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BUTTERFLY

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R. E. SNODGRASS

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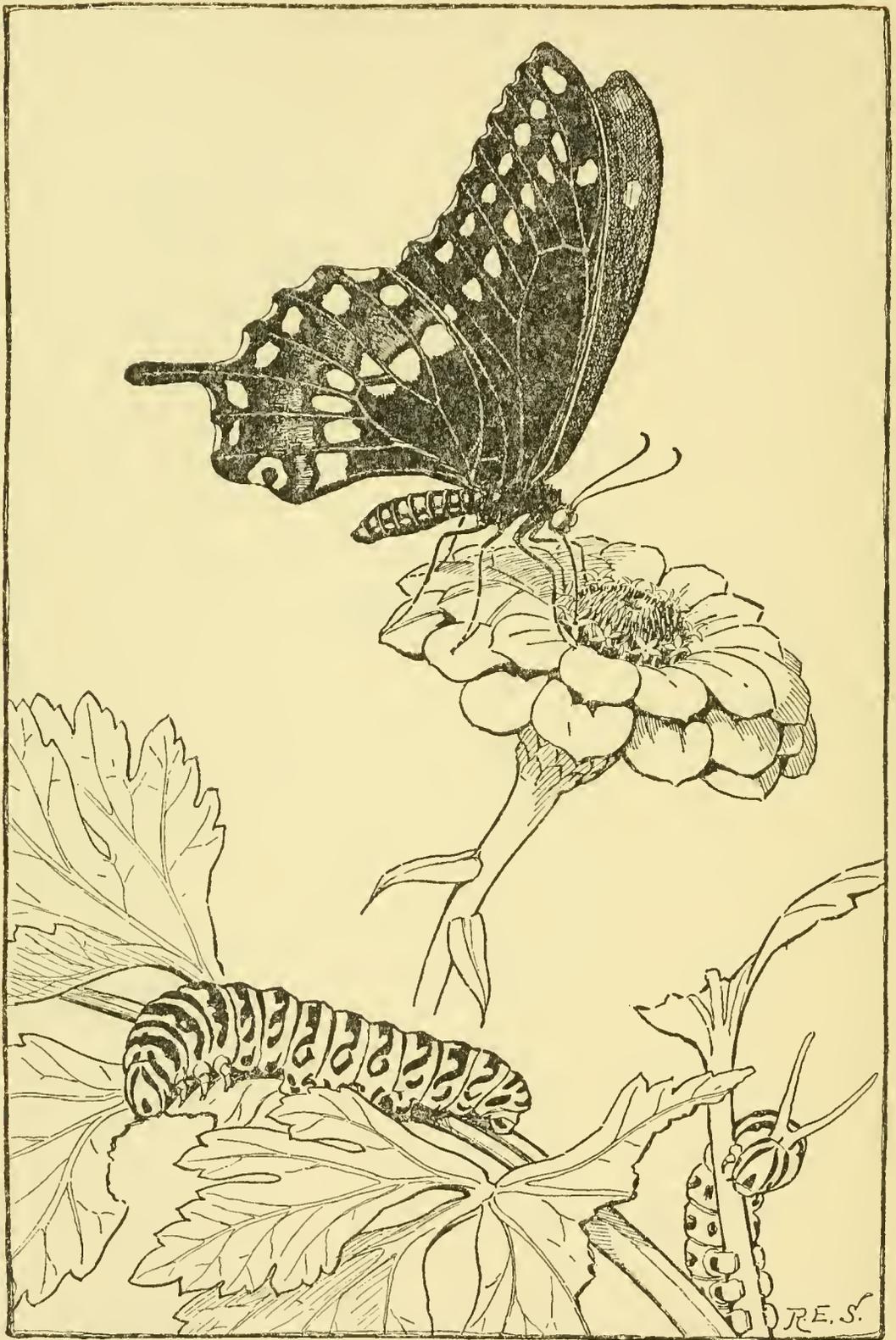


FIG. 1.—The celery caterpillar and butterfly, *Papilio polyxenus asterius* Stoll.

# THE CATERPILLAR AND THE BUTTERFLY

By R. E. SNODGRASS

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## INTRODUCTION

The caterpillar and the butterfly are here given the title role because they are a familiar example of those insects in which the young differ so much from their parents that they must go through a reconstruction called a metamorphosis in order to attain their own adult form. So well known, in fact, is the apparent transformation of the wormlike caterpillar into the splendid winged butterfly, and so marvelous does it seem, that it has been taken as a symbol of human resurrection. In ancient Greek the human mind or soul was called *psyche*, and the same name was given to the butterfly, presumably the emancipated soul of the caterpillar. Though the process of resurrection is obscure, and the fact has perhaps not been fully demonstrated, we now know almost the whole story of how the caterpillar appears to become a butterfly. Furthermore, in recent years students of insect metamorphosis have given much attention to the role of hormones in controlling the life of the young insect and the development of the adult. In short, almost the whole of modern studies on insect metamorphosis has been devoted to understanding the change of the larval insect to the adult, or imago.

On the other hand, little attention has been given to the question as to how or why did the young moth or butterfly ever become such a thing as a caterpillar, a creature so different in every way from its parents. It would indeed be a wise butterfly that knows its own child, since probably it has no memory of its own youthful life as a caterpillar. Equally certain is it that the caterpillar has no idea that it will ever be a butterfly.

With most animals, including many insects, the young resemble their parents except in matters of immaturity. Consider the young grasshopper or the young cockroach—they differ from their parents principally in the incomplete development of their wings and the external genital organs. They have no need to fly since they live in

the same habitat as their parents, have the same kind of mouth parts, and eat the same kind of food. There is no reason why the young of such insects should be radically different from their parents. They are able to develop gradually into the adult form. Many other insects are in the same class and go through life without any metamorphosis.

Let us suppose now that the adults of some other insects far back in the early days of their evolution adopted a way of feeding that depended on their ability to fly and became structurally adapted to obtaining a special kind of food. If the young of these insects had to inherit the new kind of feeding organs of their parents, being unable to fly, they would be left to starve and the species would die out. To prevent such a calamity the usual laws of heredity have somehow been set aside in such cases, allowing the young insect to undergo an evolution on its own part adapting it structurally to some suitable environment where it could live and grow to maturity. A good example is the dragonfly; the flightless young insect could not catch mosquitoes in the air as do its parents, so it took to the water where plenty of live food was available, and has become structurally so individualized that it now has no resemblance to its parents. Likewise the young mosquito without wings could not practice bloodsucking as does its mother, or the nectar-feeding of its father, so it also became aquatic and has been equipped for its own way of feeding in the water. Adult fleas are wingless, but they have substituted jumping legs for wings and are able to feed on the blood of vertebrate animals. The larval flea thus left where it was hatched has to make the best of the circumstances by feeding on whatever it can find, but its form and mouth parts are suitable to the life it has to lead. The wasps and the bees take care of their helpless larvae, but the young of insects deserted by their parents receive special attention from nature.

Most any of the lower insects undergo some changes at the last moult, such as the completion of the wings and the external genital organs, or a remodeling of the shape and proportions of the body. Such changes may be called "metamorphosis" in a literal sense, but they are merely the final stage of normal adult development. A true metamorphosis involves the discarding of specialized larval characters, which allows the completion of adult development, and differs in degree according to the degree of aberration of the young from the adult structure. Various cases might be cited in which the young insect differs from its parents only in some minor character of its own, which is discarded at the last moult.

A very simple example of metamorphosis due to juvenile specialization is seen in the cicada. The young nymph of the seventeen-year

cicada (fig. 2 A) as compared with the adult is more elongate and cylindrical, with the front of the head strongly protruding and rounded, but it has a special juvenile feature in the form of the front legs. These legs are modified for burrowing during the underground life of the nymph, and later (B) for climbing when it comes out of the ground. The under surface of the femur is armed with strong

