has been available for study are provided with four pairs of median larvapods with the first two pairs usually not strikingly smaller than the others. In certain Phytometrinae the vestiges of the lost larvapods can be discerned as heavily chitinized small protuberances bearing the setae in about the same position which they occupy in the fully developed appendage. *Epizeuxis lubricalis* of the Hypeninae has the first pair fairly well developed but completely lacking crochets. The number and relative size of the larvapods furnish very fundamental characters, altho no noctuid subfamilies can be reliably diagnosed upon this basis alone.

Since the caterpillars of the most generalized families and of the great majority of all Lepidoptera bear four well developed pairs of median larvapods, this is most reasonably regarded as the generalized condition. Their reduction has taken place in a few very distantly related groups, this process having proceeded to a different extent in each. In the Cochlidiidae they are entirely absent and in the Geometridae only the last pair of median ones and those of the anal segment persist. Certain groups of Noctuidae, apparently represent an incipient stage in this process of reduction, as exemplified by the Agrotinae, in which the first two pairs are typically somewhat smaller than the rest. In the Catocalinae the same tendency is exhibited to a much greater degree. The Phytometrinae and Hypeninae, whose larvae are generally the most highly specialized in the family in this respect, are placed by Hampson among the most specialized noctuids on the basis of the structure of the adults, whereas the larvae of the Acronyctinae, which he regards as a relatively generalized subfamily, always have the full number of larvapods well developed.

There appears to be no very definite correlation within the family between the mode of life and the loss or reduction of the first two pairs of larvapods, although this condition is accompanied by the habit of walking with a looping gait and of moving more rapidly, a point to be discussed in connection with the postembryology of the larvapods. The lengthening, however, of the two latter pairs of median and of the anal ones, which is so pronounced in larvae of Catocala, appears to be a modification for arboreal life. The same specialization is found to a lesser degree in many arboreal caterpillars. This type of larvapod seems to be found only in larvae that climb extensively. The fact that the development of this modification has proceeded further in the catocalas than in most other arboreal larvae is consistent with the occurrence in this genus of a number of marked adaptations to life in the tree stratum of the deciduous forest. The eggs, larvae, and adults are protectively colored like the bark of the trees on which they rest. Practically all of the species feed upon the foliage of deciduous trees or upon plants of the deciduous forest.

The number of crochets is larger in Catocala than in most noctuid larvae, which is apparently a further specialization for climbing on the trunks and twigs of trees. From the first to the anal pair of larvapods respectively the number of crochets in *Catocala grynea* is 30, 36, 43, 55. The other extreme is presented by some of the subterranean forms, *Feltia gladiaria* having 8, 12, 14, 14, 18 and *Sidemia devastatrix* 12, 14, 14, 14, 14. In general the anal pair has the largest number and the first pair often bears a few less than the others. The formula for *Cirphis phragmitidicola*, 22, 24, 26, 30, represents an average one for the family. Some individual variation occurs in this respect, the number varying two or three each way from the mean. It is frequently different on the two sides of the same individual, as Dampf has shown it to be in the psychid, Eumeta. Considerable difference in the number of crochets is sometimes exhibited by closely related species, *Polia meditata* having 16, 18, 18, 20, 26, and *renigera* 12, 12, 16, 18, 19. These two species are decidedly subterranean. The closely related *Ceramica picta*, on the other hand, which enters the soil only to pupate, frequently climbing shrubbery to feed, has 26, 27, 30, 32, 35. Beyond the presence of a larger number in the arboreal forms, there appears to be no marked correlation between the mode of life and the number of crochets, altho the smallest number is apparently best represented among species which burrow in the soil. Specific determinations may often be facilitated by these formulae, altho a considerable difference in this respect according to the instar necessitates a positive knowledge of the stadium before applying this character.

POSTEMBRYOLOGY

Ecdysis is undergone by noctuid larvae four, five, or six times, depending chiefly on the species, but somewhat on other factors. They present, then, five, six, or seven stadia. After each molt the postembryonic changes which have taken place during the previous stadium are suddenly revealed. These changes may be highly conspicuous, but are more often so very slight that careful observation or accurate measurement is necessary to detect them. Before considering the structural changes undergone in larval postembryology, we shall discuss at this point the significance of the number of stadia, and of the amount of increase in size from one stage to the next.

NUMBER OF MOLTS

Although not absolutely fixed, the number of molts characteristic for species of lepidopterous larvae is not subject to the considerable variation found in some other orders. Wodsedalek, for example, greatly increased the number of stadia in the larvae of Trogoderma (Dermestidae) by starvation. It is certain that environmental factors may at times cause one molt more or less in certain lepidopterous larvae. Payne found that those of *Ceramica picta* pass but five stadia in both generations in Nova Scotia, whereas those reared in Illinois by the author have uniformly undergone one molt more than these northern individuals. Hibernating butterfly larvae have been known to molt once more than those of the summer broods. This phenomenon has not been found in the noctuid larvae, *Agrotis c-nigrum* and *Polia renigera*, which have been reared through both winter and summer broods. Weniger reduced the number of stadia in *Eacles imperialis* and *Antheroca mylitta* from the normal six to five, by rearing them at about 25 degrees C. coupled with high humidity. By rearing the cutworm, *Agrotis ypsilon*, at 21 degrees C., 100% humidity, and at 28 degrees C., 100% humidity, in ventilated jars, the author has similarly decreased the normal number of molts by one. It is a curious fact that the cutworm, *Polia renigera*, adds one stadium to its usual number when reared under these same conditions, being affected in an opposite manner by the same stimulus.

Sexual differences in the number of stadia were first recorded by C. V. Riley in *Hemerocampa leucostigma*, the males always molting four times, the females either four or five. Payne has recorded the same phenomenon in a few other members of this family (Liparidae). This peculiar condition has been observed by the author in but one noctuid species, *Caenurgia erechtea*. Its significance will be discussed later.

Besides these environmental and sexual variations in the number of stadia, there are very probably hereditary tendencies toward individual differences in this respect. Davis records one individual of *Cirphis unipuncta* passing seven stadia instead of the usual six. Since this exceptional individual was reared under the same conditions as hundreds of others, it seems evident that heredity and not environment must account for this exceptional instance, the possible significance of which will be considered later. Similarly, one larva of *Agrotis ypsilon*, reared with fifty-two others, molted but six times instead of seven, according to our records.

In 1890 Dyar called attention to the fact that the widths of the successive heads of any lepidopterous larva in all its stages bore a certain definite relation to each other. His presentation of this point may be summarized as follows: the quotient obtained by dividing the width of the head of any instar by that of the previous one is a constant, which is characteristic for the species. This principle has been termed Dyar's Law. Its utilitarian value is obvious, enabling one to determine what instar he is dealing with when a specimen or a published measurement of any other known instar is available. A fair indication as to the number of stadia may also be obtained if the size of the first and of the last instar is known.

An inspection of a large number of species will reveal the condition in this regard within the Noctuidae. Although the measurements represent averages derived from the number of individuals indicated, in many cases a much larger number has been examined to insure the determination of a fair average, as well as to find the extremes of variation. The material studied was either preserved when collected or grown under approximately natural conditions. Individual variation in size is not as great as might perhaps be expected, usually rendering the identification of instars a simple matter. The figures expressing the percentage of variation are obtained by dividing the maximum variation found, by the average, multiplying by 100, (to express as percentage) and dividing by 2, so that the deviation from the mean in either direction, not in total, is represented. The later instars naturally present the greatest variation, having been longer subject to external influences. Where the measurements are based on individuals of different broods the variation is usually larger than otherwise, since the larvae of certain generations often grow larger than those of others in an ordinary season. All measurements have been made with an ocular micrometer.

The inconstancy of Dyar's supposed constant, which we will refer to as the index of growth, is striking, varying in *Agrotis ypsilon*, for instance, from 1.28 to 1.84. The average for any particular species ranges from 1.44

to 1.61. The increase from first to second stadia is usually greater, from penultimate to last more often less than for other molts, this latter condition being explainable by the fact that the more rapid development of adult structures in the later instars leaves proportionately less energy available for growth. The other noticeable differences in indices of growth within a species present no uniformity. In one species, for instance, the index from second to third stadia is greater than from third to fourth, in another the reverse may be true, or in a third species these indices may be equal. The question must arise, then, as to whether the relation between these different indices within a species be definite to any extent.

An examination of the successive exuviae of isolated individuals, shows us that the variations in the index of growth for any species are of no uniformity, with the exception of the tendency toward largeness of the first and smallness of the last. All other variations are to be accounted for, then, by environment, all indices but the first and last probably tending to be equal under uniform external conditions. Any influences affecting the rate of activity of the moulting mechanism differently from that of the general metabolism must necessarily either increase or decrease the index of growth. Thus, if growth be impeded without interfering proportionately with hypodermal activity, or at least with the molting mechanism, a small index will result. Wodsedalek, by starving larvae of Trogoderma (Dermestidae), obtained many exuviae, some of the last of which were actually smaller than the earlier ones. In like manner factors favoring growth more than molting necessitate a large index.

The effect of external factors on the index is characteristic. Starvation and parasitism, of course, greatly reduce growth, but do not retard the molting processes proportionately, since the number of stadia is not affected, larvae continuing to molt when very little growth is undergone. Favorable climatic factors, on the other hand, increase the index. The unusually large increase from second to third stadia in *Agrotis ypsilon* is to be explained by the fact that the individuals upon which the given figures are based were reared simultaneously under like natural conditions, which were evidently optimum for growth, or nearly so, while these individuals were passing the second stage.

We have demonstrated the fact that some species increase in size from first to last stages considerably more than others, the total amount of growth being characteristic for the species, although variable according to external factors. It may vary widely in closely related species as in *Lycophotia margaritosa* and *infecta*. Although molting has been generally considered to be primarily a phenomenon necessitated by growth, some entomologists have been inclined to question this point, tending rather to emphasize its excretory significance. It is to be noted, however, that the seven-staged species grow more than the six-staged. This obvious correlation between the total growth index, obtained by dividing the width of the head of the last instar by that of the first, and the number of molts lends weight to the former more general view. In Caenurgia, moreover, where there is a sexual difference in the number of stadia the females, which often molt once more than the males, average larger in size. The number of individuals of this species used in Table II is too small to justify our drawing conclusions from the fact that the growth index of the males exceeds that of the females. The fact that *Cirphis unipuncta*, which presents the greatest total growth index of the six-staged species, has been known to pass seven stadia in one instance, is of especial interest in this connection.

It follows mechanically that species with a large total increase, in other words, those with a first instar whose head is proportionately small for that of the last instar, produce eggs relatively small for their adults, the small first instar being correlated with a small egg, and the large last instar producing naturally a large moth. The egg measurements in Table I have been made from alcoholic specimens and are, therefore, somewhat larger than certain corresponding published measurements based on fresh eggs. The figures given represent the diameter of the largest circumference, the periphery of the typical noctuid egg being circular. In those species whose eggs have one diameter slightly greater than the one at right angles to it, an average has been given. Altho the correlation between egg-diameter and the width of the head of the first instar is clearly demonstrated in Table I, the ratio between these two measurements varies considerably according to the species. *Ceramica picta* presents an extreme condition where the egg is small relative to the larval head, the ratio being 1.65. In the catocalas, on the other hand, we find the width of the egg proportionately large for that of the larval head, the ratio reaching 2.62 in *C. illia*. This condition may possibly bear a direct relation to the habit of hibernation in the egg, which is general in this genus.

The shape, as well as the general internal structure of the abdomen of all noctuid moths is very nearly uniform, approximately the same proportional amount of space being used for egg-carrying in all species. It follows, therefore, that a moth producing eggs proportionately small for its size must bear a larger number than one whose eggs are large relative to the size of the adult. We should remember when considering this point that the moths of this family have but a short period for oviposition, usually laying all their eggs in a few successive nights, which permits of no egg-development during the life of the adult, such as occurs in the queen bee.

The data for the fecundity is based upon the number of fully developed eggs in the abdomens of reared moths and represents potential fecundity. Since the number of eggs actually laid in breeding cages is determined by external stimuli, all eggs in the abdomen being oviposited only under optimum conditions, which for many species are difficult to obtain artificially, the published records of the number of eggs laid by various species are unreliable as indices to the potential fecundity. The undeveloped eggs, which are never laid, occupy a quite uniformly small space in the abdomen. Accurate data on fecundity can be obtained only with difficulty, since counts must be made of the eggs contained in the abdomens of moths emerging in captivity only. Moreover, a large number of individuals should be examined, because of the great individual variation in this respect. In spite of the regrettable insufficiency of data, the column headed potential fecundity presents significant indications.

A consideration of the mechanical relations already discussed enables us to understand the significance of the correlation between high fecundity and large total growth. Although a general relation between these conditions is clearly indicated, we note that certain irregularities occur. *Feltia subgothica* and *Ceramica picta* lay an exceptionally large number of eggs relative to the amount of their larval growth. An examination of the ratios between the diameter of the egg and the width of the head of the first instar in these two species reveals the fact that both bear eggs proportionately small for the size of their first instars. This condition enables the moths to lay a large number of eggs relative to the amount of larval growth for the species, accounting for the irregularity in the correlation. The relation between fecundity and growth is not direct, since the former increases more rapidly than the latter, as is evident when we read from top to bottom in these columns, a relatively slight increase in growth corresponding to a large increase in fecundity. It is highly probable that the factors determining fecundity are many. Of these factors the amount of growth is an important one in this family.

It should be noted that *Cirphis unipuncta*, with the largest total growth index of the six-staged species, having seven stadia rarely, attains the highest fecundity of those with six stadia. This destructive species has three broods in Illinois. The larvae developing in June grow markedly larger than those of the following brood, which pass the larval period in midsummer, the individuals of the fall-brood being nearly as large as those of the spring-generation. This relation probably holds only for the latitude and climate of Illinois in a usual season. Since the eggs of all generations are of the same size, the total growth is different for each brood under normal weather conditions. Altho our data as to the fecundity of the moths of different broods is inadequate, it seems quite evident that those developing from the large September larvae must have relatively high fecundity. This is suggested as a factor contributing to the fact that the spring-larvae, offspring of moths from the September larvae, almost always constitute the brood which attains such great numbers in Illinois, accompanied by the well known army-worm devastation. Altho the larvae of this brood also attain a large size, they become greatly reduced in numbers by wilt disease and parasites, so that the midsummer -brood is usually not large. The small individuals of the midsummer-generation yield moths of low fecundity, accounting for the usual inconspicuousness of the third brood, altho infrequent outbreaks have been observed in September. It seems probable that this principle may prove to be an important one to be considered in the prediction of these outbreaks.

The fact that fecundity is hereditary in animals has been well established. Geneticists have found that the tendency to bring forth twins and triplets is hereditary in mammals. By artificial selection, Pearl and Surface have greatly increased the egg-laying propensities of a certain strain of Plymouth Rock fowls. It has been well established that fecundity in Drosophila is an hereditary trait. Individual variation in fecundity is considerable within the Noctuidae. Since those strains, in a species of this family, with a tendency to lay many eggs must transmit this trait to many more individuals than would those inclined toward low fecundity, it seems evident that in general species must increase fecundity in the course of evolution up to a point where it is checked by some sort of barrier, mechanical or physiological. The only possibility for a non-prolific strain to untimately persist would involve necessarily its accompaniment by inheritable, advantageous properties not possessed by prolific strains, such advantages offsetting their low fecundity. We have no evidence indicating that this latter, seemingly unlikely possibility has taken place within the Lepidoptera.

In the light of the correlations demonstrated, it seems evident that the amount of growth, or the number of molts, would act as a barrier to an increase in fecundity, furnishing mechanical limits, which would prevent further expression of this tendency. An hereditary increase in the number of molts, such as the one cited with regard to a single individual of *Cirphis unipuncta*, would allow the individuals possessing this trait to attain a larger size and consequently a higher fecundity. This would, therefore, be transmitted to a larger number of offspring than would the tendency toward a lesser number of molts. The persistent variation, then, would be the one with the largest number of stadia.

On the basis of this theory, the largest number of larval stages is the most specialized condition in this family. This conclusion is supported by all the other evidence available. As shown by Dyar, the great majority of lepidopterous larvae undergo ecdysis four times, five times frequently, and three, six, seven, eight, nine or ten times rarely. According to our data the molting five times appears to be the general condition throughout the Noctuidae, four molts occurring only in the two species of Phytometra, and in the male of *Caenurgia erechtea*, and six being found in but three species. We should be justified apparently in regarding the passing of seven stadia as a specialized condition, merely on account of its exceptional occurrence.

Since the two species of *Phytometra*, *brassicae* and *biloba*, which have been reared through all larval stadia by the author, present but five stadia and *contexta*, according to Thaxter, passes six, it would seem that this biological character is not a fundamental one. The persistence of the generalized condition of molting but four times in this structurally specialized group is parallelled by the situation found in Hepialus, whose moth is very generalized structurally, but whose larva has developed the specialized habit of root-boring.