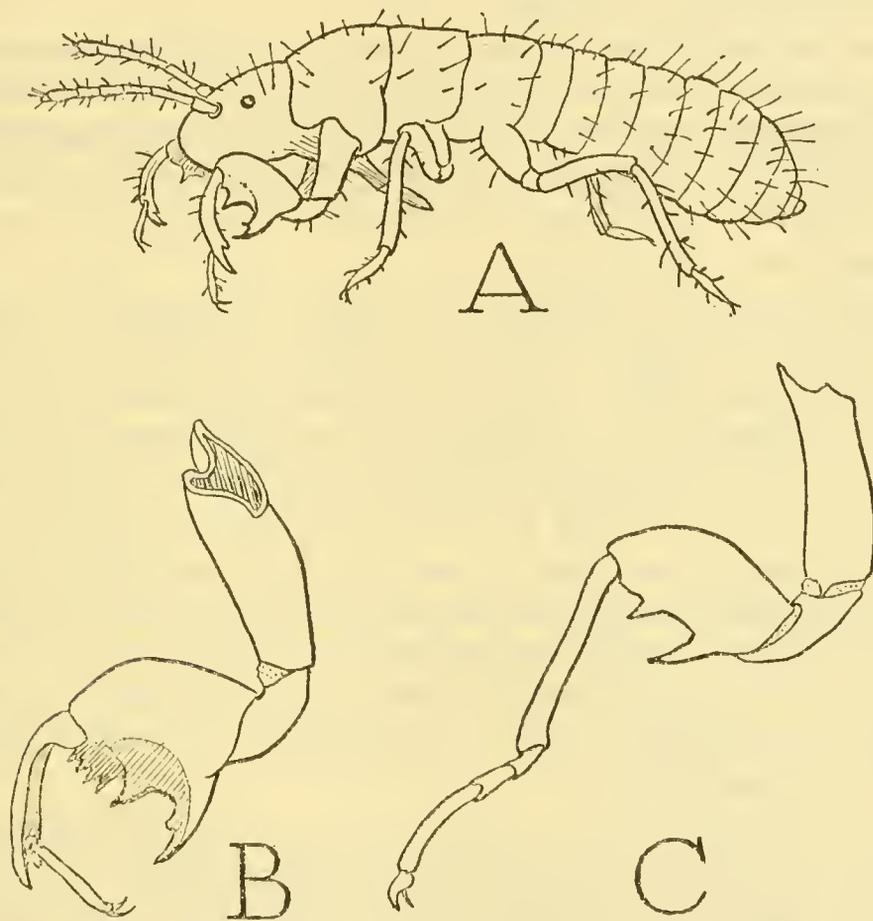


FIG. 2.—Young nymph of the seventeen-year cicada, and change in the front leg from nymph (B) to adult (C).

teeth, the tibia is toothed at its end, and the slender, undivided tarsus is freely attached to its mesal surface. At the moult to the adult the cuticle of these larval legs is cast off, and the adult leg (C) appears in the typical mature form. The leg epidermis simply forms two kinds of legs, one for the nymph, the other for the imago, but the nymphal leg is a special adaptation for the nymph.

It would be interesting to know when and how the young cicadas first became adapted to underground life. With most insects of which the young have a special habitat, the female lays her eggs where the young will live. The female cicada, however, following the tradition

of her race, inserts her eggs into the stems of trees, suggestive that formerly the young cicadas lived on the trees, as do young aphids and scale insects. At present, the young cicadas simply drop off the trees to the ground, a habit that may have been accidental at first, but gave a better chance of survival. Here, then, is a case where the young insects have deserted their parents, and fortunately became structurally adapted to a subterranean burrowing life. Also in the ground they were able to prolong their lives.

From the case of the cicada it is only a step, though perhaps a long one, to that of the dragonfly in which the young insect has become entirely different from its parents in adaptation to living and feeding in the water, but still it reverts to the adult structure at one moult. The same is true of some other insects, such as the mayflies and the stoneflies.

As this process of independent juvenile specialization is carried still farther in the higher insects, affecting not only the external form but the internal organs as well, many of the larval tissues and organs become so different from those of the adult that they have to be destroyed. The corresponding adult parts are then newly built up, in which case it can hardly be said that the larva is metamorphosed into the imago. It now becomes necessary for a reconstructive stage, or pupa, to intervene between the larva and the fully formed imago, which is liberated by a final moult. The insect is now said to be "holometabolous." The holometabolous insect becomes virtually two distinct animals separated by the pupa, in which one is broken down and the other newly constructed.

Now the question comes up as to how does one egg produce two individuals so different as the larva and the adult may be. This is probably a question for the geneticists to explain, but so far as known to the writer they have not done so. However, since gene mutations affect adult structures, they should produce modifications also in juvenile stages. If a mutation is beneficial to the adult, it can be preserved; when useful *only* to the young insect, it must be discarded at the moult to the imago, but restored to the next larval generation.

Experimentally it has been shown that the egg is potentially both larval and adult, but the fact does not explain how it has come to be so. We can surmise that the egg contains two sets of chromosomes or two kinds of genes, but how did this condition arise only in cases where the young insect could not lead the life of its parents and had to be given a form of its own? In the course of normal development the young animal naturally comes first, so in the case of double

development the larval form, whatever it may be, precedes the adult. The larva is the direct development from the egg, but it carries the factors of adult development suppressed temporarily until the larva has completed its growth, which then allow the adult development to proceed.

It may be disputed whether the holometabolous insects represent one or several lines of descent. There is no modern larva that might plausibly be selected as of the type from which the others may have been evolved. Yet all holometabolous larvae have one feature in common, which is the internal development of the wings. Just what essential survival value the endopterous condition may have had is difficult to see, since the young of numerous other insects seem to get along very well with external wing pads. However, whatever may have been the form of the primary holometabolous larva, or why it became endopterous, it seems highly probable that external winglessness was a condition favorable for many potential habitats, and thus led to the great diversification of modern larval structure in adaptation to various ways of living. The association of the endopterous condition of the larva with holometabolism is probably because internal wing rudiments could become fully developed external wings only in a pupal stage.

Of all the holometabolous larvae, the lepidopterous caterpillar is structurally one of the most standardized. Though caterpillars differ in size and details of structure, they never depart from the fundamental caterpillar organization. By way of contrast consider the difference among the Diptera between a mosquito larva and the maggot of a muscoid fly, or in the Hymenoptera the contrast between a sawfly larva and the larva of a wasp or bee. Some function of the caterpillar has demanded a basic uniformity of structure in all species.

In conformity with the principle already discussed that the adult insect is responsible for the structure of the larva, we must look to the moth or butterfly to find the reason for the caterpillar.

#### EVOLUTION OF THE ADULT

The moths and butterflies are named Lepidoptera because of their scaly wings, but their scales do not make them what they are, any more than do the bright colors that many of them wear. The mosquito has scales on its wings, and some moths have clear wings. The typical lepidopteron is distinguished from all other insects by the possession of a tubular, nonpiercing, maxillary proboscis, coiled beneath the head when not in use (fig. 3 E). The other mouth parts are much

reduced or suppressed, and the proboscis limits the diet of the moth or butterfly to readily accessible liquids, which are mostly the nectar of flowers. This fact determines the essential structure not only of the adult lepidopteron, but that of the caterpillar as well. The intake of liquid food necessitates the possession of an efficient sucking apparatus connected with the alimentary canal, while the alimentary canal itself can be much simplified by comparison with that of an insect that feeds on solid food.

Butterflies, it is true, do not feed entirely on nectar; some are able to rasp fruit for the juice, others may suck up sap exuding from trees, or imbibe honeydew from aphids, and they have been seen apparently feeding on carrion and excreta. They all drink water. So far as known, the only digestive enzyme of adult Lepidoptera is invertase. Swingle (1928) reports the presence of only this enzyme in the oriental fruit moth, and in elaborate studies on digestion in various adult Lepidoptera Stober (1927) found no other digestive enzyme than invertase. It appears, therefore, that adult Lepidoptera can digest only cane sugar. When small quantities of starch, fat, or protein (blood) are mixed with their food, these substances, Stober says, remain unchanged in the stomach. Glucose, of course, can be absorbed as obtained in nature. Species with reduced mouth parts that do not feed as adults were found to have no digestive enzymes. It is not known what butterflies seen apparently feeding on carrion or excrement may get from such sources. Possibly the juices contain products of bacterial decomposition that can be directly absorbed as predigested food.

Inasmuch as a few modern moths have vestigial mandibles, there can be little question that present-day Lepidoptera are descended from adult progenitors that fed on solid food. Their adaptation for a liquid diet, therefore, must have been made when the early ancestors of the moths and butterflies renounced solid food for liquids. The proboscis is formed of the maxillary galeae, and is probably not a functional organ of great antiquity, since early stages of its evolution are still preserved in two primitive families, the Eriocraniidae and the Mnesarchaeidae. Except for one doubtful form, fossil Lepidoptera are not known much before the Eocene.

At the time when the Lepidoptera first appeared in evolution, the mutual relationship between flowers and insects had already been established. Flowers had bright colors and probably attractive odors, and their pollen formed a nutritious food for insects. Thus the plants fed the insects, and the insects pollinated the plants.

The Micropterygidae have long been regarded as a primitive

lepidopterous family, but taxonomists now assign them to a separate order, the Zeugloptera (Chapman, 1917), which Hinton (1946) contends is more primitive even than the Trichoptera. However, whatever may be the correct classification of the micropterygids, their

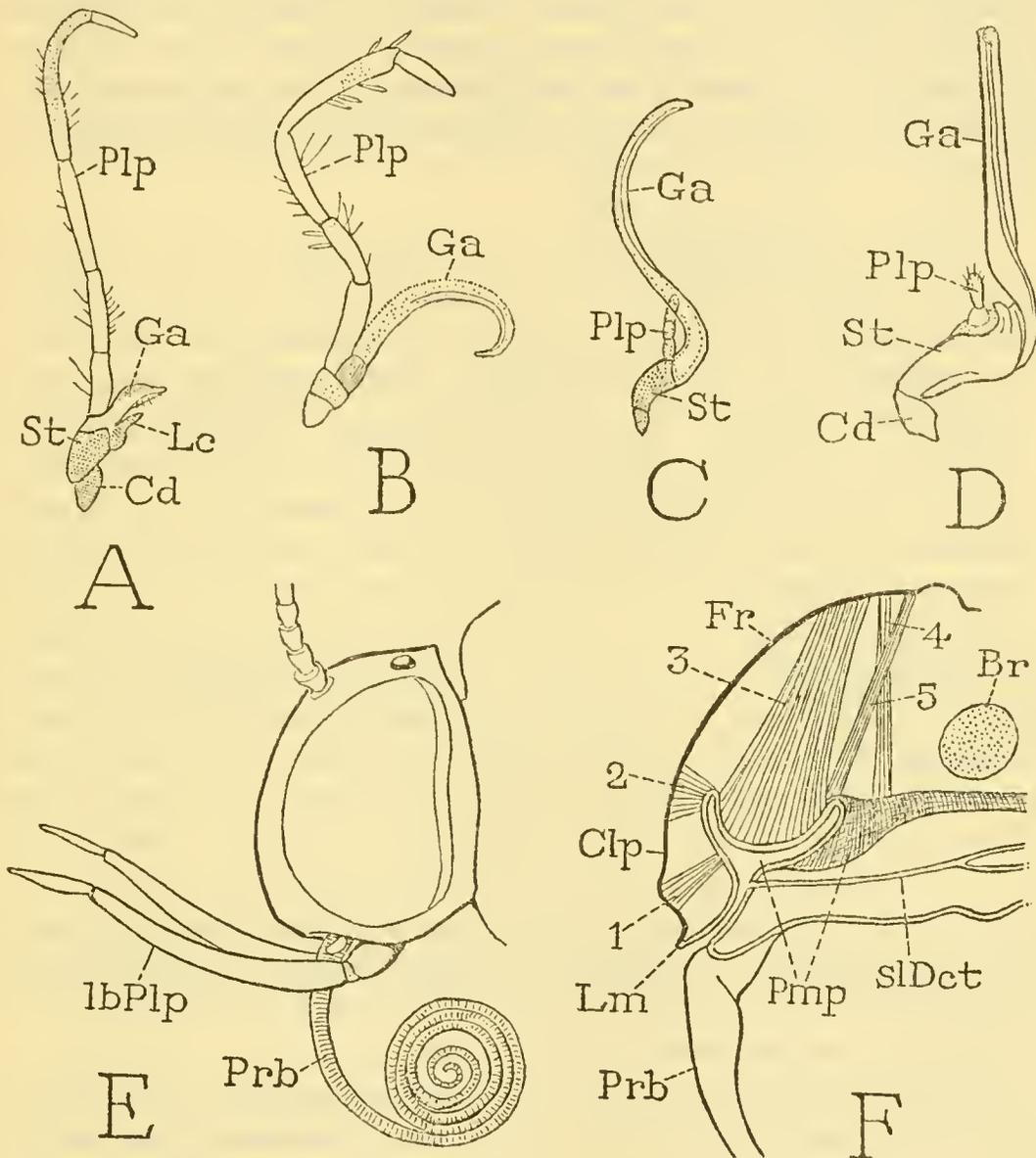


FIG. 3.—Evolution of the lepidopterous proboscis, and the sucking pump (A,B,C, from Tillyard, 1923).

A, Maxilla of *Micropteryx auruncella*. B, Maxilla of *Eriocrania semiperpurella*. C, Maxilla of *Mnesarchaea paracosma*. D, base of a typical, fully developed lepidopterous maxilla. E, Head of *Saminoidea exitiosa*. F, Section of head of sphinx moth, diagrammatic, showing the sucking pump and its muscles.

ancestors must have had some relation to the ancestors of the Lepidoptera, and their modern mouth parts may be taken as an approximate example of the feeding organs of the lepidopterous progenitors. The adult micropterygids have well-developed functional jawlike mandibles. The maxillae (fig. 3 A) are of generalized structure, each organ

having a small, simple lacinia and a galea, and a long 5-segmented palpus. A detailed comparative description of the mouth parts of several micropterygid species is given by Issiki (1931), but he says nothing of the food or feeding habits of the insects. According to Tillyard (1923) the mandibles of *Sabatinca* "work in conjunction with the epipharyngeal and hypopharyngeal brushes and the triturating basket of the hypopharynx as grinders of the minute pollen grains or other fine vegetable matter which form the food of the imago." Hannemann (1956) says the long flexible maxillary palpi are used for bringing the food into the mouth.

If the mandibulate progenitors of the Lepidoptera fed on pollen, they had easy access to nectar, their problem being how to obtain it from the depth of the flower corollas. If, then, some fortunate mutation happened to lengthen the maxillary galeae, the latter may have enabled their possessors to get a taste of nectar. The next step in the evolution of a maxillary proboscis is seen in the modern Eriocraniidae, in which the galea of each maxilla is much elongated, curved, and grooved on its inner surface (fig. 3 B), while the lacinia is entirely suppressed. According to Busck and Böving (1914) in *Mnemonic auricyania* the galeae have marginal serrations that serve to connect them with each other. In the Mnesarchaeidae the galeae are still more lengthened (C), and the maxillary palpi are reduced to three small segments. From the condition in these two primitive lepidopterous families it is but another step in the same direction to the long, coiled proboscis typical of the other Lepidoptera (fig. 3 E), in which the base of the maxilla (D) retains the form it has in the eriocraniids. Along with the development of the proboscis the mandibles underwent a reduction until they became functionless vestiges or disappeared altogether. From an early stage in their evolution, therefore, the Lepidoptera became entirely liquid feeders.

The fully developed proboscis of modern Lepidoptera is a truly remarkable instrument. When not in use it remains tightly coiled beneath the head, but it can be straightened out to its full length for insertion into flowers to serve as a nectar conduit. A detailed study of the structure and mechanism of the proboscis of *Pieris brassicae* has been made by Eastham and Eassa (1955), in which they critically review and correct certain ideas on how the proboscis works expressed by earlier writers.

A proboscis alone could not serve for the ingestion of liquid food; a sucking apparatus must have been developed along with the evolution of the proboscis. In *Micropteryx* it is shown by Hannemann (1956) that the slender oesophagus opens directly from the preoral

cavity and that there is no pharyngeal dilatation. All Lepidoptera that feed in the adult stage, however, are provided with a sucking pump in the head connected with the base of the proboscis and continuous into the oesophagus. In a comparative study of the pump, Schmitt (1938) shows that the organ varies somewhat in size and structure in different species, but is always operated by two sets of dilator muscles separated by the frontal ganglion and its brain connectives. The preganglion muscles arise on the clypeal region of the head, the post-

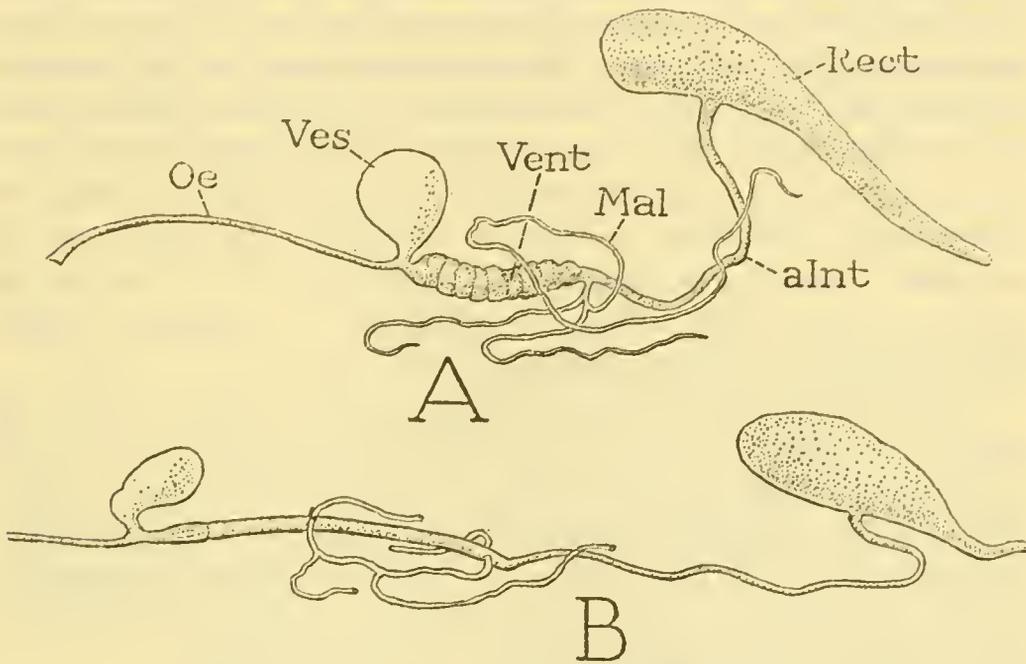


FIG. 4.—Alimentary canal of adult moths.

A, *Malacosoma americanum*. B, *Sanninoidea exitiosa*.

aInt, anterior intestine; Mal, Malpighian tubules (not shown full length); Oe, oesophagus; Rect, rectum; Vent, ventriculus; Ves, oesophageal vesicle.

ganglion muscles on the frontal region. The lepidopterous food pump, therefore, is a combination of the preoral cibarium and the postoral pharynx. The same type of pump is described by Srivastava (1957) in *Papilio demoleus*, and is strongly developed in the sphinx moth (fig. 3 F, *Pmp*). Its principal dilator muscles (3,4,5) arise on the frons (*Fr*) and are therefore pharyngeal, the anterior muscles (1,2) arising on the clypeal region (*Clp*) are cibarial. The sucking pump of the honey bee is also cibario-pharyngeal, but in most sucking insects the pump is entirely cibarial.