In *Caenurgia erechtea* the number of stadia presents an interesting secondary sexual character, the larva undergoing ecdysis but four times in the male and four or five in the female. The males of this species offer the only instance known to us outside of the Phytometrinae where a noctuid larva molts but four times. Parallel instances have been found by C. V. Riley in *Hemerocampa leucostigma* and by Payne in other liparid larvae, in which the male passes five stadia and the female either five or six. This phenomenon is most probably to be explained by the fact that the female larvae generally attain a larger size than the male. The fact that the female varies in the number of molts indicates further that the larger number of stadia represents the more specialized condition.

The species passing seven stadia, *Agrotis ypsilon*, *Lycophotia margaritosa* and *Nephelodes emmedonia*, do not constitute a phylogenetic unit, but have developed an extra molt independently, since each is more closely related to different six-staged groups than they are to each other. *Lycophotia infecta* undergoes ecdysis but five times. Specific differences in this respect in the genus Phytometra have already been mentioned.

POSTEMBRYONIC CHANGES

A study of the postembryology of noctuid larvae, as well as a consideration of the ontogeny of animals in general, convinces us that the structural changes exhibited in ontogeny are not all an expression of the same biological factor, but are of a number of distinctly different kinds. The structural changes appearing in the postenbryonic development of caterpillars may be conveniently classified as follows:- (1) Recapitulative; (2) Non-recapitulative; (a) Adaptive to unequal function; (b) Necessitated by the mechanics of growth; (3) Compound; (a) Recapitulative-adaptive; (b) Recapitulative-mechanical; (c) Adaptive-mechanical.

The Law of Recapitulation is of quite general but by no means of universal application, ontogenetic sequences which do not conform to the law being many and well known. The fact that a mammal at birth has a head large relative to the size of its body does not lead us to regard the ancestor of this animal as the possessor of a proportionately large head. Nor does our knowledge of the postembryology of the house-fly convince us that it descended from an apodous insect with vestigial biting mouth-parts. We do not look to recapitulation to account for such conditions. Such postembryonic changes may be described as non-recapitulative as opposed to those of recapitulative significance, which apparently conform to the law. This point can be determined with regard to a structure undergoing change in ontogeny with a certainty proportional directly to our knowledge of the phylogeny of the structure in question. Thus, if the changes undergone by any structure in the course of its development recapitulate its race-history, we regard that structure as of recapitulative significance, but if its phylogeny be doubtful, our decision on this point must be proportionately tentative. The successive instars of species of Leucaspis figured by Lindinger reveal beyond any reasonable doubt the recapitulative significance of the pygidial structure in these coccids, the postembryology recapitulating minutely their phylogeny, which has been well established by the extensive morphological studies of MacGillivray. The recapitulative significance of wing-venation in pupal postembryology has already been mentioned. Of many parallel instances the case of Mantispa is perhaps the most familiar, the larva of this insect passing through transitional stages from a thysanuriform to an eruciform type, repeating the generally accepted phylogeny of the latter form of larva. The taxonomic advantages gained by the establishment of the recapitulative significance of a structural change in postembryology will be demonstrated later.

Many structures are adapted to the mode of life of a particular stage or to a habit associated with a single point in the life-cycle. Such organs function unequally or even differently in different stages of development, frequently being used in only one stage. Lepidopterous pupae, notably of the Sesiidae, frequently bear spines or projections used for breaking the cocoon and for wriggling into the open. These belong distinctly to the pupae. A parallel instance is furnished by the wings of insects, which function only in adults and appear in earlier stages merely as developing adult structures. Similarly caterpillars often spin silk in certain stadia and not in others, and noctuid larvae frequently do not employ the first one or two pairs of larvapods in the first stadium. This unequal function of a structure in different stages is generally correlated with structural differences, hence a non-recapitulative factor is introduced. Postembryonic changes which are the expression of this factor will be referred to as *adaptive to unequal function.* It is evident that the two factors, recapitulation and adaptation to unequal function may act in the same or in opposite directions with reference to a particular postembryonic change. In the former event it is impossible to ascertain to what extent each of these forces has operated in the production of the change, which is consequently most reasonably regarded as the expression of the two factors combined and is referred to as recapitulative–adaptive. When these two forces conflict, the effect of the recapitulative one is completely obscured, as will be demonstrated later, the factor of adaptation to unequal function being dominant.

Since certain animal structures do not grow as rapidly as others, they are generally relatively larger in earlier developmental stages than in later. The familiar instance already cited of the newly born mammal, with its proportionately large head, is parallelled generally by insects, the heads of the first instar being markedly large relative to the body. The ocellariae and crochets of lepidopterous larvae are strikingly large in the first instar, growing slowly in comparison with the surrounding structures. These phenomena are obviously not an expression of recapitulation, but are most probably to be explained by the relative rates of cell proliferation in different kinds of tissue. This factor, like unequal function, may undoubtedly operate either with or against the recapitulative force. When the effect of the latter is obscured by that of the mechanics of growth, the resulting change is classified as *mechanical*, whereas when these two forces exert themselves in the same direction the change produced would be termed *recapitulative-mechanical*, although no clearly defined instance of this situation has been found.

The compound types involving recapitulation have been already defined. One instance noted is obviously the result of a combination of unequal function and mechanics of growth. This change is classified as *adaptive-mechanical*.

Of the possible combinations of these factors all have been actually indentified as responsible for certain postembryonic changes in noctuid larvae, except two, *recapitulative-mechanical* and *recapitulative-adaptive-mechanical*. The first of these very probably finds expression in the migration of certain head-setae to be discussed later. The second type of change possibly occurs also in these larvae.

It should be noted that, unlike the other two factors, recapitulation is to be regarded as a general law, which fails to express itself only when obstructed by other forces, which are dominant over it.

Many postembryonic changes in structure are inexplainable in the dim light of our knowledge of the factors involved. Our lack of adequate knowledge of phylogeny is probably largely responsible for this situation, since many changes such as those of the head-capsule of muscid larvae figured by Nielsen, may prove to be of recapitulative significance, when sufficient morphological work is done to establish the race-history of such structures. An investigation, moreover, of the functions in different stages of organs undergoing postembryonic changes will most probably reveal many instances of adaptation to unequal function, while the determination of the importance of the factor of the mechanics of growth awaits the researches of the histologist. Hence morphological, biological and histological investigation may be expected to explain for the most part these numerous problematical changes, such as those in the shape of the body-setae and of the antennae of caterpillars, in the number of facets in the eye of the nymphs of dragon-flies, in the heads of muscid larvae, in the structures of the caudal end of the body of tipulid larvae, in the number of tarsal segments in the Heteroptera, and many others. Such investigations will probably reveal a number of types not listed in our present classification, which is necessarily very restricted, applying only to noctuid larvae.

The postembryology of the fixed parts of the noctuid larval head reveals the following changes:

(1) Appearance of the adfrontal sutures; (2) Change in the relative length of the epicranial stem; (3) Mesal extension of the postgenae; (4) Change in the shape of the labrum; (5) Reduction in the relative size of the ocellariae and sensoria; (6) Change in the position of the setae; (7) Change in the shape of the setae; (8) Change in the coloration.

ADFRONTAL SUTURES

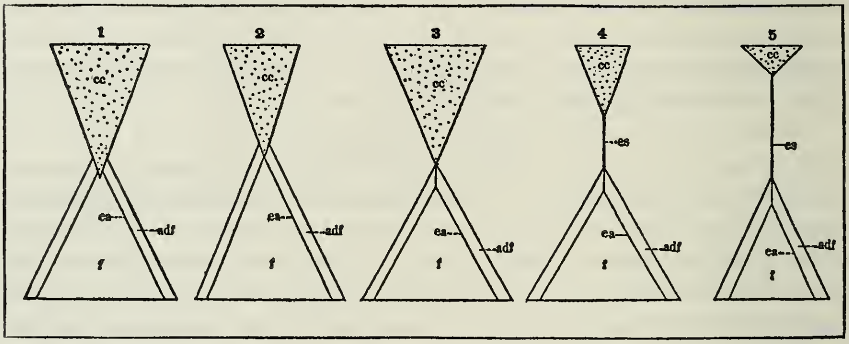
Although the presence of the adfrontal sclerites has long been regarded as a condition diagnostic for lepidopterous larvae, the fact that this area appears only in the later stadia, at least in noctuid larvae, has apparently not been discovered. Very frequently the coloration of the early instars gives the appearance of adfrontal sclerites where no structural differentiation exists, which has most probably been conducive to the general overlooking of the true situation. In the noctuids these sutures are distinct only in the larvae of the two later stadia, very faint indications being sometimes distinguishable in exuviae or treated heads of the third from last stage. The adfrontal sclerites have been regarded as bearing a direct structural relation to the infoldings along the epicranial arms. Fracker speaks of them as the "external expression of the attachment of the anterior arms of the tentorium." An inspection of a section thru this region (Fig. 1) reveals absolutely no connection between the adfrontal suture and the epicranial parademe, to which the pretentorium is attached. This suture appears externally as a narrow light-colored line constant in general position throughout the family but varying much in its irregular curving, even within a species. In sections it is not distinguishable from the general cuticle, except by its lighter pigmentation. Since the older ideas of its significance are obviously incorrect, our present problem is to account for its existence.

The usual place of splitting in the head-capsule at molting and at pupation is along the epicranial stem and arms in all but the more specialized forms such as dipterous or coccinellid larvae or coccid nymphs. We regard this, therefore, as the generalized condition in insects. As was stated in our consideration of the morphology of the tentorium, the great reduction of this originally supporting structure has been accompanied by the development of a number of deep infoldings, one of which occurs along the epicranial suture. As might be expected, the marked specialization in this region is accompanied by a specialized condition in molting, the entire head-capsule being shed intact. So far as we know the larvae of no other order molt without breaking the exuvia of the head, altho some nymphs do so. It seems probable that the deep infolding along the epicranial suture has rendered the usual splitting impossible. The great change in form undergone at pupation, however, makes a break in the last head-capsule mechanically necessary. This occurs along the epicranial stem and adfrontal sutures. So far as we have been able to determine they have no other function. These structures are to be regarded, then, as a modification for pupation due indirectly to the greatly reduced condition of the tentorium and to the deep parademe along the epicranial suture, which has taken over the supporting function of the tentorium.

The well developed condition of these sclerites in the next to the last instar, where they do not function, is paralleled by the general occurrence of adaptive structures in stages earlier than the one in which they are used. Altho the adfrontal sutures appear in larval development as they presumably did in phylogeny, beginning as a very faint line which becomes prominent later, the fact that they function only in the last instar indicates that the factor of unequal function also plays an important part in their development. If recapitulation alone were operating on this postembryonic change, we should, moreover, expect these sutures to appear in the first instar, as shown by the following facts. Their universal occurrence throughout the order indicates very strongly that they were present in the ancestral lepidopterous larva. Since the first instar of the noctuid larva is typically noctuid, it presumably represents with reference to recapitulation a period in phylogeny later than the one in which the Noctuidae appeared, certainly much later than the period in which the adfrontal sclerites originated. Hence on the basis of recapitulation alone the first instar would exhibit well developed adfrontal sutures. Their failure to appear until late in larval development is evidently due to the fact that they function only in the fully grown larva. This postembryonic change is evidently the expression of the two factors recapitulation and unequal function and is to be classified as recapitulative-adaptive.

EPICRANIAL STEM

As has already been shown in our consideration of the morphology of the head, the relative length of the epicranial stem varies widely in the larvae of this family, (Figs. 2, 15, 16, 17) furnishing a character second only to the number of larvapods in conspicuousness. The proportional length of this suture is most conveniently expressed in terms of its ratio to the length of the front. The quotient obtained by dividing the length of this sclerite by that of the epicranial stem will be referred to as the epicranial index and expressed by F/Ep. The great majority of lepidopterous larvae have a fairly long epicranial stem, Types 4 and 5 predominating. Type 5, with the epicranial stem longer than the front, occurs more frequently than Type 4, with the front exceeding the stem in length, in the Noctuidae and their allies, as well as in the Sphingidae and Rhopalocera. The average epicranial index normally found in the Noctuidae is about 0.7, the stem being somewhat longer than the front. Within the great superfamily Noctuoidea, the markedly short epicranial stem occurs only in certain genera of the Noctuidae. This condition is very frequently seen, nevertheless, since many of our commonest and most economically important noctuid larvae present this type of head. The infrequent occurrence of the reduced epicranial stem in the Noctuidae and allied families indicates that this is a specialized condition, at least in this group.



Hypothetical figures showing the relation of the front and epicranial stem. *adf*, adfrontal sclerite; *cc*, cervacoria; *ea*, epicranial arm; *es*, epicranial stem; *f*, front.

Moreover, wherever found in lepidopterous larvae, the short epicranial stem is associated with a specialized feeding-habit, that is, a habit other than the usual leaf-eating one, which we may reasonably attribute to the ancestral lepidopterous larvae, on the basis of its general occurrence in existing forms. Similarly, the parasitic life of certain of the family Oryssidae is to be considered as a specialized one, since the larvae of the horntails are typically borers. Leaf-mining larvae whether coleopterous, dipterous, or lepidopterous furnish an instance of specialized habit. The root-boring habit of the larvae of Hepialus is to be regarded as a biological specialization, altho their adults are structurally generalized. The larva of the noctuid, *Epizeuxis lubricalis*, feeds upon dry dead-wood, that of *Scolecocampa liburna* on moist dead-wood. Various cut-worms are subterranean to a greater or less extent. Each of these modes of feeding represents a departure from the leaf-eating habit and free-living existence, which were most probably characteristic of the ancestral lepidopterous larva.

There is a correlation between the short epicranial stem and specialized feeding-habit. It will be seen that Types 1 and 2 occur only in leaf-miners, Type 3 being also confined to larvae of this habit except in the seed-eating or stem-boring Prodoxidae, in the wax-eating bee-moth larvae, and in the leaf-rolling Tortricidae. Similarly in the Noctuidae the reduced epicranial stem is always associated with a specialized habit, the subterranean mode of life. The more pronounced this habit the shorter is this suture.

It has been necessary in order to establish this correlation to find criteria by which we may compare larvae of various species with reference to their subterranean proclivites. Cut-worms have generally been described in economic literature as larvae which hide beneath the ground by day, eating at or beneath the surface during the night. Our experiments have shown, however, that there is considerable diversity of feeding-habit, even within this biological group. Certain so-called cut-worms never enter the soil, others do so only under extreme stress, and some, on the other hand, never come above ground except for ecdysis. In addition to observations made on larvae reared under natural conditions, two series of experiments have been performed to determine the relative extent of the development of the subterranean habit with as many species of noctuid larvae as possible. The first of these determines which species are able to burrow into the soil and to what extent this ability has been developed in each. The second series of experiments determines the extent of the power to resist submergence in water, a resistance which subterranean animals have generally developed. The combined results derived from these two lines of investigation enable us to form a fairly accurate idea as to relative "subterraneanness" of various species. We will now consider these experiments.

DETERMINATION OF BURROWING HABIT

The determination of the relative extent of the development of the power to burrow into the soil in the larvae of various species is the object of the first series of experiments. The logical method for making manifest an ability or tendency to burrow into the ground, however slight, involves the subjection of the organism to an irritating factor to which it reacts in a markedly negative manner, at the same time excluding all means of avoiding this factor except by entering the soil. Lepidopterous larvae generally avoid direct sunlight, a large proportion of them being nocturnal in habit. This is especially true of noctuid larvae, the cut-worms being notoriously active at night. Altho precise experiments on the reactions of these insects to light are much to be desired, anyone who has worked with them extensively will have noticed, without doubt, a generally marked negative response to light. The author knows of no other natural factor calling forth such immediate and pronounced response. These experiments have been performed, therefore, in the following manner:

An ordinary fifty watt electric light bulb was suspended above the center of a glass-jar three inches in diameter, containing soil, with the lowest point of the bulb six inches above the soil. A thermometer was suspended with its bulb touching the soil in the center of the jar. The typical black earth of Illinois was used in a finely pulverized condition and sufficiently humid to eliminate dust. It was packed down lightly on top, leaving an even surface. The temperatures ranged from 33.3 to 35.5 degrees C. which was much higher than that of the laboratory due to the heat from the light. Except in Experiment 3 all material used was reared outside under approximately natural conditions and well fed. It was not brought into the laboratory until immediately before the experiment was to be started, except in Experiment 3. To avoid interference with one another, not more than five larvae were put together in the same jar. Frequently several instars of the same species were used, altho they always reacted alike, so far as could be observed. Observations were taken every few minutes, account being kept of the time required for the larvae to become visibly stimulated, as well as of the time elapsed before each individual should become buried, wholly or partially. These experiments were performed in April and May, except where otherwise indicated in the tables, consequently the temperatures to which the larvae were subjected during the experiments were unnaturally high, probably adding to the irritation produced by the light.

It has been shown that stimulation is usually immediate. Well fed larvae, which lie motionless when brought into the laboratory from the outside, generally exhibit pronounced irritation as soon as subjected to the light, running rapidly about the jar. The phrase "time required for submergence" expresses the time from the beginning of activity to the time when the individual is entirely or partially buried. In several instances certain individuals ceased activity as soon as the head and thorax were beneath the surface. This feature seems to be an individual rather than a specific trait. While the larvae of some species commence burrowing within two or three minutes after they become stimulated, entering the soil perpendicularly and disappearing within a few seconds after they begin to dig, others crawl for half an hour, making an occasional abortive attempt to thrust their heads beneath the earth, finally very gradually burying themselves by entering the soil at a small angle with the surface. Other species make no attempt to burrow, continuing to crawl actively about for two hours, at the end of which time the experiments were usually ended. We find represented in these species evidently several stages in the development of the subterranean habit, some entering the soil very readily, others with apparent reluctance, and some not at all.