In contrast to the highly developed sucking apparatus, the alimentary canal of adult Lepidoptera is much simplified, as might be expected of a nectar-feeding insect. In the moth of the tent caterpillar (fig. 4 A), for example, the oesophagus (*Oe*) is a long slender tube

traversing the thorax from the sucking pump in the head to the anterior part of the abdomen, where it joins the stomach, or ventriculus (*Vent*). Just before the stomach the oesophagus bears dorsally a diverticulum in the form of a thin-walled vesicle (*Ves*), which has been supposed to be a reservoir for liquid food, but generally it is found to contain air. The very short ventriculus has no caeca, and its walls are thrown into circular folds. Following the ventriculus is a long, slender intestinal tube (*aInt*), which opens into the under side of a large rectal sac (*Rect*). In a peach borer moth (B) the alimentary canal is an even more slender tube, except for the oesophageal diverticulum and the rectal sac. The alimentary canal of the monarch butterfly *Danais plexippus*, as described by Burgess (1880) under the name *archippus*, and recently figured by Ehrlich and Davidson (1961) differs in no essential way from that of the moths, though the oesophageal diverticulum is half or two-thirds the length of the abdomen. According to Burgess the delicate walls of the diverticulum are well supplied with slender longitudinal and transverse muscle fibers, but the sac contains nothing but air.

Long coiled glands opening by a common duct at the base of the labium have been described or figured in various adult Lepidoptera (see Schmitt, 1938; Srivastava, 1957; Ehrlich and Davidson, 1961). These glands have replaced the larval silk glands, and are presumably salivary in function. In the honey bee larva the silk glands completely break down after spinning, and the salivary glands of the adult are regenerated from anterior remnants of the larval ducts.

The Malpighian tubules arise from the anterior end of the intestine as a pair of tubes varying in length, in some species swollen into bladderlike vesicles. Each primary tubule divides into two, and usually one of these again divides, giving three tubules in all on each side. The tubules may form a tangled mass around the stomach and the intestine, and in some species at least their posterior ends are inserted beneath the muscular coat of the rectum.

It is clear that the basic specialization of adult Lepidoptera is a structural adaptation for feeding on nectar contained in the depths of flower corollas. That sugars are their only food is evident from their lack of digestive enzymes other than invertase. Though nectar was formerly a favorite drink of the gods, it must be a very inadequate diet even for a moth or butterfly. The female at least needs proteins for the production of yolk-filled eggs. Hence it should be the duty of the caterpillar to store up food reserves in its body to supplement its diet in its own adult stage. The tent caterpillar moth, *Malacosoma americanum*, is a species that takes no food in the adult stage, but

the ovaries are fully stocked with ripe eggs on emergence of the female, ready to be laid as soon as fertilized. In this case the egg-forming material must have been received from the caterpillar. The lepidopterous caterpillar, therefore, should be a larva primarily constructed for the function of general feeding. According to Stober (1927) it is provided with enzymes for the digestion of sugar, starches, fats, and proteins. Babers and Woke (1937) report that digestive enzymes of the southern armyworm include amylase, maltase, glycogenase, invertase, rennin, lipase, trypsin, and erepsin. The caterpillar is thus evidently equipped to handle any kind of food. It is the dietetic limitation of the adult, therefore, that has brought about the structure of the caterpillar, and the caterpillar is responsible for the life of the adult. An investigation of the caterpillar now will show just how well it has met its obligations.

### THE CATERPILLAR

A typical modern caterpillar (fig. 5 A) has a long, soft, cylindrical body of 13 segments, and a sclerotized head. On each side of the head (B) is a group of six small simple eyes. The antennae (*Ant*) are very short, sometimes minute. The mandibles are strong biting-and-chewing jaws (F). On the under side of the head (C) the closely associated labium and maxillae form a prominent lobe containing the silk-spinning apparatus, which opens by a small tapering spinneret (*Spn*) at the end of the labium. The thoracic legs (A) are very short, but each has the usual six segments of an insect leg (D). The abdomen bears generally a series of short, paired, unsegmented appendages, known as *prolegs* (*PrL*), commonly present on segments III-VI and X.

It is always of interest to know something of the ancestry of any modern animal we are trying to understand, but we know nothing of the nature of the primitive lepidopterous larva. Larvae of the Micropterygidae (fig. 6 A,B) have been described and figured by Chapman (1894) and by Tillyard (1922). They look as much like caterpillars as anything else, and the well-developed mandibles could pass for those of a modern caterpillar. The antennae, however, are long and slender (B,C), and in place of prolegs the larvae have either minute points (A) or more slender processes on the first eight abdominal segments (B), each ending in a single curved claw (D). According to Hinton (1955), these organs lack muscles, and it is unlikely that they are prototypes of the lepidopterous prolegs. Some micropterygid larvae feed in the open and spin silken cocoons.

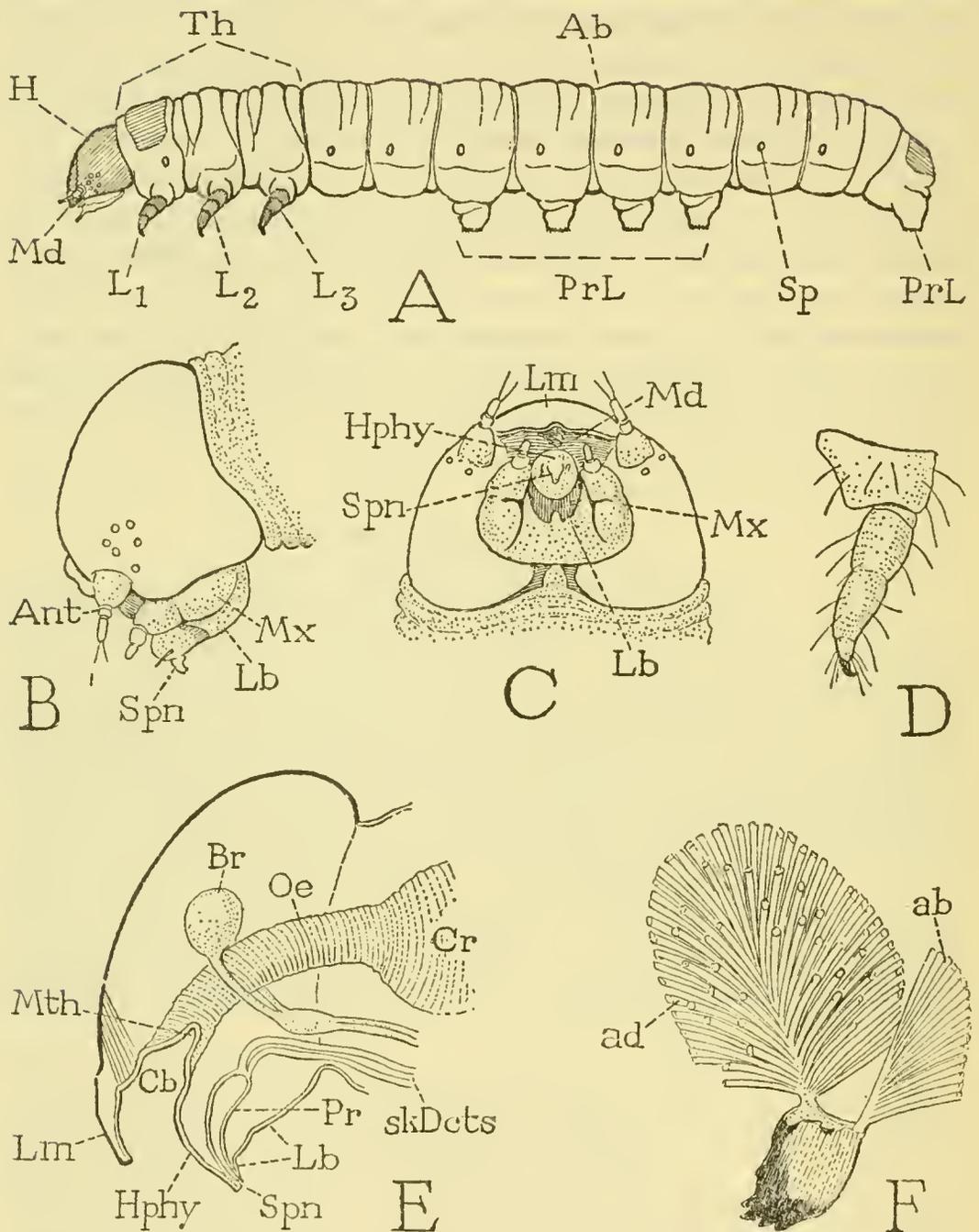


FIG. 5.—External features of a caterpillar.

A, Typical structure of a caterpillar. B, Head of a silkworm, lateral. C, Same, ventral. D, A thoracic leg. E, Longitudinal section of a caterpillar's head, diagrammatic, showing united hypopharynx and labium enclosing the silk press (salivarium). F, Left mandible and muscles of a tomatoworm, anterior.

*Ab*, abdomen; *ab*, abductor muscle; *ad*, adductor muscle; *Ant*, antenna; *H*, head; *Hphy*, hypopharynx; *L*, thoracic leg; *Lb*, labium; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *PrL*, prolegs; *Sp*, spiracle; *Spn*, spinneret; *Th*, thorax.

A larva of the primitive lepidopterous family Eriocraniidae, *Mnemonic auricyania* (fig. 6 E), as shown by Busck and Böving (1914), has a small head and a simple tapering body of 13 segments, but being a leaf miner it lacks both thoracic and abdominal legs. It is in the Hepialidae that we first encounter a typical caterpillar (F), though in this case a stem borer.

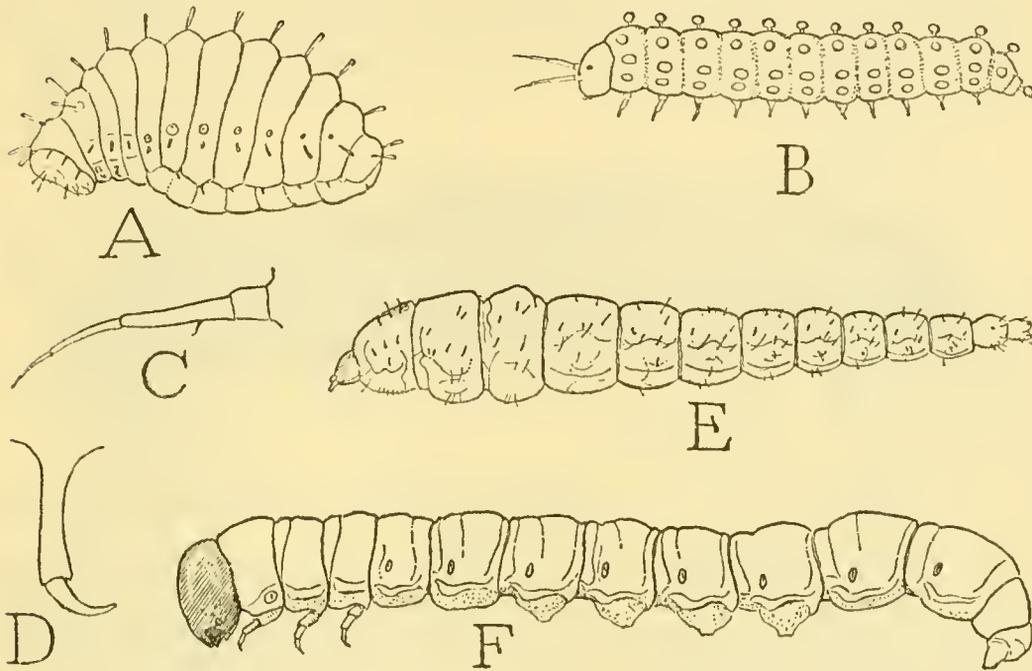


FIG. 6.—Larvae of Micropterygidae and lower Lepidoptera. (A, from Tillyard, 1922; B,C,D, from Chapman, 1894; E, from Busck and Böving, 1914.)

A, *Sabatinca barbarica* (Micropterygidae). B, *Erioccephala calthella* (Micropterygidae). C, Same, antenna. D, Same, abdominal "proleg." E, *Mnemonic auricyanea* (Eriocraniidae). F, *Hepialus* sp. (Hepialidae).

To effectively perform its function of feeding, after the adult had adopted a nectar diet it was first necessary for the caterpillar to have strong biting-and-chewing mandibles, and these it inherited from its ancestors. At the same time it needed a stomach of a size capable of digesting a constant supply of leafy food, and this the modern caterpillar has. Descriptions of the alimentary canal of various caterpillar species may be found in the papers here cited by Bordas (1911), Peterson (1912), Stober (1927), Neiswander (1935), Woke (1941), El-Sawaf (1950), and Teotia and Pathak (1957).

The alimentary canal of a typical caterpillar almost fills the body (fig. 7). Beginning with the pharyngeal region (*Phy*) following the mouth (*Mth*) a narrow oesophagus (*Oe*) curves back through the head and in some species expands in the thorax into a huge, strongly muscular crop (*Cr*). The crop is followed by a long, thick

stomach, or ventriculus (*Vent*), occupying half the length of the body, and its walls are thrown into circular folds that evidently allow of much expansion. The proctodaeum (*Proc*) is differentiated into a short pyloric section (*Py*) into which open the Malpighian tubules (*Mal*), a colon, or anterior intestine (*AIInt*), and a large pear-shaped rectal sac (*Rect*). Clearly, the caterpillar did not inherit its alimentary canal from its parents (cf. fig. 4). It has been provided with a digestive system adequate to handle all the food it can eat, and there is no limit to its appetite. In a tent caterpillar with a full stomach

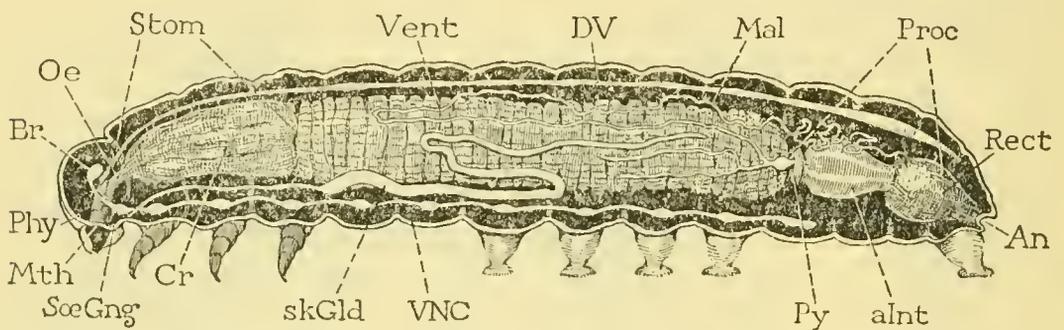


FIG. 7.—Internal organs of a caterpillar, except the fat tissue, exposed from the left side.

*aInt*, anterior intestine; *An*, anus; *Br*, brain; *Cr*, crop; *DV*, dorsal blood vessel; *Mal*, Malpighian tubules; *Mth*, mouth; *Oe*, oesophagus; *Phy*, pharynx; *Proc*, proctodaeum; *Py*, pylorus; *Rect*, rectum; *skGld*, silk gland; *SoeGng*, suboesophageal ganglion; *Stom*, stomodaeum; *Vent*, ventriculus (stomach); *VNC*, ventral nerve cord.

(fig. 8 A) the latter (*Vent*) may extend from the thorax into the seventh segment of the abdomen. In an individual just after a meal (B) the crop (*Cr*) is expanded to a long sac more than twice its length before eating, and the stomach is correspondingly shortened. Crowell (1943) found that a measured amount of food goes through the alimentary canal of the fifth or sixth instar of the southern army-worm in about  $3\frac{1}{4}$  hours. During resting periods the fore gut is cleared of solid food.

Experimental studies on the feeding reactions of caterpillars and their senses of smell and taste have been described by Dethier in a series of papers (1937, 1939, 1941a, 1941b). Odor is shown to be the principal factor by which a phytophagous caterpillar recognizes its food plant. The olfactory sense organs are on the terminal segments of the antennae and maxillae. The caterpillar's perception of odor is of very short range, but its head is always close to the feeding surface. In a study of *Papilio* larvae, which feed almost exclusively on umbelliferous plants, Dethier shows that the attractive odor is that of the

complex chemical components of the essential oils of the Umbelliferae, which impart a characteristic odor to plants of this family. Caterpillars greedily drink sweet solutions, but give a decisive avoidance reaction to a salt, sour, or bitter solution. Tests on *Apamea velata* and *Mala-*