Unavoidable differences in the physiological condition of the individuals account, most probably, for the considerable variation in the "time required for submergence" with different larvae in the same experiment. During the rest period prior to ecdysis and some six hours before it, larvae make no attempt to burrow when subjected to the test, no matter how pronounced this habit may be in the species. Three individuals of *Polia renigera* which reacted differently from the rest, failing to enter the soil, were isolated and found to be parasitized by chalcids when they died several days later. One larva of *Agrotis c-nigrum*, presenting a similar non-conformity to specific habit, died of the fungus, *Botrytis rileyi*, some time afterward. This individual revealed a marked negative geotropism, crawling up on the sides of the jar and onto the thermometer, a reaction exhibited by no other larva investigated. It is interesting to note in this connection that grasshoppers diseased by *Empusa gryllidae* and army-worms or cut-worms affected by wilt present the same response, crawling always to the top of some plant to die. Underfed larvae require a much longer time to bury themselves than do well-fed ones of the same species, the hunger stimulus seeming to partially overcome the negative response to light. Experiment 3 illustrates this point very clearly, the material having been kept without food for twenty-four hours in the warm laboratory at a temperature at which the metabolism is high. Since the larvae were very hungry, they resisted the tendency to burrow for a much longer time than in the other experiments, where they were well-fed. For this reason the averages given in this table do not include Experiment 3. The difference in the time of day when these experiments were performed bears a direct relation to the hunger, since the larvae feed principally at night. In Experiment 1, performed at 9 P.M., the slower response may be due to the fact that feeding was interrupted. The difference in weather conditions prior to the performance of Experiments 1, 2, and 4, undoubtedly has contributed further to the lack of physiological uniformity in the material used, introducing an additional source of error.

Altho accurate data as to the relative facility with which various species enter the soil can be obtained only by a long series of experiments carried on under carefully controlled conditions, employing a much larger number of individuals than have been available for use in our investigation, the data presented afford, nevertheless, some significant indications. Since species such as the arboreal *Homoptera lunata* or the cabbage looper, *Phytometra brassicae*, which we know to be not subterranean, are not induced to enter the soil under the conditions of the experiments and since notoriously subterranean species readily manifest their ability to burrow when stimulated by light, we are justified in applying this test in order to determine whether larvae have subterranean tendencies in species with which this point is doubtful. It has been determined thus that the bronzed cut-worm, *Nephelodes emmedonia*, and the cut-worms of the genus Cirphis (the army-worm genus) are not subterranean. Furthermore, in the subterranean species the relative facility with which the larvae enter the soil, as indicated by the "time required for submergence," as well as by various peculiarities already discussed associated with burrowing, serves as an indication of the extent of the development of the subterranean mode of life in these species. It may be noted, for example, that *Sidemia devastatrix* presents an extreme case of development of the under-ground mode of life in noctuid larvae. The larva of this species rarely comes above the surface except to molt. Unlike other cutworms it has lost its body pigment and has been aptly described as "half way between a cut-worm and a white grub." Owing to the insufficiency of material and to the sources of error previously mentioned, it would seem unwise, however, to attach undue significance to the relative lengths of time required for burying given in this table.

RESISTANCE TO SUBMERGENCE

The object of the second series of experiments is to determine the relative resistance to submergence in water in various species of noctuid larvae. Immediately after an unusually heavy thunder-shower, several arboreal noctuid larvae were found dead, clinging to the trunks of trees in crevices in the bark, where water had been running during the hardest part of the rain, which had lasted about twenty minutes. Since lightning had not struck in the vicinity, it seemed evident that these larvae were drowned by the water running down the tree-trunks. They bore the characteristic marks, to be described later, of drowned larvae. A few days afterward a cut-worm, *Feltia subgothica*, accidentally left in water for two days in the laboratory, recovered after a number of hours and resumed feeding. This striking difference in the ability to resist submergence in water between the arboreal caterpillars and the subterranean Feltia suggested the use of the length of time during which larvae could resist such submergence as an index as to the extent of the development of their subterranean habit. During early spring land infested with cut-worms, many of which hibernate as partly grown larvae, is often saturated with water for days at a time, without seemingly affecting their numbers. We should naturally expect such insects to be able to withstand these conditions successfully and to have developed, in common with subterranean animals generally, a resistance to submergence. Non-subterranean larvae of the ground- and field-strata might be expected to possess this power to a lesser extent, and arboreal species would presumably lack it almost entirely, since the nature of their habitat usually renders it unnecessary for them to withstand extensive drenching. Caterpillars which hibernate in the soil must be subjected to water from the melting snows as well as to the spring rains and consequently might reasonably be expected to present the most extensive resistance to submergence of any lepidopterous larvae.

This subject has been investigated experimentally in order to obtain so far as possible a means of expressing mathematically the relative "subterraneanness" of various species of noctuid larvae. The material used in these experiments was reared under approximately natural conditions. Before being submerged in water the larvae were washed to remove all soil and particles of foreign matter such as might carry minute air bubbles beaneath the surface. Immediately after washing, each larva was put in 150 cc. of distilled water five cm. deep contained in a small glass jar. When the larvae were small, two or three were usually put together in the same jar. In order to keep conditions as constant as possible throughout this series of experiments, the jars were kept in a constant temperature chamber at about 17 degrees C., there being occasionally a deviation of one or two degrees in either direction for a few hours at a time. They were exposed to natural light but not to direct sunlight. At the end of the period of submergence the larvae were dried on filter paper, then placed on a blotter six inches below a fifty watt Mazda electric light. Subjected to the stimulation of this irritating factor, manifestations of life could be most readily brought forth. While in this situation, the time required for the individuals to regain various degrees of activity was recorded. They were kept under the light for lengths of time varying from fifteen minutes to three hours or more, depending upon the readiness with which activity was regained. When stimulated as much as possible by this means, the individuals were isolated, each being placed under approximately natural conditions with food, in order that observations on the later effects of submergence might be made for several days.

The first few seconds of submergence are always spent in violent movements of the entire body, after which the larva suddenly becomes motionless, remaining so until removed from the water. Individuals undergoing ecdysis float, necessitating their being weighted down by a small piece of metal tied to the anal uropods by a fine thread. It seems probable that there may be a layer of air between the old and new cuticle, which would account for the low specific gravity of larvae in this condition. When not molting, they always sink immediately. After being removed from the water, dried, and placed under the light, the first signs of life are usually represented by the beating of the heart, which can be observed according to the transparency of the integument. Slight movements of the antennae and thoracic legs are next to be seen, followed by a feeble curling of the thorax caused by contractions of the longitudinal muscles, often accompanied by an extension and retraction of the crochets. As various kinds of motion of the trunk and appendages become more marked, water is expelled in quantity from the mouth and anus. When in this stage of recovery, larvae placed with the ventral surface uppermost gradually turn over. Sometime later they will crawl a little when mechanically stimulated, still expelling water. Often after a few hours they appear normally active, altho seldom feeding until several hours after apparent recovery. The evidences of the regaining of activity take place almost invariably in the above order.

The stage of activity reached with individuals which fail to recover varies according to the resistance of the species and to the length of time submerged. When kept under water for a time much longer than that required for drowning, sometimes no movement can be produced by stimulation. More often, however, the earlier stages of activity are passed through, followed by a decline evidenced by a repetition of the same stages in reverse order. Frequently larvae which have apparently thoroly recovered, crawling actively about, refuse to eat and die within two or three days. This indicates that the length of time for which they were submerged is very close to the minimum time required for drowning for the species in question.

The extent of activity developed before the decline sets in offers a valuable guide to the determination of the minimum time required for drowning, which is the object sought in these experiments, since this factor enables us to express in numbers the resistance to submergence of various species. From the data collected it has been possible in most cases to determine within rather narrow limits the average minimum time required for drowning. When one-half or one-third of the individuals of an experiment die and the rest survive, the time for which they were submerged is taken as representing approximately the resistance to submergence for the species.

Altho different instars of the same species present no uniform difference in resistance, we find some individual variation in this respect, which is most probably to be accounted for by unavoidable physiological differences in the material. Such factors as the time expired since molting, the amount of food in the alimentary canal, and the weather conditions under which the material was reared undoubtedly influence the resistance to submergence to a greater or less extent. The first of these, which will be discussed later, is probably the most important. It is to be regretted that data regarding the resistance of larvae of different broods have not been obtained, since such data would be of considerable interest with respect to those species having several broods a year and hibernating as partly grown larvae. Our experiments with such species have been performed solely with larvae of the hibernating brood after hibernation had been passed. Very probably those of the summer broods are less resistant. If this be true, it would be of great interest to determine whether the difference in resistance in different broods is innate or induced by climatic factors.

The specific variation in resistance to submergence is extreme, ranging from 25 minutes to 48 hours. The exact nature of the adaptations, morphological or physiological, which permit of such striking differences in this respect, is problematical. We find no external structures which throw light on this question. The spiracles offer no variations which seem to bear on this point. Internal structures or histology, a study of which the scope of this work does not permit, may be found to bear relation to the development of the power to withstand submergence. It seems probable that differences in the efficiency of the mechanism for closing the tracheae just entad of the spiracles may be found.

There are indications that death from drowning in these larvae is caused by two factors, oxygen starvation and mechanical injury due to the filling of the alimentary canal with water. The drowned larvae have always exhibited a black girdle around the body, varying in extent from one segment to five or six, so that in the latter case it extends for half the length of the larva. Those which almost recover from submergence show but a slight ring around the metathorax or first one or two adbominal segments, while individuals which die before their removal from the water often turn black from the head to about the sixth abdominal segment. Larvae killed by pinching have exactly the same appearance. This appears to indicate mechanical injury caused by distending the alimentary canal with water. The expulsion of water from both mouth and anus during recovery has already been mentioned. It is a significant fact that larvae in the prepupal condition and those undergoing ecdysis are much more resistant than others. Of these the prepupae swallow water and the moulting larvae do not, owing to the fact that the mouth-parts cannot function during ecdysis; yet the former show at least as great a resistance as the latter. Larvae passing through these two stages are physiologically similar in the following respects: they are quiescent; they are not digesting food, having expelled the contents of the alimentary canal; and they are preparing to shed their cuticle. We have reason to suppose that the oxygen requirement for both prepupae and molting is relatively low, due to the reduction of motion and to the lack of digestion of food. In the light of this probability the great resistance to submergence of larvae in both of these stages becomes understood. Death by drowning seems to be effected, then, both by lack of oxygen and by mechanical injury due to gorging the digestive tube with water. How subterranean larvae are equipped to withstand either or both of these factors, we do not know.

The resistance to submergence in different species, as determined experimentally, varies according to the extent to which the larvae are subjected to submergence or to drenching in their natural habitats. This resistance is not only correlated with the proximity of the habitat to the ground during the active life of the larva, but also with the stage in which the hibernation is passed, since larvae passing the winter in the soil must withstand considerable submergence without regard to their habitat while in an active condition. In order to present more clearly the relations shown in the data collected, it has been divided into two sections, the first of which includes only those species hibernating as larvae on or beneath the ground, the second section embracing those not passing the winter in this stage. If we compare two equally subterranean species, one of which hibernates in the soil as a larvae, the other as a pupa, we note that the former is very much more resistant to water. *Feltia subgothica* and *Agrotis ypsilon* or *Nephelodes emmedonia* and *Phytometra brassicae* afford examples of this point. It is evident, then, that we should confine our comparisons of the resistance to submergence of species, with reference to their habitats, to those which fall in the same section. By so doing the factor of the stage of hibernation is eliminated.

It has been found that the subterranean species present the greatest resistance. *Epizeuxis lubricalis*, because of its exceptional mode of life, cannot properly be compared to other species in this section. Altho never entering the soil, it remains in wet weather in or beneath water-soaked pieces of decaying wood on the ground, dead-wood furnishing the food for this biologically specialized species. Consequently, it presents a high resistance, altho non-subterranean. The relative development of the power to resist water in species of the subterranean-, field-, and tree-strata is indicated in Section 2, in spite of the insufficiency of the data. Most resistant is the fairly subterranean *Lycophotia margaritosa*, next the non-subterranean cabbage looper, *Phytometra brassicae*, of the field-stratum, and least so the arboreal forest-species, *Homoptera lunata*.

EPICRANIAL INDEX AND SUBTERRANEAN HABIT

This investigation of the resistance to submergence in water leads us to conclude that this factor is an index to the extent of the development of the subterranean mode of life, altho hibernating larvae cannot be directly compared in this respect with those not passing the winter in this stage. We have now established two criteria for determining the relative "subterraneanness" of species, namely, the readiness with which the larvae enter the soil and their resistance to water. The latter, since it is capable of numerical expression much more accurately than the former, is far more significant as a guide to the extent of the development of this habit.

It has been stated previously that the epicranial index is correlated with the subterranean habit, those species presenting the most marked underground mode of life having the shortest epicranial stem. Having necessarily disgressed from our principal line of thought, in order to establish the relative "subterraneanness" of various species, we are now prepared to continue our consideration of this suture. We have already shown that the short epicranial stem or large epicranial index isan exceptional condition in lepidopterous larvae, associated with a specialized feeding habit. The data confirms not only that this condition in the Noctuidae is confined to subterranean larvae, but that the extent of the development of this habit is correlated very definitely with the relative length of the epicranial stem. We have ample reason, therefore, for stating that the short epicranial stem is a specialized condition in noctuid larvae, associated with a specialized mode of life, the subterranean one.

Our understanding of the mechanics of this correlation is by no means complete. Subterranean larvae are characterized in general by an extensive chitinization of the pronotum, beneath which the caudal part of the head is retracted most of the time. The mouth-parts tend to become directed cephalad instead of ventrad in such larvae. A parallel, but more extreme condition is exhibited by the lepidopterous leaf-miners, where we find the greatest reduction of the epicranial stem correlated with mouth-parts directed cephalad, the caudal portion of the head remaining beneath the chitinized pronotum. It seems evident that mandibles in this position are better adapted for burrowing than those directed ventrad, and that this change in the position of the head has induced a shortening of the epicranial suture, a point which has been discussed in the morphological section of this paper. When we consider the profound specialization in the heads of beetles, which has been brought about in correlation with the change in the position of the mouth-parts from a ventral to a cephalic direction, it seems quite reasonable to suppose that a less marked specialization in the position of the head, such as we find in subterranean noctuid larvae, would be accompanied by proportionately less pronounced modifications of the head-capsule.

Our knowledge of this relation between the epicranial stem and the feeding habit should be of some value to the economic entomologist. Cut-worms attacking well-cultivated crops, such as corn or tobacco, must be able to enter the soil in order to protect themselves from the heat of the sun. The larvae of those species which do not burrow must depend upon an abundance of grass or weeds, among the bases of which they can withdraw during the brighter part of the day. Noctuid larvae with a long epicranial stem, such as the bronzed cutworm, *Nephelódes emmedonia*, or the members of the genus Cirphis, to which the army-worm belongs, are unable to enter the soil and are therefore seldom found attacking well cultivated crops. When such crops are attacked by army-worms, it is during migratory outbreaks, when their reactions are abnormal. It is a significant fact that all of the fourteen species dealt with by Crumb in his key to tobacco cutworms are of the short-stemmed type. The army-worm's abstinence from tobacco is not a matter of appetite, since this author has found them to eat it as readily as grass, but it is rather because of the inability of this species to burrow into the earth and thus escape the rays of the sun. Hence an examination of the length of the epicranial stem of an undetermined cutworm may inform the field-man whether or not it could consistently attack any well cultivated crop.

The changes in the epicranial index, length of front divided by length of epicranial stem, undergone in the postembryology of various species are presented in the tables. The percentage of variation has been computed in the same way as in Table I. The measurements were made with an ocular micrometer. It will be noted that the greatest individual variation occurs in the last instars of the most subterranean species, which present the most specialized condition of the epicranial stem. The postembryonic development of the epicranial index has been graphically expressed in Plate I. The horizontal axis has been divided into six equal parts representing stadia, this being the usual number within the family. With those species presenting five or seven stadia, the units on the horizontal axis have been respectively lengthened or shortened so that the total length of this axis remains the same for all curves. By this means curves of species having a different number of instars can be more easily compared. The interpretation of this chart presents some very significant points, which we shall consider singly. These curves may be conveniently divided into two types. The curve of the first type turns upward toward the right and shows a marked shortening of the epicranial stem in the later stadia, while that of the second type continues downward and reveals a continuous lengthening of this suture. The significance of this turning upward, presented by the first type, will be considered at this point.

It has been well established in our discussion of the phylogeny of this structure that in this family the short epicranial stem has descended from the longer more primitive one. Since the curves of those species whose last instars present a reduced condition of this suture reveal the presence of a longer one in one or more of the preceding stadia, we must conclude that the postembryology of this structure recapitulates its phylogeny. In our classification of the kinds of postembryonic changes, those involving the relative length of the epicranial stem fall, therefore, under the recapitulative type.

The curves of all species of Noctuidae examined reveal a lengthening in the stem from earlier to later stadia or to the stage in which the turning upward takes place. In the three species examined representing the families Notodontidae, Liparidae, and Psychidae, we find this same condition, altho not very marked in the first of these, indicating apparently that this suture was short in the ancestral larva of these families, and possibly in all the Lepidoptera. We have, however, no phylogenetic evidence in support of this indication, since the larvae of the most generalized families usually have specialized feeding habits, rendering it unsafe to regard a structure whose condition is correlated with the feeding habit, as we have shown that of the epicranial stem to be, as representing a generalized condition in these larvae. This suture is fairly long in the root-boring larvae of the three species of Hepialus examined. In the larva of the European cossid, *Cossus cossus,* we find an unusually short epicranial stem, while *Zeuzera pyrina* shows the opposite extreme, altho both are borers in live-wood. The bag-worm, *Thyridopteryx ephemeraeformis,* offers an average condition of the epicranial index. It is probable that none of these species presents a generalized condition with respect to this structure, altho they represent generalized families. Since the turning upward toward the right of the chart, wherever it is found in these curves, evidently expresses a recapitulation of the phylogeny of this structure, it seems reasonable to conclude that the turning downward toward the left in the same curves represents also a recapitulation. The lack of change in epicranial index from first to second instars in the two species of Phytometra examined, as well as the turning upward shown by the curves of various other species, precludes all possibility of explaining this lengthening of the epicranial stem in terms of the mechanics of growth. There is no mechanical force, in other words, producing more rapid growth in the vertex than in the front. Hence, in the absence of knowledge concerning the early phylogeny of this suture, such data as we have indicate that the ancestral noctuid larva possessed a short epicranial stem, altho this condition is found in existing forms only as a secondary development associated with the subterranean mode of life.

We will consider now the interpretation of the fact that the change in direction in those curves which turn upward takes place in different stadia in different species. This interpretation involves, in the first place, an analysis of the postembryological relation which corresponding stadia in different species bear to one another. Do corresponding instars in species having the same number of stadia necessarily represent identical postembryological stages? Various mammals at the time of their birth present somewhat different developmental stages. The kangaroo, for instance, brings forth its young in a very immature condition, corresponding to that found in the late embryonic life of the majority of mammals. It seems not unlikely that insects may offer a parallel situation, the early postembryonic life of some corresponding, perhaps, to the latter embryonic life of others. Within a group as closely related as the noctuids it seems very improbable that such a condition should exist to any appreciable extent, altho we cannot be sure that all noctuid larvae are equally mature at hatching. However, this may be, it is certain that the passing of corresponding stadia requires quite different proportional lengths of time in different lepidopterous larvae, even within the same family, suggesting the possibility that the postembryological value of such stadia may differ according to the species. If we find, for example, the first stadium of one species requiring one-third of the total larval life and that of another species but one-eighth, we naturally begin to doubt that this stadium represents the same stages of development in these species. The data presented will serve to illustrate this condition. We note that the time required to pass various stadia relative to the total larval life varies considerably in species and to some extent in individuals. The question arises as to how much of this difference is due to external factors and what proportion of it is attributable to innate tendencies. The effects of change of temperature, of starvation, and of parasitism upon individuals of *Polia renigera* are very marked, as is the influence of seasonal conditions upon different broods of *Coramica picta,* demonstrating the pronounced effect of external factors upon the length of stadia. The innate tendencies in this respect can be determined accurately for various species only by rearing their larvae under constant conditions, as has been done with *Polia renigera* and *Agrotis ypsilon.* These were reared at both 28 degrees C. and 21 degrees C. in ventilated jars at 100% relative humidity. The individual variation in the relative length of the stadia of the few individuals which were so reared we cannot satisfactorily explain. Larvae of these two species reared outside do not differ uniformly in the proportional length of their stadia from those grown under constant conditions.

The lack of data derived from rearing larvae in this manner precludes our drawing definite conclusions as to the innate relations existing between the duration of different stadia in different species. Nevertheless a comparison of species reared outside may offer us significant indications regarding this point. It will be noted that the larvae of two species of tussock-moths, *Notolopha antiqua* and *Hemerocampa leucostigma*, which were reared by Payne in Nova Scotia under natural conditions, present a relatively long first stadium. Larvae hatching from forced hibernating eggs of the latter species in Illinois and grown in a warm laboratory by the author also required an unusually long period for passing this stadium, indicating that this unusual condition is not to be explained by the effect of external conditions upon the larvae. Nor is it correlated with hibernation in the egg stage, since three species of larvae of Catocala hatching from hibernating eggs about the same time failed to show this condition, the first and second stadia requiring about an equal amount of time. In all noctuid larvae reared by the author the last stage has been markedly the longest, whereas in these two species of liparid larvae the last two stadia are nearly equal in duration. The three larvae of *Dipterygia scabriuscula*, showing the long first stadium, hatched on the same day as the fifty-one individuals of *Agrotis ypsilon* and were reared under the same conditions, yet all of the latter species required approximately the same amount of time for passing first, second, and third stages. In *Polia renigera* there seems to be a general increase in the length of the two latter stadia, while only the last stage is long in *Agrotis ypsilon* and *Lycophotia margaritosa.* These facts all indicate the presence of innate differences in the relative length of corresponding stadia in different species, even within families.

The presence of such a difference, however, need not necessarily indicate a difference in postembryological value of the corresponding stadia of the species compared, since the longer stadia may be associated with slower development. The fact that the amount of increase in the width of the head-capsule from one stage to the next remains practically constant for the species, bearing no relation apparently to the duration of the stadia, shows that the longer stadium represents the slower growth. For example, *Dipterygia scabriuscula* requires a much longer relative time for passing the first stadium than does *Lycophotia margaritosa,* yet both species grow approximately equal amounts during this stage, the former growing more slowly than the latter. Since the first instars of these two species grow relatively the same amount, it seems quite probable that they present the same postembryological stage at the end of the first stadium, nowithstanding the specific difference in the duration of this stadium. However, this is not necessarily true, for it is easily conceivable that corresponding instars of two species might grow relatively equal amounts and yet attain different stages of development. Much investigation on the postembryology and physiology of these larvae must be completed before we shall be able to settle definitely this question as to the exact relations which the duration of the stadium and the amount of growth bear to the stage of postembryonic development.

It is highly probable, however, that corresponding stadia in closely related species represent about the same stages in postembryology. Altho the first stadium of one species may possibly correspond embryologically to the first and part of the second in another or perhaps the third instar of one may represent in development the latter part of the third and first half of the fourth in another, it seems practically impossible that the developmental differences within this family could be sufficiently profound to render the first stadium of one species equivalent postembryologically to the third of another or the fourth of one to the sixth of another. Whatever minor variations in this respect may exist in those species whose curves turn upward would certainly not be sufficiently extensive to mislead us in interpreting these curves.

From our conception of the law of recapitulation it follows as a corollary that identical stages of development in different species must represent the same period in phylogeny with reference to the recapitulation of a particular structure. This corollary may be stated thus: Any recapitulative change must recapitulate in equivalent stages of development in different conditions of species which have developed during the same phylogenetic period. It follows, of course, that postembryological stages which are not equivalent must present conditions with respect to a particular recapitulative change which have developed at different times in race-history, the earlier stage in the ontogeny representing the earlier phylogenetic period. For example, when we find the epicranial stem, which we have shown to be a recapitulative structure, beginning to shorten in the second stadium of one species and not until the fifth of another, we conclude that this condition developed in the former species in a much earlier phylogenetic period than in the latter.

We cannot be reasonably certain of locating equivalent postembryological stages in different species unless they be rather closely related. In attempting to find developmental stages in a lepidopterous and a coleopterous larva, for instance, which we could be certain were identical, we should encounter, no doubt, considerable difficulty. The former might be more mature at hatching than the latter and they might pupate at somewhat different postembryonic stages. Furthermore, various structural and developmental specializations might render it practically impossible to locate exactly corresponding postembryological conditions in the larvae of these two orders. Tower has shown that beetle larvae present marked developmental diversity within themselves, the wings of certain chrysomelids being distinguishable at the time of hatching from the egg, whereas in the Curculionidae, and some other families they do not appear until the last larval stadium. By going back sufficiently far into the embryology we could undoubtedly locate equivalent stages in the most diverse orders of insects, but in the postembryology we must confine the application of this corollary to closely related species, where no marked developmental or structural diversity threatens to mislead us.

We have already concluded that corresponding stadia of those species whose curves turn upward may be regarded as representing approximately equivalent postembryonic stages. It becomes evident upon the application of the corollary just discussed that these stadia also correspond to more or less definite periods in phylogeny. Each unit on the horizontal axis of the chart represents roughly, then, a definite postembryological stage and an equally definite period of time in race-history. The relation which these units bear to one another we need not consider at this point. It will be shown later that certain biological evidence supports the application of this corollary to our intepretation of these curves.

Plate I shows conclusively that the short epicranial stem has appeared independently in different species during widely separated periods in the ancient history of this family, since the shortening of this suture begins as early as the second period in some but not until the last in others. Hence the short-stemmed species do not constitute a phylogenetic unit, a point which will be discussed in detail later.

The progressive nature of the tendency toward the shortening of the epicranial stem is very apparent in these curves which turn upward. In but one or two instances among the noctuid larvae examined has the relative length of this suture remained unchanged after it has ceased to lengthen and never has it grown subsequently longer after once beginning to shorten, but it has continued to become progressively more reduced with the passing of time. The species which began to exhibit this reduction earliest in their race-history generally present the shortest stem in their last instars. This does not necessarily hold true in all cases, however, since some species had a much longer epicranial stem than others at the time when this suture commenced to decrease in length, so that the greatest reduction in the last instar is not always correlated with the earliest appearance of this shortening. A comparison of the curves of *Polia renigera* and *meditata* will serve to illustrate this point. Moreover, there is a marked diversity in the angle at which the curves of different species turn upward, so that a form which has been developing in this direction during the last period only may have a shorter stem in its last instar than one in which this suture has been decreasing for a much longer period. To use a convenient analogy, some have run faster than others, some have had farther to go, and some began to run much earlier than others, the latter having won the race in the majority of cases.

Certain species, such as *Cirphis phragmitidicola*, apparently represent an incipient stage in this process of reduction, which, if it continues to operate progressively in the future, as it has in the past with other species, must result eventually in reducing the epicranial stem of this species to a fraction of its present length, a condition typified at present by the last instars of *Agrotis ypsilon* and *Feltia subgothica*.

To summarize the conclusion which we have thus far reached regarding the shortening of the epicranial stem in the postembryology of noctuid larvae: This process is a recapitulative one. It represents a secondary development occurring only in certain species with subterranean proclivities. It is of independent origin in different species, having begun at widely different times in race history. It is a progressive process, species in which it has begun continually undergoing greater reduction in the length of this suture. The intensity of this process has varied in different species, that is, it has gone on more rapidly in some species than in others.

In the following discussion, it will be shown that the rate of reduction in the length of the epicranial stem has been subject to an acceleration. The significance of the slopes and angles of both types of curves will now be considered. Certain of them turn upward at a smaller angle than others in the same period, indicating unequal rates of reduction in the stems of such species, as has been stated previously. A parallel situation may be seen in the left-hand portion of the curves, where some turn downward much more abruptly than others, showing that this primary lengthening process has also developed at very different rates according to the species. It should be clearly borne in mind that these conclusions are based on a comparison of angles presented by different curves in the same horizontal unit. Such a comparison can be directly interpreted without danger of going astray, but in comparing the slopes of parts of the same curve or of portions of different curves in different units, we are confronted with a situation which is liable to be misleading without an understanding of the relation which these units bear to one another.

For the purpose of analyzing this relation let us suppose that a certain species has a larval life of sixty days, which we will divide without regard to stadia into six equal periods of ten days each. Suppose further that we represent the curve of this species as we have those in Plate I, using for units, however, these six equal periods instead of stadia. Now in this graphic representation, the periods in phylogeny to which these ten-day divisions correspond are given equal value, whereas in reality this is very far from true. According to the general conception of the working of the law of recapitulation, the first ten days would represent a much longer phylogenetic period than the second ten, which, in turn, would correspond to a portion of the race-history of much greater duration than would the third ten days, and so on until the last ten day division, whose corresponding phylogenetic period would be, perhaps, but a minute fraction of that of the first ten days. The fact that the change in the position of the setae of the trunk, a recapitulative one, is very much greater from first to second instars, than thruout the entire remainder of the larval life illustrates this principle. To represent graphically this condition it would be necessary to extend greatly the length of the first unit, lengthening the second one to a lesser extent, the third a still lesser amount, and so on. We have no means of knowing what the relative lengths of these units should be in order to render the slopes of different parts of this hypothetical curve exactly representative of the relative rates at which these changes in epicranial index have evolved during different phylogenetic periods. We merely know in which direction to apply this sort of correction.

Another means of correction may be applied to this hypothetical curve, by leaving the units equal, as they are in Plate I, but dividing the sixty day larval life into six unequal periods, which gradually increase in length from younger to older. The same result would be accomplished in this manner as by keeping the periods equal and altering the length of the units, in the manner just described. For mechanical reasons it has been necessary to use stadia for our units in Plate I. As already demonstrated the lengths of stadia generally do not present a gradual increase from younger to older in this family, but are often about equal, except for the last, which is usually much longer, and for the first, which is long in some species. The employment of stadia as units, then, offers no correction, except possibly for the last unit, where this stadium is long. It is questionable whether or not this correction, brought about in consequence of the longer duration of the last larval stadium, where this condition is found, is sufficiently extensive to render significant a comparison of the slopes of the last two units without further correction. Possibly these two units may remain equal as they stand in Plate I, the long last stadium having taken care of the correction, which would otherwise have to be introduced by increasing the length of the next to last unit. Where we find a long first stadium we should perhaps increase the length of the first unit even more than otherwise. It is well to recall at this point, however, that the length of a stadium may not be an index to the amount of postembryonic development undergone during it, since, as has been previously suggested, the longer stadium may be correlated with a slower development. If this be true the long first stadium requires no greater correction than the shorter one.

When we compare different parts of the same curve, then, with reference to slope, it must be remembered that the units should not be of equal length, as they stand in Plate I, but that each should be somewhat longer than the one which follows it. The possibility that the last two units may need little or no alteration in order to represent the true condition should also be considered. Furthermore, the first unit may require greater lengthening than otherwise for species with a long first stadium, such as *Dipterygia scabriuscula.* The general effect of this correction is to make the primary curving downward on the left of the chart very gradual and to accentuate the secondary curving upward on the right. Upon applying this correction mentally to Plate I, we note that this secondary shortening of the epicranial stem has proceeded with much greater rapidity than its primary lengthening. It becomes evident, moreover, that this primary process has generally accelerated with the passing of time, altho the curves seem to indicate the opposite condition before the necessary correction is applied. Straight lines, where they occur on the uncorrected chart, do not indicate a constant rate of evolution, but an acceleration. The secondary shortening process has also progressed at an increasing rate, the acceleration being much greater than in the lengthening process.

The two species of the genus Phytometra examined present a distinct type of curve in which the epicranial index remains unchanged thruout the first two periods, followed by the usual accelerated lengthening. The epicranial stem of the last instar of these larvae is as short as that of the average species whose curve turns upward. This condition is evidently due to the fact that in this genus the primary lengthening has been delayed until the third period, so that the epicranial stem has not been evolving in this direction for a sufficiently long time to enable it to attain the length common to species in which this suture has not undergone secondary reduction.

This postembryological study has provided a source of evidence as to the evolution of habit within this family. The correlation between the reduced condition of the epicranial stem and the subterranean mode of life has already been discussed. We have seen that an anatomical relation exists between the short epicranial stem and the cephalic direction of the mandibles, this latter condition being apparently an adaptation for burrowing in the soil. The period in phylogeny in which the shortening of this suture began, as indicated by the curves in Plate I, is to be regarded, then, as the one in which this biological specialization took place. The point of turning upward in one of these curves represents, in other words, the origin of the subterranean habit in the race history of the species in question. It is apparent that this mode of life has originated independently at different times in the phylogeny of different species. Entomology furnishes numerous instances of such independent origin of the same biological specialization in various groups of insects. The aquatic and parasitic modes of life, as well as the leaf-mining and wood-boring habits exemplify this situation, the same habit having developed independently at different times in different groups.

We have demonstrated the accelerative nature of the secondary shortening of the epicranial stem. In the light of the established correlation between this structure and the subterranean habit, it becomes evident that species developing tendencies to enter the soil have gradually become more markedly subterranean at an increasing rate with the passing of time. From this it follows that those forms having developed this habit earliest in race-history must present the most pronounced subterranean mode of life at present. From the data we have collected it is clear that this is precisely the case. The species whose curves turn upward earliest in postembryology reveal the greatest degree of "subterraneanness," as evidenced by their resistance to submergence and other biological traits. Those forms which have been subterranean longest, in other words, are the most subterranean now. This point supports further the corollary that corresponding postembryological stages in different species represent the same phylogenetic period, inasmuch as the conclusions obtained on the basis of this corollary agree with the biological data regarding the relative "subterraneanness" of species.