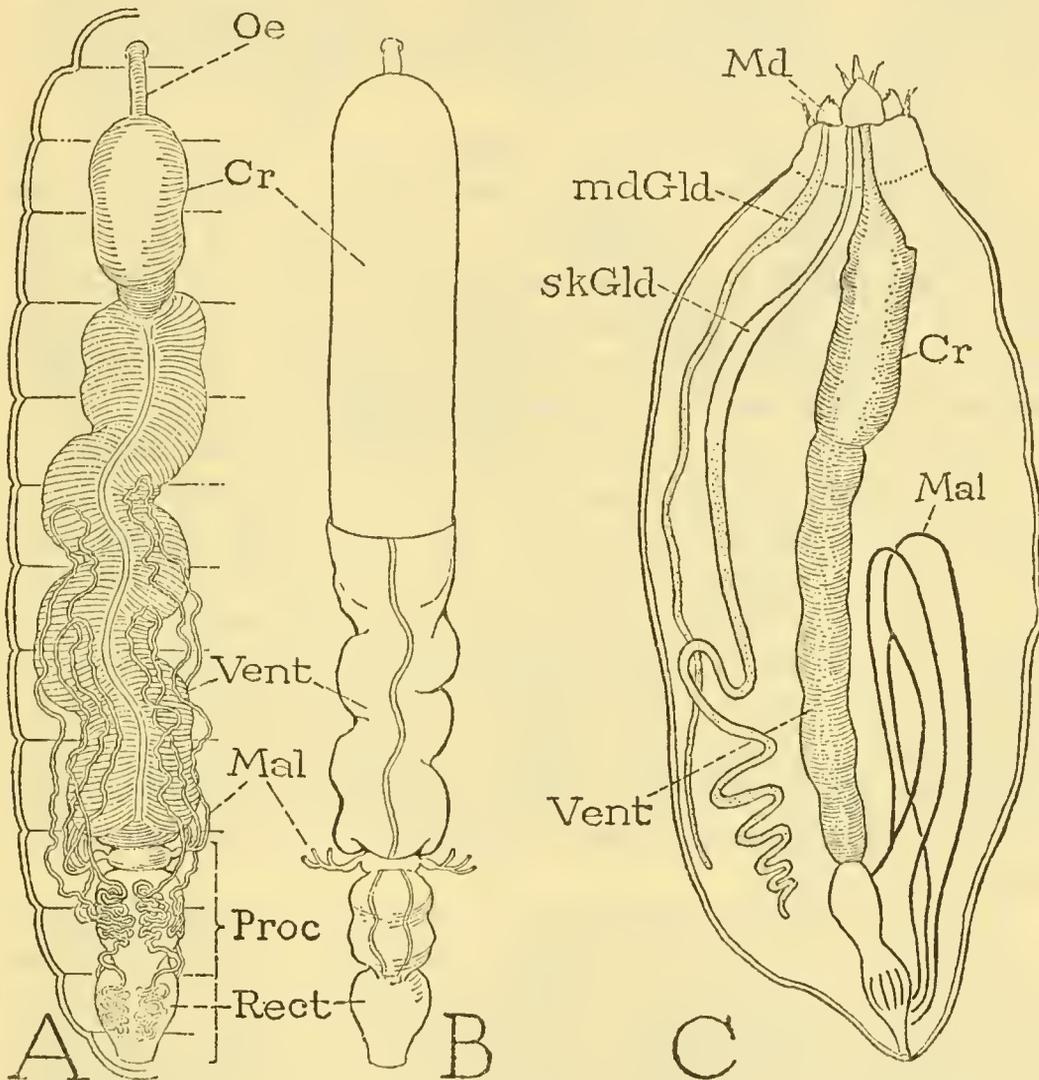


FIG. 8.—Alimentary canal and head glands of caterpillars. Lettering as on figure 7, except *mdGld*, mandibular gland.

A, Tent caterpillar, *Malacosoma americanum*, crop contracted, stomach full of food, greatly extended. B, Same after a period of feeding, crop extended, stomach contracted. C, Caterpillar of *Enarmonia pseudonectis* opened from above, showing alimentary canal, silk gland (*skGld*), and mandibular gland (*mdGld*) of left side (from Teotia and Pathak, 1957).

*cosoma disstria* gave their sensitiveness to sugars as follows: sucrose, fructose, dextrose, and lactose in decreasing order. The final food test by the caterpillar is the taste of the leaf. The organs of gustation, according to Dethier, are primarily on the epipharynx, but probably also on the hypopharynx. Most young caterpillars do not have to hunt

for their food, because the female moth or butterfly usually deposits her eggs on the proper food plant for the larva.

Since the usual labial salivary glands of other insects are converted into the silk glands of the caterpillar, many caterpillars at least have long tubular mandibular glands (fig. 8 C, *mdGld*). The secretion of these glands might be supposed to have a salivary function, but from analyses that have been made Uvarov (1928) suggests that the secretion may be of an excretory nature.

The cylindrical body of the caterpillar accommodates the large alimentary canal, but the abdomen is too heavy to be held up by the thorax in the manner of adult insects. The reduction of the thoracic legs, therefore, allows the abdomen to follow in line with the thorax, and also brings the mouth parts into close contact with the feeding surface. The prolegs support the heavy abdomen, and serve for holding on tight when the caterpillar is climbing or feeding.

The prolegs occupy the position of the abdominal limb vestiges of the embryo, and for this reason some writers have regarded them as appendages serially homologous with the thoracic legs. In structure and musculature, however, the prolegs have nothing in common with the thoracic legs, and they are not moved in the manner of legs as organs of locomotion. Hinton (1955) has thoroughly discussed the whole subject of larval prolegs, not only in the Lepidoptera but in the other orders as well, and gives cogent reasons for believing that in all cases these legs are secondary adaptive structures of the larva having no relation to former abdominal appendages represented by vestiges in the embryo.

A typical caterpillar proleg (fig. 9 A, G, J) is a short, thick, hollow outgrowth of the body wall ending with a flattened foot lobe known as the *planta*, which is armed with small hooks, or *crochets*. Muscles from the body wall are attached on the base of the leg (figs. 9 E, 10 A), and in some cases within the leg; but the principal proleg muscles are a group of long fibers from the lateral body wall inserted on or near the center of the planta (fig. 9 E). These muscles are plantar retractors. Inasmuch as the Onychophora and Tardigrada have a leg musculature similar to that of the caterpillar's prolegs, Pryor (1951) points out that this type of musculature simply meets the need of a similar mechanism in legs of a similar structure, and can have no phylogenetic significance.

The crochets are arranged in various patterns on the planta in different caterpillar species. Fracker (1930) and Peterson (1948) have made comparative studies of the crochets from a taxonomic standpoint without correlating their arrangement with the habits of

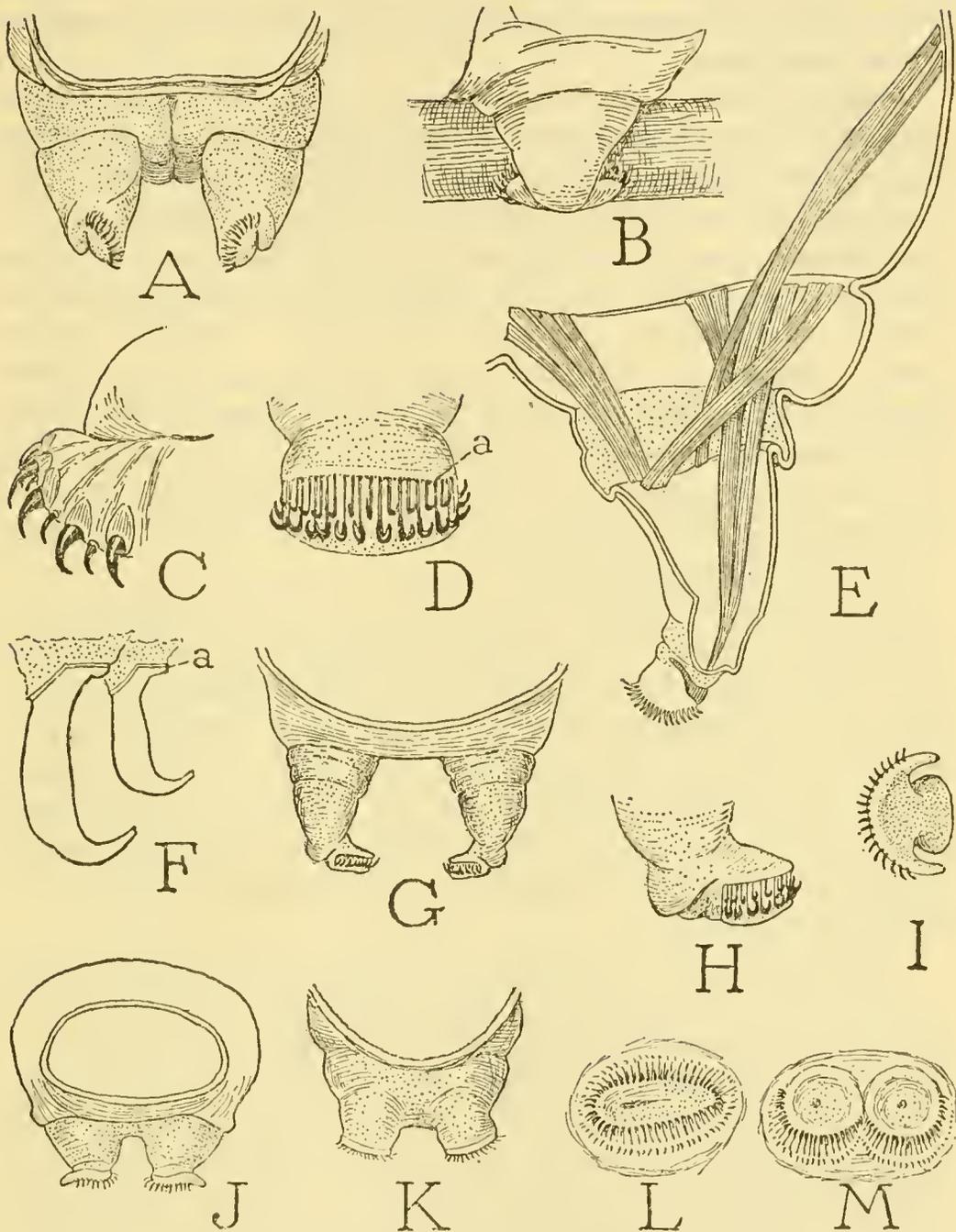


FIG. 9.—Examples of larval prolegs and crochets.