It has been noted that certain species, typified by *Cirphis phragmitidicola* and *Ceramica picta*, appear to represent an incipient stage in the development of the subterranean mode of life, entering the soil only under extreme stress during the feeding period. The curves of such forms turn upward but slightly, in the last unit only. If the development of this habit continues progressively in the future as it evidently has in the past, such slightly subterranean species must eventually become markedly so, like *Agrotis ypsilon* or *Feltia subgothica*. This suggests the interesting possibility that we may have in the remote future a larger number of species of subterranean noctuid larvae than at present. However speculative this proposition may seem, it is undoubtedly indicated by the data at hand.

When we compare subterranean and non-subterranean larvae with reference to the number of individuals parasitized, the advantage of the former mode of life becomes obvious. From more than a thousand individuals of *Feltia subgothica* reared during three successive years, but four or five have been infested with insect-parasites, whereas larvae remaining above ground during the daytime, such as the cabbage-looper or the army-worm, are frequently 90% parasitized by many insect-enemies. Subterranean cutworms are similarly free from attack by birds. Egg-parasites affect both classes equally. Fungi and wilt diseases seem to be as generally found in non-subterranean hosts as in those whose habitats are associated with the earth. The only nematodes thus far recorded from noctuid larvae were taken from a single subterranean cutworm, Agrotis sp., by the author. The apparent rarity of these parasites in cutworms indicates that they are not to be regarded as important enemies. Large carabid beetles are evidently the only important natural enemies affecting subterranean lepidopterous larvae to an appreciably greater extent than those which do not enter the soil. Yet these feed extensively upon larvae above ground, some even climbing trees in search of their prey. From the point of view of protection from natural enemies, the subterranean habit unquestionably offers important advantages, which probably accounts to a large extent for its progressive nature in the course of evolution.

The interpretation of certain exceptional curves in Plate I is problematical. That of *Agrotis clandestina* fails to turn upward, altho the larva of this species is to some extent subterranean. The primary lengthening of the epicranial stem of this species is but slight in the last period, indicating the retarding of this process, which must necessarily precede the secondary shortening. Not only does the curve thus indicate an incipient condition in the reduction of this suture, but the bright coloration of this cutworm points further to recent development of the subterranean habit. Cutworms which enter the soil generally tend either to lose their pigment, like *Sidemia devastatrix*, or to become indistinctly marked and dully colored. We know of few equally subterranean larvae with such bright colors and distinct markings as clandestina. *Agrotis c-nigrum*, to which this species is very closely related, exhibits similar but much less distinct markings and duller colors, its curve being typical of cutworms which burrow in the ground. Clandestina is probably one of our "youngest" cutworms, this habit, altho quite well developed, being too young phylogenetically to be accompanied by a marked shortening of the epicranial stem.

Catocala ? vidua presents the opposite situation, where we have an arboreal form whose curve turns upward slightly in the last unit. Possibly the larva of this species enters the soil to pupate, altho the members of this genus typically spin cocoons above the ground. The epicranial stem of the arboreal *Heterocampa bilineata* (Notodontidae) undergoes a marked secondary shortening, showing that this condition in families other than the Noctuidae is not necessarily associated with the subterranean mode of life. In spite of the marked turning upward in the curve for this species, the stem of the last instar is much longer than in larvae which enter the soil. The peculiar curve of the bag-worm bears some relation, perhaps, to its unusual feeding habit. A much more extensive postembryological study of this structure must be made, embracing many families of lepidopterous larvae, before we can hope to understand the significance of these changes.

Having discussed the postembryology of the epicranial stem and its biological significance, it now remains for us to consider the phylogenetic evidence which this study may afford. A certain degree of correlation between the types of curves in Plate I and taxonomic groups can be observed. Attention has already been directed to the peculiar type of curve presented solely by the two representatives of the Phytometrinae examined. Whether or not this type is characteristic for the entire subfamily we cannot state. When we consider the pronounced uniformity of the larvae of this group, however, it seems fairly probable that this is so. The species of Catocala represented exhibit an unusually great increase in the length of the epicranial stem during the first two periods. Species of the same genera have curves similar in position and shape, except where the secondary turning upward has interfered. This process, being associated with the subterranean habit, which often differs in closely related species, cannot be relied upon as an indication of phylogenetic relationship. With curves which turn upward the primary portions only can be safely compared from a taxonomic point of view. For instance, *Cirphis unipuncta* presents a typical non-subterranean type of curve, whereas those of *phragmitidicola* and *pseudargyria*, which are very closely related to this species, are of the incipient subterranean type. The difference in the later postembryonic development of this suture in *Agrotis c-nigrum* and *clandestina* has already been referred to. A comprehensive series of such curves would unquestionably afford valuable phylogenetic information.

All of the species examined were established earlier than the first phylogenetic period represented in Plate I. In other words, none of the curves of closely related species have started from the same point in the first unit. A more extensive series might very possibly discover species so recent that their curves would unite in a common line in the first one or two units.

The race-history of the reduced epicranial stem may be represented by the diagram shown in figure 61, which indicates both the independent origin and progressive nature of this condition. In this figure 1 represents the persistence of the long-stemmed ancestral condition to the present. A form which has departed relatively recently from the condition of 1 and which tends toward the development of a shorter stem is illustrated by 2. The most ancient departure from 1 is represented by 6, which reveals the shortest epicranial stem at present. The conspicuousness and apparently fundamental nature of this character would tempt taxonomists to employ it for the division of larger groups within this family. Our knowledge of its phylogeny, however, derived from this postembryological study limits its taxonomic use to the separating of species and in some cases, perhaps, of genera. The taxonomist studying this structure without regard to postembryological evidence, but drawing his conclusions entirely from the comparative morphology of the last instar, would, in all probability, be misled as to its phylogeny. He would, of course, without the aid of postembryology correctly conclude that the short stem represented a specialized condition but, on the other hand, no clue as to the independent origin of the shortening of this suture would be afforded him. Working on this basis, he would most naturally be led to believe that the species with the short epicranial stem represented, at least for the most part, a phylogenetic unit. The fact that this condition is often found in closely related genera would add to this impression. Its independent origin in different species in the same subfamily or genus could not possibly be deduced without a postembryological study. Figure 60 represents diagrammatically the erroneous interpretation of the evolution of the short epicranial stem, which would be most naturally derived from a study confined to full-grown larvae. In this diagram 1 represents the persistence of the primitive long-stemmed condition, as in Figure 61. The short-stemmed condition, on the other hand, is shown as descending from a common ancestor. The preservation of the condition of the most ancient departure from 1 is illustrated by 2, whereas in reality the condition of 2 is the most recent departure in this direction. According to Figure 60, 6 has developed most recently and reveals the most extreme specialization. In reality the condition of 6 at the present time is found in species in which this tendency appeared earliest in phylogeny, as shown by Figure 61. A comparison of these two diagrams, the correct and the false, derived respectively with and without regard to postembryology, demonstrates in a convincing manner the phylogenetic value of this neglected source of evidence.

POSTEMBRYOLOGY OF LABIUM AND SPINNERET

The most profound postembryonic changes undergone by noctuid larvae are those in the form of the spinneret, while other parts of the labium also present considerable difference according to the instar. The stipular setae frequently increase in relative size during larval life (Figs. 40, 43, 44), altho they may remain about the same (Figs. 33, 38). A striking decrease in relative size is always undergone by the two sensoria of the palpiger and by the pair of smaller ones on the proximal semicircular sclerite of the spinneret (Figs. 29-32, 33-36, 38, 40, 41, 43-45). As previously mentioned the same situation is presented by those of the head, altho not so marked. This appears to be a non-recapitulative change due to the mechanics of growth. The pronounced decrease in the relative size of the ocellarae already discussed offers an apparently parallel situation. It seems evident that the modified hypodermis of sensory organs, whether of visual or of chemical sense, grows more slowly than the ordinary hypodermis.

In the first instar of some species the proximal sclerite of the spinneret is continuous between the sensoria, forming a complete ring instead of a semicircle, as it sometimes does in the older noctuid larvae (Figs. 33-38). The fact that the former condition is of quite frequent occurrence thruout the order suggests that it may be the primitive one, in which case this change is to be regarded as a recapitulation, the semicircular sclerite of the noctuid larva representing the remnant of a complete ring. The first instars of *Polia renigera* and of *Agrotis ypsilon*, on the other hand, exhibit the condition typical of fully grown noctuid larvae with respect to this point (Figs. 29-40). In the former species, however, a secondary chitinization appears in the last instar, connecting the two ends of the semicircle (Figs. 31-32).

The palpi undergo changes in form and in the shape and relative size of their setae. A comparison of Figures 30 and 31, 33 and 38, and 40 and 44 reveals the fact that both segments of the palpus become relatively longer and narrower during development. Since there appears to be no evidence indicating whether or not the ancestral palpus was shorter and broader than the typical one of existing forms, we cannot attempt to classify this change. The significance of the striking reduction of the seta of the proximal segment during larval growth is also problematical. Usually, altho not always, the terminal seta of the distal segment becomes much more slender and relatively shorter in the later stadia. *Lycophotia margaritosa* appears to present an exceptional situation in the development of all of the setae of this region. Those of the stipula fail to increase in relative size as they usually do and the terminal one of the palpus becomes relatively larger in the course of growth, whereas the reverse is typically true. The reduction of the terminal seta commonly found in the Noctuidae is paralleled in certain leaf-miners figured by Trägardh. Moreover, the terminal setae of the antennae and maxillae of caterpillars are frequently short and stout in the first instar, becoming normal in form during development. The significance of these changes cannot be definitely determined in the present state of our knowledge of their phylogeny. They are probably non-recapitulative but are evidently not to be explained by the mechanics of growth, since exceptional instances occur.

It was mentioned in the morphological part of this paper that the seta of the proximal segment of the palpus presents a specialized condition with reference to position in *Lycophotia margaritosa*, where it is located mesad instead of laterad of the small terminal segment (Fig. 38), a very exceptional situation. The location of this seta is normal in the first instar (Fig. 33), the unusual position found in the later instars being the result of its migration around the cephalic side of the distal segment. This process is unquestionably a recapitulation.

The postembryology of the spinneret of noctuid larvae is a highly complicated and most interesting subject. Four distinct types of development of this structure have been observed and most probably a more extensive study will reveal the existence of a number of additional ones in the order. In Type I the spinnerets of both first and last instars are subequal in length and distinctly longer than in the intermediate stadia. The species of Phytometra examined present this condition. Type II is represented by *Lycophotia margaritosa*. The spinneret of the first instar of this species (Fig. 34) is much longer than the palpi and fairly slender, the condition most frequently found in the fully grown larvae thruout the family. In the second stadium it is very much shorter and reveals slight projections on both upper and lower distal margins (Figs. 35, 36). The reduction in length proceeds a little further in the third instar and the distal projections become longer (Fig. 37). Moreover the lateral emarginations, which are very rudimentary in the first two stadia, are fairly deep in this one, so that the upper and lower lips, previously described, become evident. From this stadium to the last there is no appreciable change in relative length, but the projections gradually become elongated on both lips, forming a well developed fringe, and the proximal fold and its sclerite decrease considerably in relative width. The lower lip shows a tendency to become bilobed. The decrease in the relative size of the sensoria has already been discussed. *Polia renigera* exemplifies Type III. The spinneret of the first instar is somewhat shorter than the palpus (Figs. 29, 30). In the following stadia a gradual increase in its relative length occurs and the proximal fold becomes markedly elongated on the cephalic aspect. The condition in the fully grown larva is shown in Figures 31 and 32, where the spinning organ is somewhat longer than the palpi and the extension of the proximal fold reaches about half way to its distal end. The secondary chitinization of the spinneret and of the proximal fold, like that between the sensoria of the proximal sclerite, does not appear until the last instar. Type IV presents very little change in the relative length of the spinneret in different instars, as may be seen by comparing Figures 40, 41, 43, and 44, representing the postembryology of the spinneret of *Agrotis ypsilon*, which typifies this type of development. The proximal sclerite descreases in relative width as in the other types. The fold in this species increases as it does in *Polia renigera* but to a much lesser extent. A secondary chitinization appears on the fold continuous with the primary sclerite but of a lighter color, again recalling the somewhat similar condition in *renigera*. The fringe develops much as in *Lycophotia margaritosa*, its first indication appearing as slight rounded projections on the upper lip of the second instar (Fig. 42). Unlike *margaritosa*, however, the lateral emarginations are well developed in this stadium and the distal projections appear only on the upper lip. In the following instars the lower lip becomes distinctly bilobed and a small fringe, which presents considerable individual variation, develops on the upper one from the projections which appear first in the second instar (Figs. 43-46).

The essential basis for the recognition of these four types is the difference in the relative length of the spinneret in different stadia. The other changes described will be considered later. In Type I the spinneret is longer in the first and last instars than in the others; in II it is long in the first stadium, becoming short in the course of development; the condition in III is exactly the opposite, the first instar having a short spinneret which develops into a long one; in IV it is short thruout all stadia. Each of these types of postembryonic development of this structure is correlated with a different distribution of the spinning habit with reference to the instars. The species falling under Type I, long in first and last stadia, spin threads in the first instar and a well developed cocoon in the last. In Type II, long to short, the first instar only spins silk, the cocoon-spinning habit having been entirely lost in correlation with subterranean pupation. Type IV, short thruout, has lost the spinning power in all stadia.

These changes in the relative length of the spinneret during postembryonic development are obviously to be explained by the unequal function of this structure in different stadia rather than by recapitulation. Inasmuch as the ancestral noctuid larva had a long, slender spinneret, as has been shown on the basis of morphological evidence, the expression of the recapitulative force would result in a relative shortening of this organ from first to last instars in those forms where the spinneret of the last stadium has been reduced. Whereas this condition is found in Type II, where the first instar spins silk and the last one does not, it fails to occur in IV, where the spinneret is short in all stadia, the spinning habit being absent thruout. Similarly species which have preserved the long ancestral spinneret in the last stadium would exhibit this condition in all instars, if recapitulation were the only factor operating, whereas marked inequality in the relative length of this organ in the different stadia is found in both Types I and III, where the spinneret is long in the last instar. This situation exemplifies what may prove to be a general zoological law, namely, *When the expression of the recapitulative law conflicts with the development in successive instars of a series of adaptations to different functions, or to different degrees of the same function, the latter is dominant* .

In species where either all or none of the instars spin silk it might be argued that the recapitulative force would be allowed to express itself, since the factor of unequal function would be eliminated. Instances are rare in the Noctuidae where the larvae of all stadia spin silk in approximately proportionally equal amounts, as in the tent-caterpillar, *Malacosoma americana*. *Sidemia devastatrix* furnishes the only instance known in the Noctuidae where this habit appears to be equally developed thruout larval life, and the data in this case are not conclusive, since live larvae of only the first and last three stadia have been seen by the author. The first instar spins silk threads during the feeding period, the fourth and fifth form slight cocoons in which to molt and the last pupates within a cocoon. Since the long ancestral spinneret has been preserved in this species, the expression of recapitulation would not involve any postembryonic change and so far as known none occurs, the spinneret of all stadia examined being long. Type IV presents the opposite condition where there is no silk-spinning in any stadium. In this type the recapitulative law is not followed with respect to the relative length of the spinneret, which remains approximately the same thruout larval development.

An analysis of the possibilities with regard to the original use of the habit of spinning silk in the order and in the family reveals the fact that we cannot reasonably expect to encounter an expression of the recapitulative force in species where the factor of unequal function has been secondarily eliminated, as it has in Type IV. There are at least three ways in which this habit may have originated in the ancestral lepidopterous larva. It may have developed originally in the first instar, functioning as a means of dissemination by the wind, as it does in various existing species, or in some other capacity. Apparently better grounded is the hypothesis that the spinning of a cocoon by the fully grown larva represents the primitive condition, the other instars having in certain forms subsequently developed the habit of spinning threads. Perhaps most probable of all is the possibility that this habit was originally equally developed in all stadia, as it is now found in the case-bearers, tent caterpillars, borers which line their burrows and miners which line their mines with silk. The frequent occurrence of this condition among larvae of the more generalized families lends weight to this view, altho the limitation of the spinning of silk to cocoon-spinning often met with thruout the order favors the conclusion that this situation is the ancestral one.

However this may be, the very exceptional occurrence among noctuid larvae of the equal development of the silk-spinning habit in all stadia strongly indicates that the spinneret functioned unequally in different instars in the primitive caterpillar of the family. The spinning of silk most probably occurred in the last instar or in both first and last, these two conditions being the only ones of general occurrence in forms which retain the primitive long spinneret in the fully grown larva. Thus the factor of unequal function in the postembryology of the spinneret of noctuid larvae is most probably an ancestral one. In Type IV this factor has become secondarily eliminated by the loss of the power to spin silk in both first and last instars. We cannot reasonably expect, therefore, that recapitulation would find expression in the postembryology of this type with respect to the relative length of the spinneret.

As previously concluded in the treatment of the morphology of the spinneret the fringe is a specialization which has developed in correlation with the habit of subterranean pupation, apparently functioning as a brush for the lining of the earthen cell with a secretion of the silk-glands. The fact that it is well developed only in the last instar also supports this conclusion. The four types of the development of the spinneret just discussed are based only on its relative length and do not apply to the fringe, which often appears in both Types II and IV where the reduced spinneret occurs in the last instar. The appearance of the fringe in postembryonic development apparently represents a recapitulation. Since it functions only in the last instar, however, the factor of unequal functions has operated in the same direction as the recapitulative force, so that this process is not the expression of recapitulation alone. It falls under the same group in our classification of postembryonic changes as the development of the adfrontal suture, recapitulative and adaptive to unequal function.

The appearance of the lateral emarginations, which are present only in the reduced type of spinneret, have presumably developed in phylogeny as they do in postembryology. Since the upper and lower lips thus formed probably have to do with the function of the spinneret, which is performed only in the last instar, unequal function as well as recapitulation has operated in the production of this postembryonic change.

The appearance of the elongated proximal fold and of the secondary chitinization in the postembryonic development of *Polia renigera* (Figs. 29, 32) also recapitulates the phylogeny. Since these structures serve as a support for the spinneret, which is functional only in the last instar, unequal function also plays its part in these changes, which are evidently to be regarded as recapitulative and adaptive to unequal function.

The reduction in the relative width of the proximal sclerite is apparently of general occurrence within the family, this process always manifesting itself regardless of the trends of development along other lines. Until more definite knowledge is gained of the phylogeny of this sclerite no definite conclusion can be reached as to the significance of its reduction in relative width during larval life. The same may be said of the loss of the portion of the proximal sclerite which lies between the sensoria in the first instar of *Lycophotia margaritosa*. Since morphological evidence indicates that both the palpiger and the proximal sclerite of the spinneret in noctuid larvae represent the remnants of a more general chitinization, it seems probable that both of these changes are recapitulative.

The taxonomic importance of the structure of the spinneret of the last instar has already been emphasized. It is obvious that the condition of this structure in the first instar also provides valuable phylogenetic information. In *Lycophotia margaritosa* and *Agrotis ypsilon*, where the spinneret of the last instar is essentially of the same type, that of the newly hatched larva is strikingly different. These two species are both of the subfamily Agrotinae. The habit of spinning threads in the first stadium, nevertheless, is apparently a comparatively fundamental one, hence the extent of the development of the spinneret in this stage, which is correlated with this habit promises to serve as a fundamental guide to relationships. It is important, therefore, that all accounts of the development of caterpillars state the situation with regard to the form of this organ and with reference to the spinning of threads in all instars. On the basis of the limited amount of data available as to the occurrence of silk-spinning in the first instar of noctuid larvae no correlation with the mode of life is apparent.

LARVAPODS

In the morphological discussion of the larvapods it was noted that the ancestral condition, where the four median pairs are well-developed, has been retained in the majority of noctuid larvae, altho in certain subfamilies the first one or two pairs tend to become reduced and are sometimes lacking. The incipient condition in the development of this specialization is exemplified by many Agrotinae, where the first two pairs are distinctly, altho not strikingly shorter than the others. In Catocala a more advanced condition is found, the first two pairs of larvapods being much smaller than the others. This process has proceeded still further in the specialized subfamily Hypeninae, where the first pair is without crochets or wanting altogether. The most specialized situation with respect to this process is exhibited by nearly all Phytometrinae, whose adults are undoubtedly among the most specialized noctuids, and by certain Catocalinae, such as Caenurgia, where the larvapods of only the fifth and sixth adbominal and of the anal segments remain.

If the postembryonic development of the larvapods were to recapitulate their phylogeny, we should expect to find a relative decrease in the size of the first one or two pairs from the first to the last instars in forms where these larvapods are reduced in size in the fully grown larva. In species where the last instar lacks the first one or two pairs they would be found, at least in a vestigial condition, in the newly hatched larvae, unless their loss took place sufficiently early in phylogeny to restrict their appearance in ontogeny to embryonic stages. Since these two pairs of larvapods are generally present in the Catocalinae, their absence being rather exceptional, and since Hampson has reported them present in one genus of the Phytometrinae, this latter possibility must be regarded as highly improbable.

A study of the postembryology of these appendages reveals the fact that these hypothetical changes based on recapitulation alone are not found and that the reverse condition usually presents itself. Instead of becoming relatively smaller during the course of development, the first two pairs of larvapods typically increase in relative size from the first to the last stadia. Moreover, where they are wanting in the fully grown larva, no trace of them is found in the first instar. On the contrary, in certain genera of Agrotinae, Hadeninae, and Acronyctinae, the first pair is absolutely wanting in the first and second stadia, appearing in the third as a minute vestige and increasing in relative size thereafter. This condition is diametrically opposite to the one which would result from an expression of recapitulation. From these facts it may be stated conclusively that the appearance or the increase in the relative size of the first one or two pairs of larvapods in the postembryonic development of noctuid larvae are non-recapitulative changes, the effects of recapitulation having been completely obscured by other factors.

The reduction or absence in lepidopterous larvae of the cephalic one, two or three pairs of larvapods is correlated with the peculiar biological characteristic of walking with a looping gait. Noctuid larvae with this gait have been referred to as semi-loopers as opposed to the loopers of the Geometridae, where this gait is even more pronounced, since but one pair of median larvapods persists in the larvae of this family. Caterpillars of this type, because of the longer steps which they are able to take, can travel more rapidly for the amount of energy expended than those which walk in the usual manner. It is a matter of simple mechanics that the looping gait is the more efficient from the point of view of rapid progress. Loopers appear to be generally more active than other caterpillars, altho certain arctiids whose aptitude for traveling at a high rate of speed is frequently displayed, furnish an exception to this rule.

The evolution of this habit in the larvae of the Catocalinae, Phytometrinae, and Hypeninae is very probably to be accounted for by the advantage of rapid locomotion which is thereby undoubtedly gained. The looping gait enables these caterpillars to withdraw from undesirable situations with the minimum loss of time and with the minimum amount of exposure to the attack of enemies. When dislodged from the trees or the plants upon which they feed, usually in more or less protected situations, or, in the case of most Catocalinae, from the twigs upon which they rest, in which situation they are protectively colored, those which can most rapidly regain a favorable environment must survive natural selection in the course of evolution. The many advantages gained by the power of rapid locomotion are so obvious that a detailed discussion of them would be superfluous.

Larvae of the ground and subterranean strata enjoy protection in a large measure by virtue of their nocturnal and subterranean habits. The proximity of their food to the ground, moreover, requires but little climbing for them to reach it. In the older comparatively inactive larvae of such forms the reduction of the first two pairs of uropods is generally not pronounced. *Caenurgia erechtea* and certain phytometrids afford exceptions to this rule. The occupation of the field stratum by the former species is very unusual for larvae of the Catocalinae and is, therefore, to be regarded as a biological specialization. The loss of the larvapods very possibly took place in the ancestor of this species previous to its migration from the tree to the ground stratum. However, this may be, the looping habit in noctuid larvae appears to be generally correlated with a relatively active mode of life and with one which often renders rapid locomotion especially advantageous. It is never found among the cutworms or their biological allies, except in the earlier stadia, being usually confined to the first two. These instars are semiloopers in the family in all instances known to the author, regardless of the gait of the older larvae. In the earlier stadia the larvae are markedly more active than in the later ones. The small size and proportionately long setae of newly hatched caterpillars render them decidedly subject to conveyance by the wind, a matter of common observation. This fact necessitates that they be generally more active than the older instars. Moreover, the large number of individuals hatching simultaneously from a single egg-mass demands dissemination either by the wind or by locomotion, considerable activity being involved in either case. The threads frequently spun only by the first instar serve as veritable parachutes in some instances and as anchors by which they attach themselves to the food-plant in others. The former employment of the thread, however, has not been actually observed in the Noctuidae, so far as known, altho it has been reported in other families and most probably occurs in this one. The apparently universal presence of the looping gait in young noctuid larvae, which is characteristic of the last instars of only the more active larvae of the family, such as the catocalas, is not at all surprising when we consider the especial need for rapid locomotion during the first one or two stadia.

The appearance or increase in the relative size of the first one or two pairs of larvapods during the postembryonic development of noctuid larvae is obviously the expression of the unequal function of these structures in different stadia. The extent of the reduction of these larvapods is proportional to the extent of the development of the looping gait, which is correlated with the amount of advantage gained by greater or less rapidity in locomotion, an advantage which is greater in the earlier instars than in the later, especially with noctuid larvae of the ground and subterranean strata. This factor of unequal function in different instars has completely obscured the effects of recapitulation, as in the parallel situation of the unequal function of the spinneret, which has been previously discussed. Thus additional support is given to the law stated to the effect than unequal function is dominant over recapitulation when these factors act in opposition to one another.

Henneguy states that the gaining of the first pair of larvapods occurs during postembryonic development in the European noctuids, *Agrotis pronuba*, (Agrotinae), *Polia nebulosa* (Hadeninae) and *Trachea atriplicis* (Acronyctinae). This condition has been found by the author in *Agrotis ypsilon* and in *Feltia subgothica*, altho the first pair of larvapods is fairly well developed in the first instars of *Agrotis c-nigrum* and *badinodis*. In *Lycophotia margaritosa*, of the same subfamily, they are present but extremely vestigial, bearing only two or three crochets. A similar difference with respect to this point is also found in the genus Polia. The American *renigera* has the first pair of larvapods comparatively well developed in the first stadium, as does the rather closely related *Ceramica picta*, whereas they are reported absent in the European *Polia nebulosa*. In like manner they are not strikingly smaller than the second pair in the newly hatched larvae of *Sidemia devastatrix*, altho Henneguy states that they are absent in those of the closely related *Trachea atriplicis*.

The difference in the development of the first pair of larvapods in closely related species indicates that this developmental character is not a fundamental one from the taxonomic point of view. The scattered occurrence of their absence in the first two stadia thruout the subfamilies Agrotinae, Hadeninae, and Acronyctinae shows that this condition, like the length of the epicranial stem and like the number of molts, has originated independently in different species. The tendency toward the reduction of the first two pairs of larvapods is, however, general thruout the family.

In the first instars of *Catocala illia*, *amatrix*, *innubens*, *cara*, and of *Homoptera lunata* the first two pairs are no more reduced than in the other subfamilies mentioned, altho the fully grown larvae of the Catocalinae are typically characterized by the very small size of the first two pairs of larvapods compared to the others. The tendency toward their marked reduction in this subfamily evidently applies to all stadia, rather than to the early ones alone, altho this process has advanced somewhat further in the young larvae than in the old ones, as it generally has throughout the family. The lack of striking difference between the relative size of the first two pairs of larvapods of the early instars and those of the later ones is a fundamental developmental character, which is evidently correlated with the active mode of life of the fully grown larvae of this subfamily.

CROCHETS

During the growth of noctuid larvae the number of crochets increases markedly on all of the larvapods. This process in *Agrotis ypsilon* may serve as a typical example. The formula for the first instar is -, 3, 5, 7, 8, the first pair of larvapods being absent, for the second it is -, 5, 7, 7, 8, for the third 3, 7, 9, 10, 14, for the fourth 9, 13, 13, 13, 16, for the fifth 12, 13, 15, 16, 19, for the sixth 16, 18, 19, 19, 20, and for the fully grown larva it is 16, 20, 20, 21, 25. Like the ocellarae and the sensoria the crochets are relatively much larger in the earlier than in the later stadia. Consequently there is sufficient space on the larvapods of the first instar to accommodate but relatively few crochets. A survey of the number found in the larvae of the more generalized families in the order, as well as in caterpillars generally, offers absolutely no evidence favoring the view that this change is recapitulative. The increase in the number of crochets is apparently to be accounted for by the mechanics of growth.

Generally throughout the order the larvapods whose distal ends have the greater diameter bear the larger number of crochets. This relation is also clearly revealed by the condition found in an individual larva whose different pairs of larvapods differ in size. Since, in such an individual, the crochets are of approximately the same size on both large and reduced larvapods, there is naturally a larger number of them on the former. Hence with the increase in the relative size of the first two pairs, previously discussed, the number of crochets increases proportionally. But this change in the relative size of the larvapods is due to unequal function, as already determined. Therefore, the increase in the number of the crochets on the first two pairs is unquestionably the expression of two factors, the mechanics of growth and unequal function. This change is, therefore, to be classified as mechanical-adaptive.

The analogous process on the other pairs is, on the other hand, not influenced by the adaptive factor, since there is no appreciable change in the relative size of these larvapods during larval growth. Hence the mechanics of growth alone is responsible for this change. The fact that the increase in the number of the crochets of the first two pairs is considerably greater than that of the others is consistent with the compound nature of the former postembryonic change as opposed to the simple one of the latter.

SUMMARY

The principal results yielded by this investigation of the postembryology of noctuid larvae may be summarized as follows:

(1) The number of molts is characteristic of species, altho influenced to some extent by external factors.

(2) The largest number of molts, the greatest amount of larval growth, and the highest fecundity are three mechanically correlated conditions.

(3) These three conditions represent a specialization, the larger number of molts and higher fecundity having been derived from the smaller number, which is correlated with lower fecundity.

(4) The conditions of larval growth, number of molts, and higher fecundity have arisen independently in different species.

(5) An investigation of the postembryonic development of all external structures of noctuid larvae has revealed the existence of many previously undescribed changes.

(6) Three factors have been identified as operating in the production of the changes observed, recapitulation, adaptation to unequal function in different stadia, and the mechanics of growth.

(7) These factors may express themselves singly or in various combinations, in which case they may operate either in the same direction or in opposition to one another.

(8) Recapitulation is essentially different from the other two factors in that it is the expression of a general law, which fails to manifest itself only when its effects are obscured by those of other factors.

(9) When recapitulation and adaptation to unequal function conflict, the latter is dominant.

(10) When the factor of unequal function becomes secondarily eliminated, the recapitulative force remains unexpressed.

(11) The postembryonic changes found have been classified according to the factor or combination of factors responsible for them. This classification is as follows:

(I) Recapitulative.—Changes in the relative length of the epicranial stem, in the extension mesad of the postgenae, and in the depth of the labral cleft; the migration ventrad of the occipital setae, of the head setae v1, v2, and probably f1; changes in the coloration of the head and body, in the sculpturing of the cuticle, in the location of the body-setae, except those of the first two pairs of larvapods, and in the form of the mandibles; the reduction of the primary chitinization and acquisition of secondary chitinization in the proximal sclerite of the spinneret; the migration mesad of the proximal seta of the labial palpus in Lycophotia; the secondary appearance of the tubercle of the seta rho in certain phytometrids.

(II) Non-recapitulative.—(a) Adaptive to unequal function in different stadia.—Changes in the form of the setae of the head and trunk and in the relative length of the spinneret; the acquisition of the first pair of larvapods; the increase in the relative size of the first two pairs of larvapods; changes in the position of the setae of these larvapods. (b) Due to the mechanics of growth.—The decrease in the relative size of the head, ocellarae, and sensoria; the migration ventrad of the head-setae v2, v4, and v5; the increase in the number of the crochets of the larvapods of the fifth and sixth abdominal segments.

(III) Compound, (a) recapitulative-adaptive.—The appearance of the adfrontal sutures; of the fringe, lips, and secondary chitinization of the spinneret; the elongation of the proximal fold of the spinneret. Compound, (b) adaptive-mechanical.—The increase in the number of crochets of the first two pairs of larvapods.

(IV) Problematical.—Changes in the form of the antennae, in the relative size of the setae of the stipula, and in the form of the labial palpi; the reduction of the setae of the labial palpi and antennae; the loss of the tubercles of the body-setae.

(12) The great value of a comparative postembryological study of species as a source of phylogenetic information has been demonstrated, chiefly by means of a detailed investigation of the development of the epicranial stem.

(13) Different types of postembryonic development of various structures, especially of the spinneret, epicranial stem, and larvapods, furnish developmental characters of considerable taxonomic importance. The condition of these structures should be given in detail in all descriptions of young caterpillars. The relative length of the spinneret of the first instar is especially important. The postembryonic development of the epicranial index offers an excellent means of determining relationships.

(14) Various correlations between structural and biological postembryonic changes have been established, such as those between the relative length of the spinneret and the amount of silk spun in different stadia, between the development of the fringe of the spinneret and the habit of subterranean pupation, and between the acquisition or relative increase in size of the first pair of larvapods and the decrease in general activity.

(15) The correlation between the subterranean mode of life, the resistance to submergence in water, and the short epicranial stem has been demonstrated. By virtue of this relation the postembryology of the epicranial stem has revealed the progressive nature and independent origin of the subterranean habit of noctuid larvae.

(16) The significance of the adfrontal suture has been determined upon the basis of postembryological evidence. This suture is a modification functioning as a means of ecdysis at the time of pupation.

(17) Sensory hypodermis, such as that of the ocellarae and sensoria, does not grow as rapidly as the ordinary hypodermis.

POSTSCRIPT

Much of the data of this investigation is included in twelve statistical tables which were submitted with the manuscript. The intricacy of these tables is such that it has been impossible to reproduce them here. They were included in the original copy of the thesis which is deposited in the Library of the University of Illinois, where they can be consulted by those interested.