A, Tomatoworm, *Protoparce quinquefasciata*, a pair of prolegs, anterior. B, Same, a proleg clasping a twig. C, Same, part of planta, ventral. D, Same, mesal surface of planta. E, Tent caterpillar, *Malacosoma americanum*, section of proleg, showing muscles. F, Tomatoworm, a pair of crochets, anterior; *a*, articular point on planta (D,*a*). G, Silkworm, *Bombyx mori*, a pair of prolegs, anterior. H, Same, planta more enlarged. I, *Diacrissia virginica*, planta, ventral. J, Same, abdominal segment and prolegs, anterior. K, *Hepialus* sp., pair of median prolegs. L, Same, ventral surface of a median proleg showing crochets. M, Same, crochets of an anal proleg, ventral.

the caterpillars. Hinton (1955) gives a good account of the mechanism of the planta that operates the crochets. Only a few special examples will be given here.

Prolegs typical of climbing caterpillars are well shown by the tomatoworm *Protoparce quinquefasciata* (fig. 9 A). The mesal part of the planta projects as a pad, which, when viewed ventrally (C), appears to be armed with a marginal row of larger upturned hooks and a submarginal row of smaller hooks. On the mesal surface of the pad (D) it is seen that each hook is supported on what appears to be a slender vertical bar in the wall of the planta. Dissection reveals, however, that these apparent bars are the exposed edges of the crochets themselves (F) which are deeply buried in grooves of the plantar surface, and that the visible hooks are only their free outer ends. The wide bases of the crochets are articulated by mesal points (F, a) in an even row on the plantar lobe (D). The same type of plantar structure is seen in the silkworm (G, H).

In the resting caterpillar clinging to a twig, the prolegs are kept extended by internal body pressure, or turgor; the crochet-bearing pads are then turned mesally and the claws firmly grasp the support (fig. 9 B). The retractor muscle of the planta is attached laterad of the base of the crochet-bearing lobe, and, as noted by Hinton (1955), a contraction of the muscle turns the lobe downward and disengages the claws. When the caterpillar is crawling, the plantae are successively lifted to allow the prolegs to be carried forward with the extension of their segments.

On flat surfaces or on the ground the crochets probably have little use, the prolegs serving merely as supports for the abdomen. The actively running arctiid caterpillars have very short prolegs (fig. 9 J). In the yellow woollybear *Diacrisia virginica* (fig. 9 I), the crochet-bearing lobe is crescent shaped with a single row of marginal upturned crochets. Some caterpillars are able to walk on glass by pressing the plantae flat against the surface. Presumably a slight contraction of the plantar muscles converts the feet into suction cups. Such caterpillars can adhere to the glass at a steep angle, but they cannot crawl on a vertical glass surface. Probably they maintain a foothold in the same way on the surface of leaves.

A different type of planta is seen in a stem-boring larva of *Hepialus* (fig. 6 F). The short median prolegs (fig. 9 K) end with flat plantar surfaces (L), each bearing a transverse oval series of larger crochets surrounded by an outer series of small crochets. The plantar muscle is attached excentrically on the plantar surface. The anal prolegs have each a pair of plantar discs side by side (M), with crochets only on

the anterior margins. Each disc has a central muscle attachment. It is not clear that the arrangement of the crochets here has any relation to the boring habits of the larva, since in other boring species the crochet pattern is highly variable.

The prolegs are clearly very useful structures to the caterpillars as props for the abdomen and for holding on while climbing, but they are not active organs of locomotion. Though usually they are present on abdominal segments *III-VI* and *X*, and are rarely more numerous, they are frequently fewer in number, and in leaf miners may be absent entirely.

A few caterpillars, such as the case makers and the bagworms, walk with the thoracic legs while the body is held erect. To the ordinary free caterpillars, however, both the thoracic and the abdominal legs are of little or no use for progression, and the caterpillars have developed a remarkable motor mechanism for direct movement of the body itself. In addition to crawling and climbing, various caterpillar species have become leaf miners and others bore into the stems or wood of plants or burrow in the ground. Furthermore, most caterpillars are able to twist and turn in all directions, and often, while holding on with the abdominal legs, they raise the anterior part of the body and swing it about in search of new foliage on which to feed. For all these movements the caterpillars have a most elaborate body musculature (figs. 10, 11), which includes the usual dorsal and ventral longitudinal bands of intersegmental muscles, and a complex outer system of small muscles going in various directions against the body wall. Similar muscle patterns in other species are illustrated by Forbes (1914).

The common caterpillar does not walk; as already said it progresses by movements of its body, not by means of its legs. It has therefore evolved a type of motor mechanism that propels it forward while the body is close to the support, and its manner of moving is not that of a worm or a snake. The locomotor movements are best seen on a slender, naked caterpillar, such as a noctuid; the following observations were made on a species of *Heliothis*. When the resting caterpillar is about to move, the thoracic legs may first become active and somewhat stretch the anterior part of the body, but they do not bring up the heavy abdomen. Forward movement is initiated by lifting the posterior end of the body, curving it downward and forward, so shifting the anal prolegs anteriorly to a new grasp on the support. Immediately then the deflected segments contract, straighten, and produce a hump on the back, while the anal legs maintain their hold, though reversed in position. A wave of successive forward contrac-

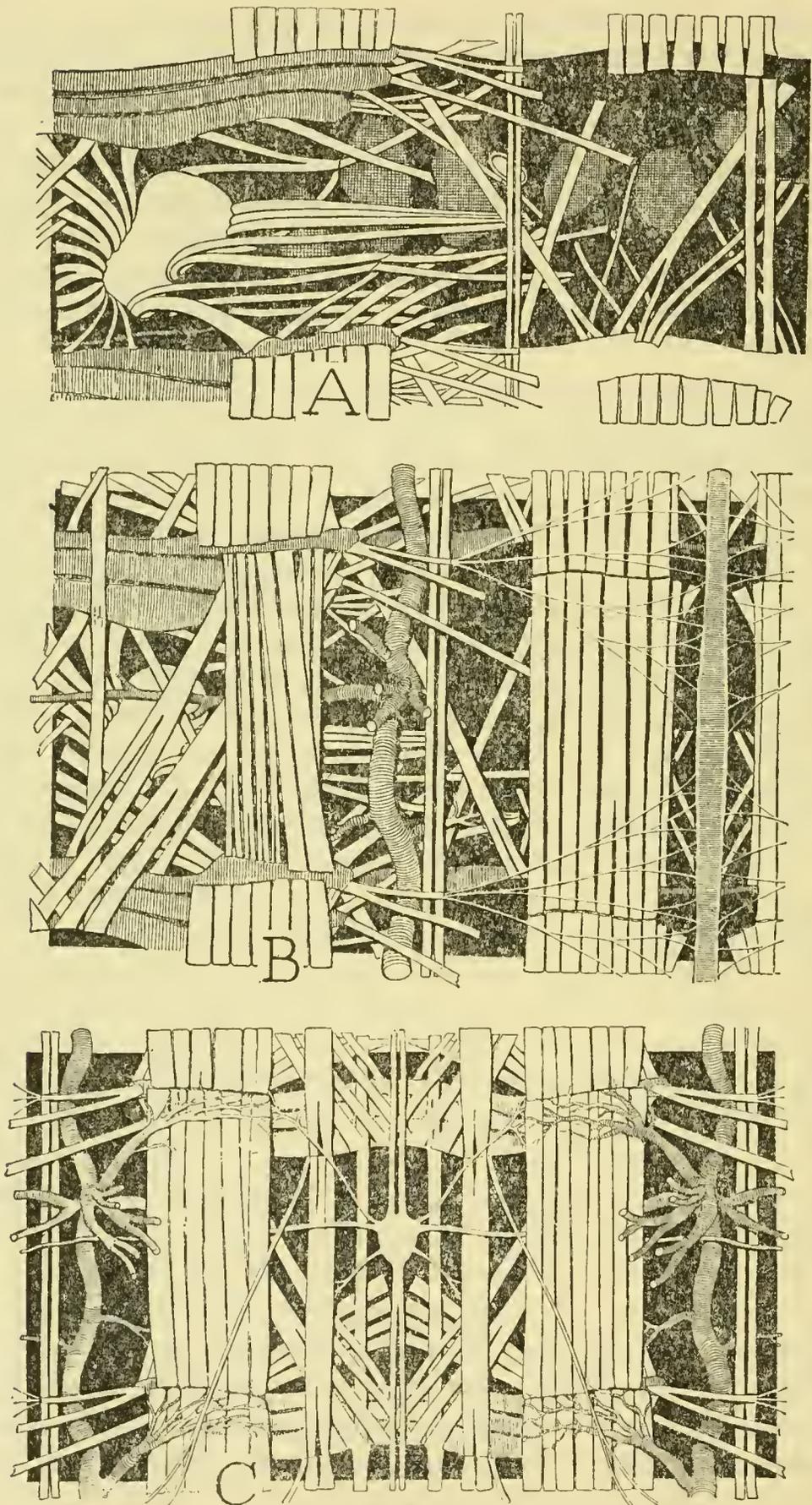


FIG. 10.—(See legend on opposite page.)