ACKNOWLEDGMENTS

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To Dr. S. A. Forbes the author wishes to express his sincere thanks for the use of the collection of the Illinois State Laboratory of Natural History. Since it has been necessary that practically all other material be collected and reared, the some thirty-five species of noctuid larvae in the collection were indispensible for the comparative morphological part of this work. Dr. C. P. Alexander and Mr. J. R. Malloch of the State Laboratory have extended numerous courtesies, which have aided very materially in the progress of these investigations and which are sincerely appreciated.

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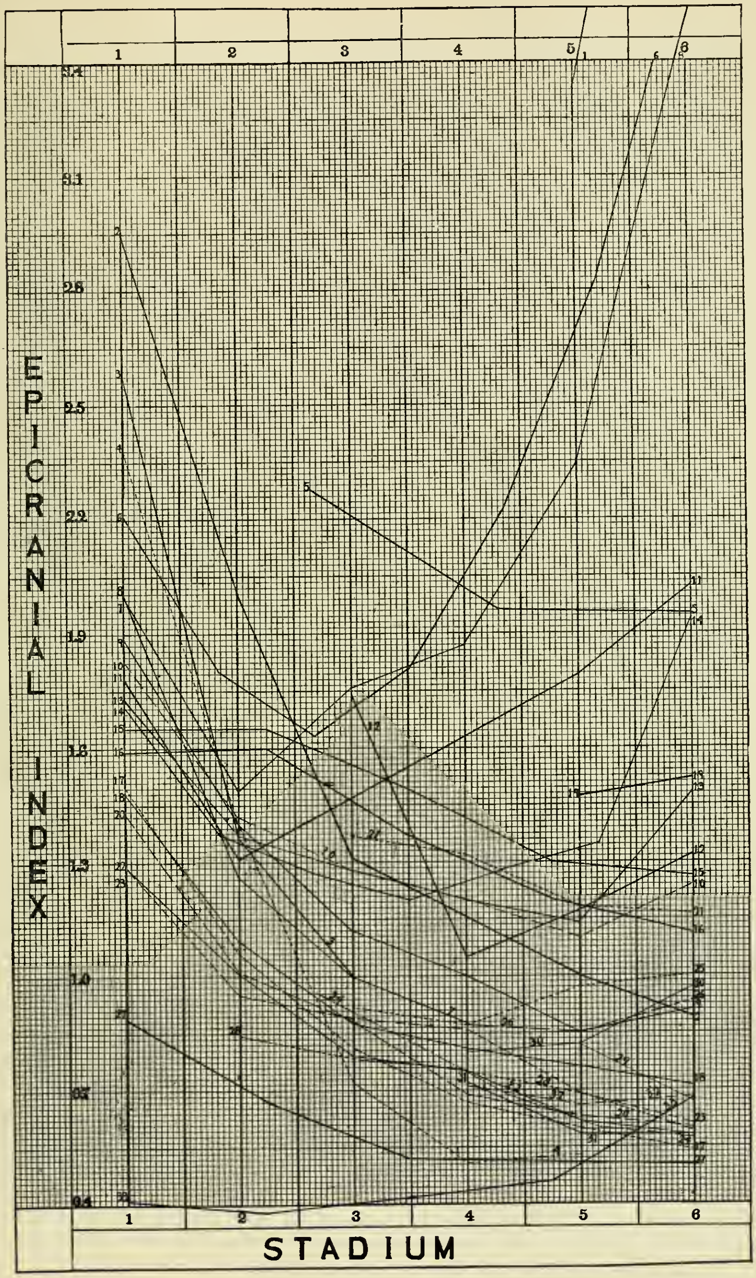
PLATE I

EXPLANATION OF PLATE I

POSTEMBRYOLOGY OF THE EPICRANIAL STEM

GRAPHIC REPRESENTATION OF THE EPICRANIAL INDEX.
EACH SPECIES REPRESENTED BY A CURVE

1. *Feltia gladiaria* (Noctuidae).
2. *Conistra* sp. (Noctuidae).
3. *Catocala amatrix* (Noctuidae).
4. *Catocala ?vidua* (Noctuidae).
5. *Vitula edmansii* (Pyralidae).
6. *Agrotis ypsilon* (Noctuidae).
7. *Catocala cara* (Noctuidae).
8. *Feltia subgothica* (Noctuidae).
9. *Ceramica picta* (Noctuidae).
10. *Agrotis c-nigrum* (Noctuidae).
11. *Sidemia devastatrix* (Noctuidae).
12. *Polia meditata* (Noctuidae).
13. *Polia renigera* (Noctuidae).
14. *Lycophotia margaritosa* (Noctuidae).
15. *Phytometra biloba* (Noctuidae).
16. *Phytometra brassicae* (Noctuidae).
17. *Catocala* sp. (Noctuidae).
18. *Dipterygia scabriuscula* (Noctuidae).
19. *Prodenia ornithogalli* (Noctuidae).
20. *Cirphis unipuncta* (Noctuidae).
21. *Agrotis clandestina* (Noctuidae).
22. *Caenurgia erechtea* (Noctuidae).
23. *Homoptera lunata* (Noctuidae).
24. *Nephelodes emmedonia* (Noctuidae).
25. *Thyridopteryx ephemeraeformis* (Psychidae).
26. *Cirphis ?pseudargyria* (Noctuidae).
27. *Hemerocampa leucostigma* (Liparidae).
28. *Papaipema nebris* (Noctuidae).
29. *Epizeuxis lubricolis* (Noctuidae).
30. *Laphrygma frugiperda* (Noctuidae).
31. *Homoptera lunifera* (Noctuidae).
32. *Cirphis phragmitidicola* (Noctuidae).
33. *Heterocampa bilineata* (Notodontidae).



RIPLEY NOCTUID LARVAE PLATE I

PLATE II

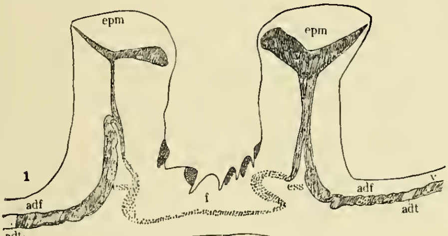
EXPLANATION OF PLATE II

EPICRANIAL STEM AND TENTORIUM

1. *Cirphis unipuncta*, last instar, transverse section thru front and adfrontals, soft parts removed by potash.
2. *Cirphis unipuncta*, last instar, cephalic aspect of head.
2a. *Cirphis unipuncta*, last instar, dorsal portion of vertex and cervacoria.
3. *Zeuzera pyrina* (Cossidae), last instar, postgenal region, ental aspect.
4. A pyralid, last instar, postgenal region, ectal aspect.
5. *Cacoecia* sp. (Tortricidae), last instar, postgenal region, ectal aspect.
6. *Thyridopteryx ephemeraeformis* (Psychidae), young larva, postgenal region, ectal aspect.
7. *Thyridopteryx ephemeraeformis*, last instar, postgenal region, ectal aspect.

a	antenna
adf	adfrontal sclerite
adt	adfrontal suture
an	antacoria
cc	cervacoria
cca	attachment of cervacoria
ccc	chitinized cervacoria
cls	clypeo-labral suture
cs	clypeal suture
ct	corpotentorium
ea	epicranial arm
epm	epicranial parademe
es	epicranial stem
ess	epicranial suture
f	front
fcs	fronto-clypeal suture
fs	frontal sensorium
l	labrum
li	labium
mi–2	mandibular setae
md	mandible
mt	metatentorium
mx	maxilla
ol–3	occipital setae
ocl–6	ocellarae
of	occipital foramen
pa	postgena
pap	postgenal parademe
pe	preclypeus
pl	paracoila
pm	parademe
pr	precoila
pse	secondary postgenal suture
pt	pretentorium
ptl	postcoila
se	secondary of suture
svl-3	sensoria vertex
v	vertex
vI–9	setae of vertex

1



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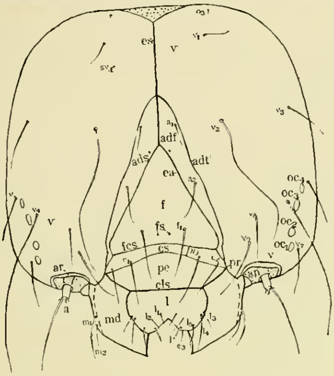

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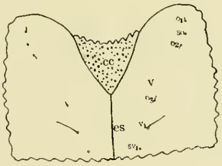

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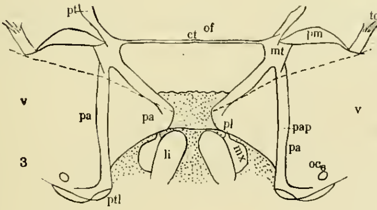

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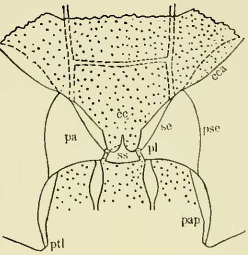

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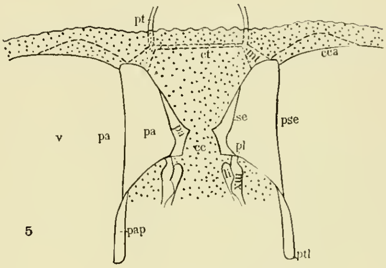

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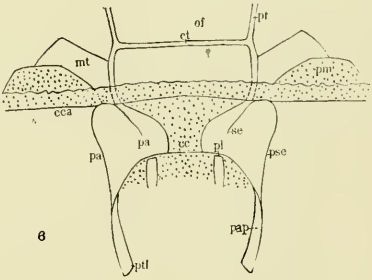

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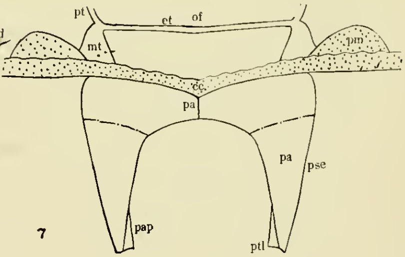


RIPLEY NOCTUID LARVAE PLATE II

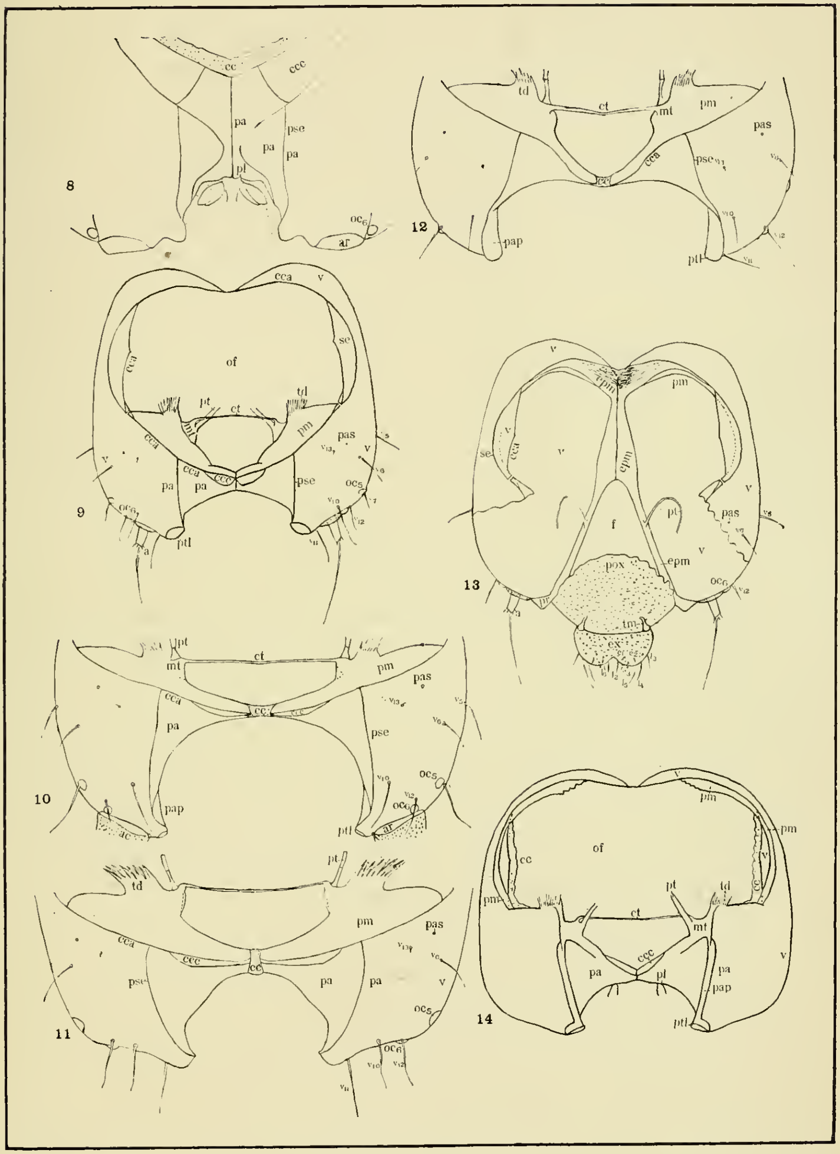
PLATE III

EXPLANATION OF PLATE III

CAUDAL ASPECT OF HEAD, TENTORIUM, POSTGENA

8. *Epargyreous tityrus* (Hesperiidae), last instar, postgenal region, ectal aspect.
9. *Cirphis unipuncta*, last instar, caudal aspect of head.
10. *Polia renigera*, last instar, postgenal region, ectal aspect.
11. *Nephelodes emmedonia*, last instar, postgenal region, ectal aspect.
12. *Feltia subgothica*, last instar, postgenal region, ectal aspect.
13. *Cirphis unipuncta*, last instar, cephalic aspect of head, ental surface.
14. *Cirphis unipuncta*, last instar, caudal aspect of head, ental surface.

a	antenna	*pap*	postgenal parademe
ar	antennaria	*pas*	postgenal sensorium
cc	cervacoria	*pl*	paracoila
cca	attachment of cervacoria	*pm*	parademe
ccc	chitinized cervacoria	*pox*	postpharynx
ct	corpotentorium	*pr*	precoila
epm	epicranial parademe	*pse*	secondary postgenal suture
ex	epipharynx	*pt*	pretentorium
mt	metatentorium	*ptl*	postcoila
ocl-6	ocellarae	*se*	secondary suture
f	occipital foramen	*td*	tendon
pa	postgena	*tm*	torma
		vl–13	setae of vertex



RIPLEY NOCTUID LARVAE PLATE III

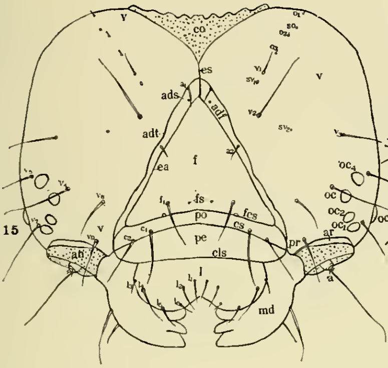
PLATE IV

EXPLANATION OF PLATE IV

CEPHALIC ASPECT OF HEAD

15. *Feltia subgothica*, last instar, cephalic aspect of head.
16. *Polia renigera*, last instar, cephalic aspect of head.
16a. *Polia renigera*, first instar, cephalic aspect of head.
17. *Chloridea armigera*, last instar, cephalic of head.

a	antenna
a1–2	adfrontal setae
adf	adfrontal sclerite
ads	adfrontal sensorium
adt	adfrontal suture
an	antacoria
ar	antennaria
c1–2	clypeal setae
cc	cervacoria
cls	clypeo-labral suture
cs	clypeal suture
ea	epicranial arm
es	epicranial stem
f	front
f1	frontal setae
fcs	fronto-clypeal suture
fs	frontal sensorium
l	labrum
l1–6	labral setae
m1–2	mandibular setae
md	mandible
o1–3	occipital setae
oc1-6	ocellarae
pe	preclypeus
po	postclypeus
pr	precoila
sv1–3	vertical sensoria
v	vertex
v1-13	vertical setae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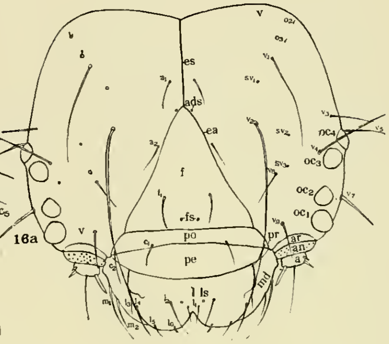
sv2
v1
v2
v3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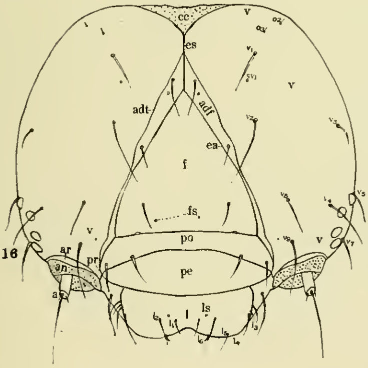
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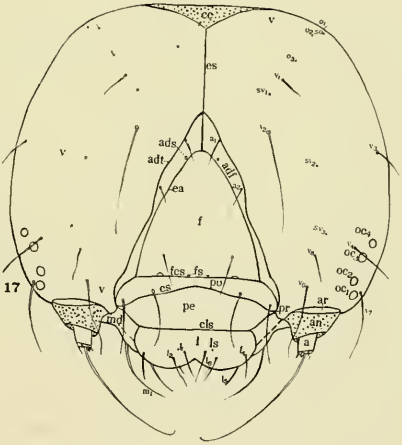
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an
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oc1
oc2
oc3
oc4
sv1
sv2
sv3
m1

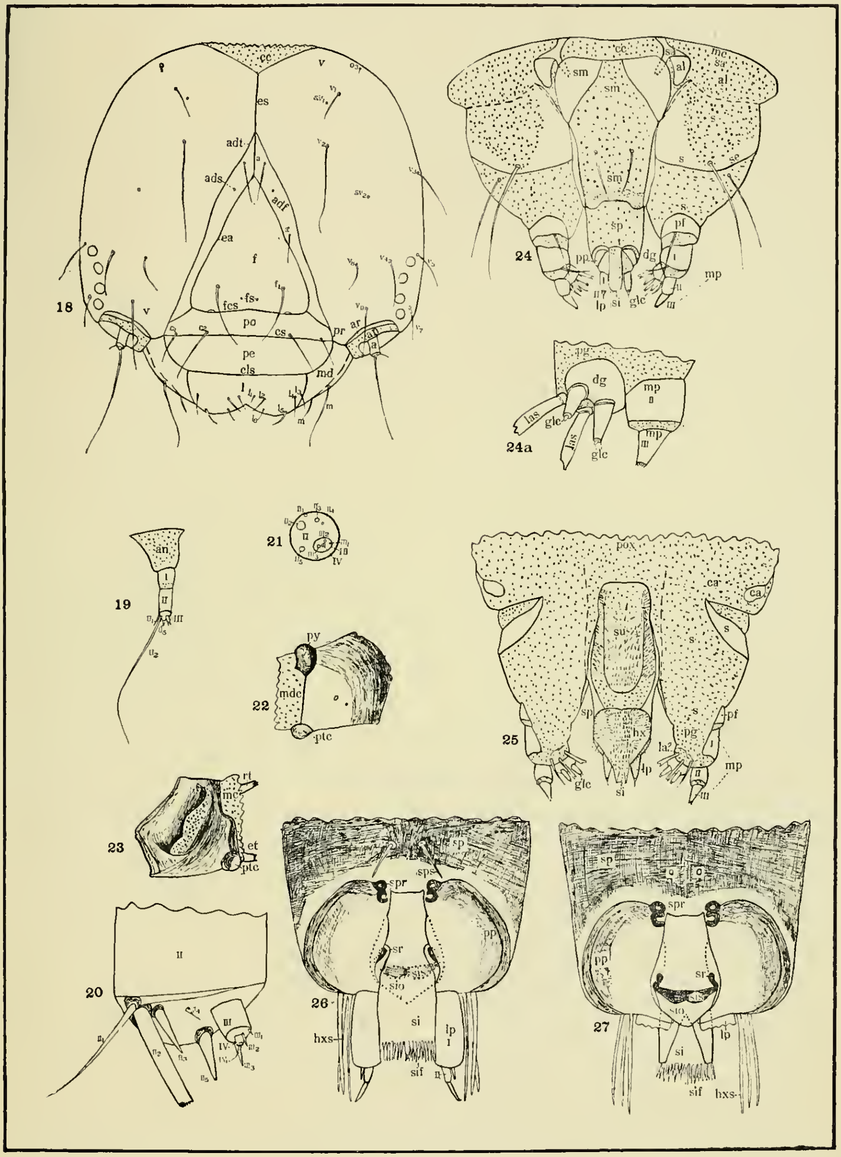
PLATE V

EXPLANATION OF PLATE V

HEAD AND MOUTH-PARTS

18. *Ceramica picta*, last instar, cephalic aspect of head.
19. *Cirphis unipuncta*, last instar, cephalic aspect of right antenna.
20. *Cirphis unipuncta*, last instar, distal end of antenna.
21. *Cirphis unipuncta*, last instar, diagram of distal end of antenna.
22. *Cirphis unipuncta*, last instar, lateral aspect of right mandible.
23. *Cirphis unipuncta*, last instar, mesal aspect of right antenna.
24. *Cirphis unipuncta*, last instar, caudal aspect of labium and maxillae.
24a. *Cirphis unipuncta*, last instar, distal end of maxilla, caudal aspect.
25. *Cirphis unipuncta*, last instar, hypopharynx and cephalic aspect of labium and maxillae.
26. *Cirphis unipuncta*, last instar, distal portion of labium, caudal aspect.
27. *Cirphis unipuncta*, last instar, distal portion of labium, cephalic aspect.

a	antenna
a1-2	adfrontal setae
adf	adfrontal sclerite
ads	adfrontal sensorium
adt	adfrontal suture
al	alacardo
an	antacoria
ar	antennaria
c1-2	clypeal setae
cc	cervacoria
cls	clypeo-labral suture
cs	clypeal suture
dg	distagalea
ea	epicranial arm
es	epicranial stem
et	extensotendon
f	front
f1	frontal setal
fcs	fronto-clypeal suture
fs	frontal sensorium
hx	hypopharynx
hxs	hypopharyngeal setae
l	labrum
l1-6	labral setae
la	lacinia
lp	labial palpus
m1-2	mandibular setae
md	mandible
mdc	mandacoria
mp	maxillary palpus
o1-3	occipital setae
pe	preclypeus
pl	paracoila
po	postclypeus
pp	palpiger
pr	precoila
ptc	postartis
py	preartis
rt	recto-tendon
s	stipes
sa	subcardo
se	secondary suture
si	spinneret
sif	fringe of spinneret
sio	proximal fold of spinneret
sis	proximal sclerite of spinneret
sm	submentum
sp	stipulae
spr	sensoria of palpiger
sps	stipular setae
sr	sensorium
sv1-3	vertical sensoria
v	vertex
v1-13	vertical setae



RIPLEY NOCTUID LARVAE PLATE V

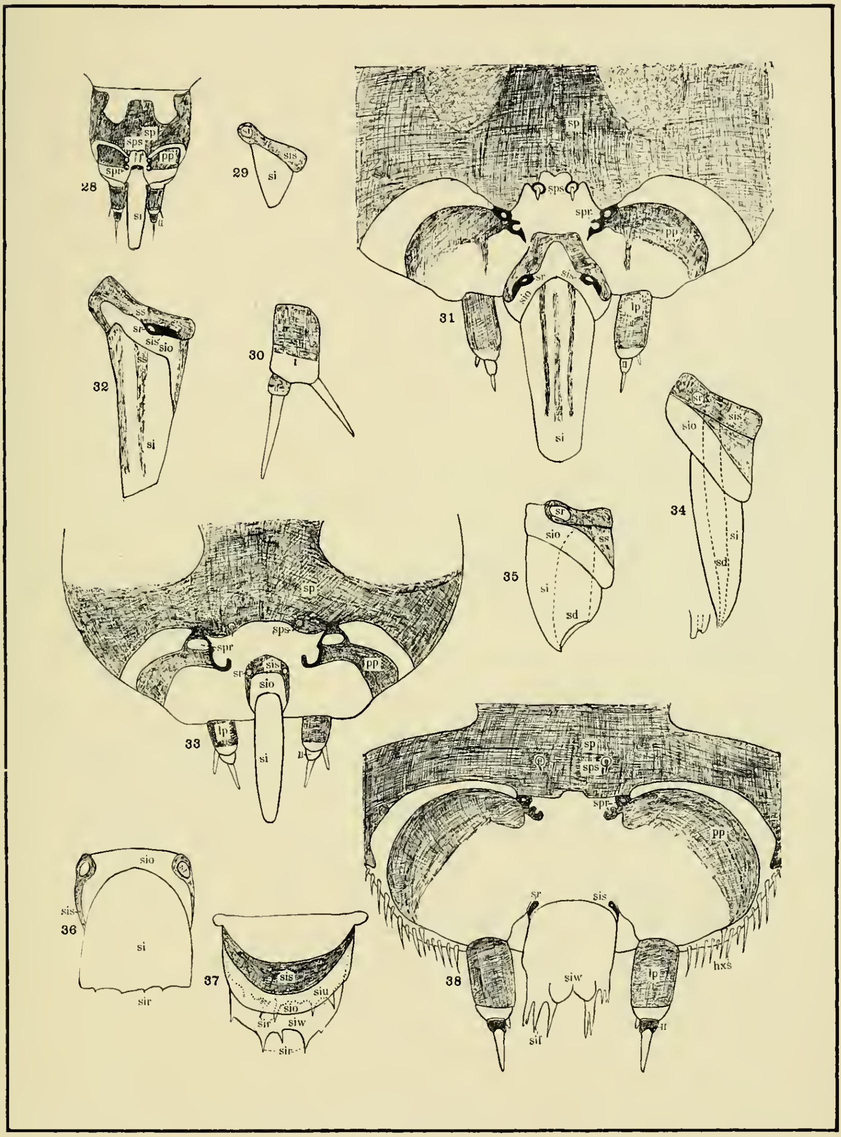
PLATE VI

EXPLANATION OF PLATE VI

LABIUM AND SPINNERET

28. *Ceramica picta*, last instar, distal portion of labium, caudal aspect.
29. *Polia renigera*, first instar, lateral aspect of spinneret.
30. *Polia renigera*, first instar, labial palpus.
31. *Polia renigera*, last instar, distal end of labium, caudal aspect.
32. *Polia renigera*, last instar, lateral aspect of spinneret.
33. *Lycophotia margaritosa*, first instar, distal end of labium, caudal aspect.
34. *Lycophotia margaritosa*, first instar, lateral aspect of spinneret.
35. *Lycophotia margaritosa*, second instar, lateral aspect of spinneret.
36. *Lycophotia margaritosa*, second instar, caudal aspect of spinneret.
37. *Lycophotia margaritosa*, third instar, cephalic aspect of spinneret.
38. *Lycophotia margaritosa*, last instar, distal portion of labium, caudal aspect.

hsx	hypopharyngeal setae	*siu*	upper lip of spinneret
lp	labial palpus	*siw*	lower lip of spinneret
sd	silk duct	*sp*	stipulae
si	spinneret	*spr*	sensoria of palpiger
sif	fringe of spinneret	*sps*	stipular setae
sio	proximal fold of spinneret	*sr*	sensorium
sir	rudimentary fringe of spinneret	*ss*	secondary sclerite
sis	proximal sclerite of spinneret		



RIPLEY NOCTUID LARVAE PLATE VI

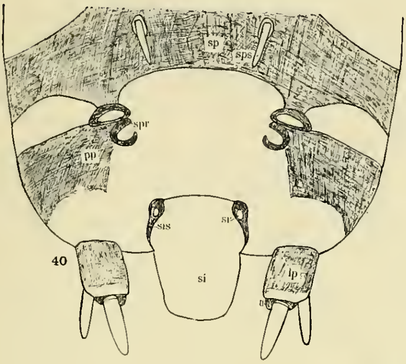
PLATE VII

EXPLANATION OF PLATE VII

SPINNERET

39. *Lycophotia margaritosa*, last instar, cephalic aspect of spinneret.
40. *Agrotis ypsilon*, first instar, distal portion of labium, caudal aspect.
41. *Agrotis ypsilon*, second instar, caudal aspect of spinneret.
42. *Agrotis ypsilon*, second instar, cephalic aspect of spinneret.
43. *Agrotis ypsilon*, third instar, distal portion of labium, caudal aspect.
44. *Agrotis ypsilon*, last instar, distal portion of labium, caudal aspect.
45. *Agrotis ypsilon*, last instar, lateral aspect of spinneret.
46. *Agrotis ypsilon*, last instar, cephalic aspect of spinneret.

hxs	hypopharyngeal setae	*sis*	proximal sclerite of spinneret
lp	labial palpus	*siu*	upper lip of spinneret
pp	palpiger	*siw*	lower lip of spinneret
si	spinneret	*sp*	stipulae
sif	fringe of spinneret	*spr*	sensoria of palpiger
sio	proximal fold of spinneret	*sps*	stipular setae
sir	rudimentary fringe of spinneret	*sr*	sensorium



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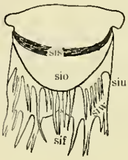

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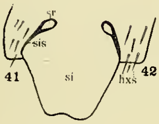

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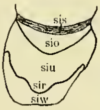

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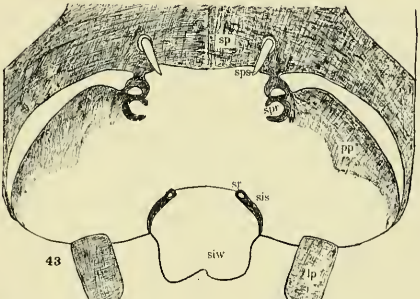

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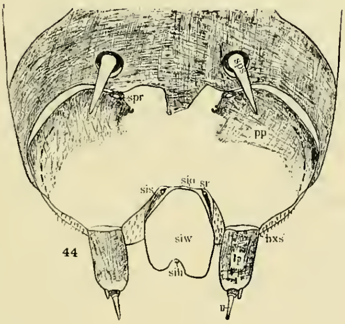

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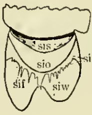


RIPLEY NOCTUID LARVAE PLATE VII

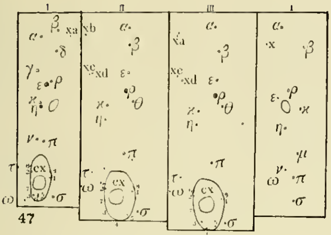
PLATE VIII

EXPLANATION OF PLATE VIII

THORACIC AND ABDOMINAL SETAE, LEGS

47. *Cirphis unipuncta,* last instar, setal maps of thoracic and first abdominal segments.
48. *Cirphis unipuncta,* last instar, setal maps of second, third, fourth, and fifth abdominal segments.
49. *Cirphis unipuncta,* last instar, setal maps of seventh, eighth, ninth, and tenth abdominal segments.
50. *Cirphis unipuncta,* last instar, a median larvapod, lateral aspect.
51. *Cirphis unipuncta,* last instar, a median larvapod, mesal aspect.
52. *Cirphis unipuncta,* last instar, anal larvapod, mesal aspect.
53. *Scolecocampa liburna,* last instar, and larvapod, lateral aspect.
54. *Cirphis unipuncta,* last instar, prothoracic leg, cephalic aspect.
55. *Cirphis unipuncta,* last instar, prothoracic leg, caudal aspect.
56. *Cirphis unipuncta,* last instar, claw of prothoracic leg.
57. *Cirphis unipuncta,* last instar, distal portion of a median larvapod, distal aspect.
58. *Cirphis unipuncta,* last instar, distal portion of a median larvapod, mesal aspect.
59. *Cirphis unipuncta,* last instar, mesal aspect of crochets.
60. Diagram representing the phylogeny of the short epicranial stem as derived from a study confined to the last instar. Erroneous interpretation.
61. Diagram representing the phylogeny of the short epicranial stem as derived from postembryological study. Correct interpretation.

co	crochet	*ma*	muscle attachment
cw	claw	*sr*	sensorium
cx	coxa	*t*	tibia
fe	femur	*ts*	tarsus
lop	larvapod		



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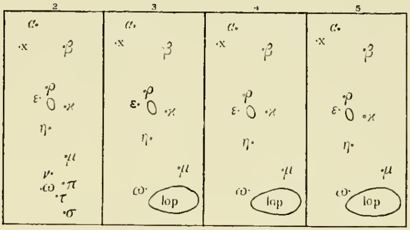

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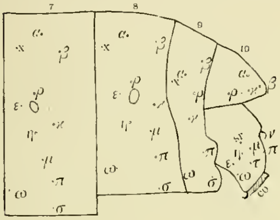

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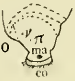

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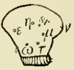

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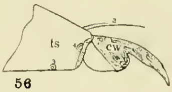

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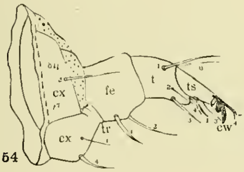

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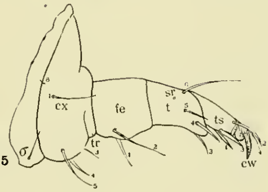

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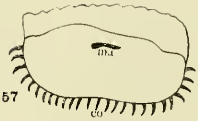

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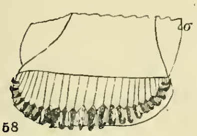

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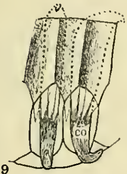

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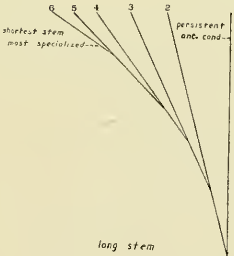

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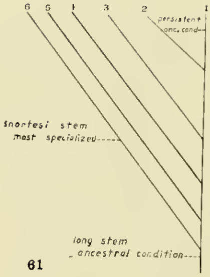

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