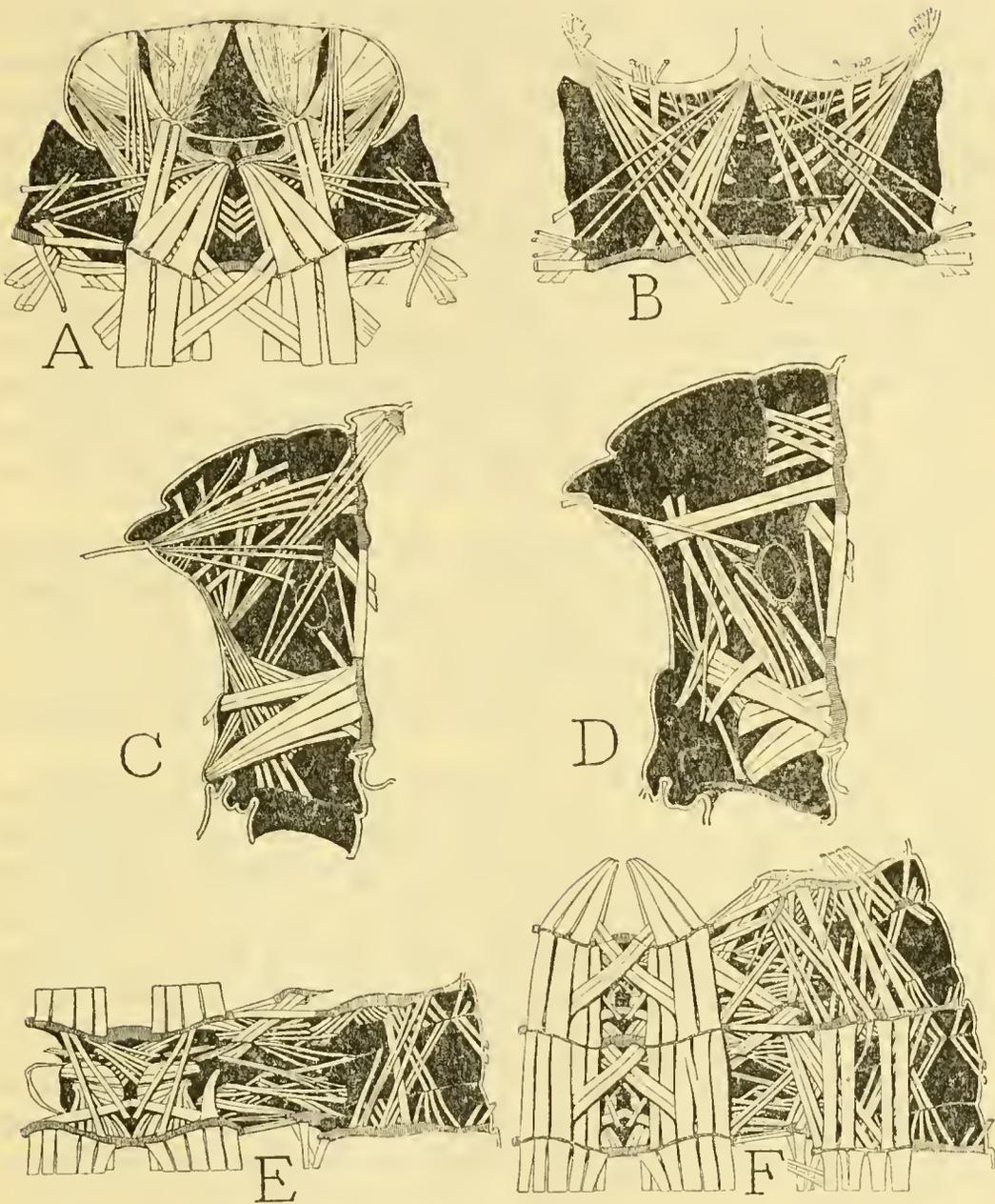


FIG. 10 (See opposite page).—Somatic muscles of the salt marsh caterpillar, *Estigmene acraca*.

A, External muscles of right half of third abdominal segment as seen after removal of longitudinal bands, showing basal muscles of proleg. B, Right half of fourth abdominal segment, ventral longitudinal muscles partly removed. C, Ventral half of fourth abdominal segment.

FIG. 11 (above).—Somatic muscles of the tent caterpillar, *Malacosoma americanum*.

A, Ventral prothoracic muscles of head. B, Dorsal muscles of back of head. C, Right half of prothorax and head muscles. D, Same after removal of head muscles. E, External ventral and right lateral muscles of metathorax. F, Ventral and right external muscles of mesothorax and metathorax.

tion and expansion of the segments now runs rapidly forward through the length of the body. Each segment contracts from the rear and is then expanded anteriorly by the following contraction of the segment in front. Thus the segments successively extend forward, and finally the head is protruded a short distance. At the same time the dorsal hump runs forward like the crest of a wave along the back, lifting successively the prolegs of segments *VI-III* and carrying them forward to a new position; on reaching the thorax the thoracic legs are carried forward in the same manner. The anal legs then again are brought up for a new hold, and the whole series of events is repeated every few seconds. The caterpillar thus progresses at a uniform rate by short forward thrusts of the body. Some species crawl with less exertion, the anal legs being simply moved forward with little humping of the body.

The only contribution of the legs to the locomotion of the crawling caterpillar is the successive forward movement of the anal prolegs. These legs are often more strongly muscled than the others. Their reversal of position as the body advances gives them the appearance of pushing forward, but it is the body moving away from them that alters their slant.

Since the motor force of the caterpillar's movement is the successive *contraction* of the body segments from behind forward, locomotion is produced evidently by the dorsal and ventral bands of longitudinal muscles of segmental length. There being no muscular mechanism of expansion, contraction has been made the effective agent of forward movement, each contracting segment expanding the segment behind in a forward direction. Other writers, as Barth (1937) and Fiedler (1938), have attributed the caterpillar's movement to contraction of the segments without noting the expansion. The locomotor mechanism of the caterpillar is clearly a substitute for leg action, but in no way resembles that of the earthworm. The legless worm moves forward by a compression of the rear part of the body, which extends the anterior part by internal pressure. Nothing of this sort is evident in the caterpillar. The caterpillar's method of locomotion depends on the soft, flexible nature of the integument, and the successive contraction of the longitudinal muscles in individual segments. In a last analysis, therefore, locomotion is controlled by the action of the nervous system in momentarily stimulating the segmental muscles in order from the rear forward.

Barth (1937) terms the locomotor movements of the caterpillar "peristaltic." Peristalsis (Gr. *peristalticos*, claspings or compressing), however, is a propagated series of circular (*peri*) contractions through

a tube, such as the oesophagus, that drives the contents of the tube through the lumen. The caterpillar type of movement, on the other hand, is a successive *lengthwise* contraction and expansion of the body segments that gives a forward motion to the tube itself, in this case the caterpillar. Barth, however, makes a detailed analysis of the muscles involved in the progressive movements of the caterpillar. He points out, furthermore, that the preservation of internal pressure, or turgor, is an important factor in maintaining the action of the muscles. This function he ascribes to the outer system of body-wall muscles, which counteracts a dilation of the soft integument of the caterpillar that would otherwise reduce the turgor. The somatic musculature, according to Barth, is thus composed of locomotor muscles and turgor-preserving muscles.

Caterpillars of the Geometridae, the loopers, or measuringworms, have adopted a method of locomotion by which they can progress at a much greater speed than the ordinary caterpillar. In these caterpillars (fig. 12 A) the prolegs of only segments *VI* and *X* are functional organs, the others have been eliminated or greatly reduced in size. Instead of making a short forward step with the anal legs and then extending the body a corresponding distance, the geometrids, while holding to the support with the thoracic legs, bring the prolegs of segment *VI* clear up to the thorax (*C*), thus throwing the first five abdominal segments into a dorsal loop. Then, retaining their grip by the prolegs, they straighten the body forward and upward, and finally bring it down on the support ready to repeat the action. By this method, with each forward step, the caterpillar advances a distance (*a*) equal to the length of the first five abdominal segments. The rate of progression can be varied; the caterpillar may go along at a leisurely pace but when in a hurry it loops and straightens in rapid succession. According to Barth (1937) the geometrids are not able to crawl in the manner of other caterpillars. In their movements there is no visible contraction and expansion of the body segments.

If the prime function of the caterpillar is feeding and the storage of food reserves in its body as fuel for the pupa or to supplement the sugar diet of the adult, it may be accredited with having fully met its obligations. Almost its entire organization is a reconstructive adaptation for feeding. This is seen in the structure of the mandibles, the long, soft, flexible body, the shortness of the thoracic legs, the presence of prolegs on the abdomen, the great size of the stomach, the abundance of fat tissue for food conservation, the extraordinary development of the muscular system, the body mechanism of locomotion, and the correlated action of the nervous system. All these features are

adaptations for procuring, consuming, and digesting an abundance of food, and for storing a surplus for the pupa and the adult. The fact that some moths have found it unnecessary to eat at all in the adult

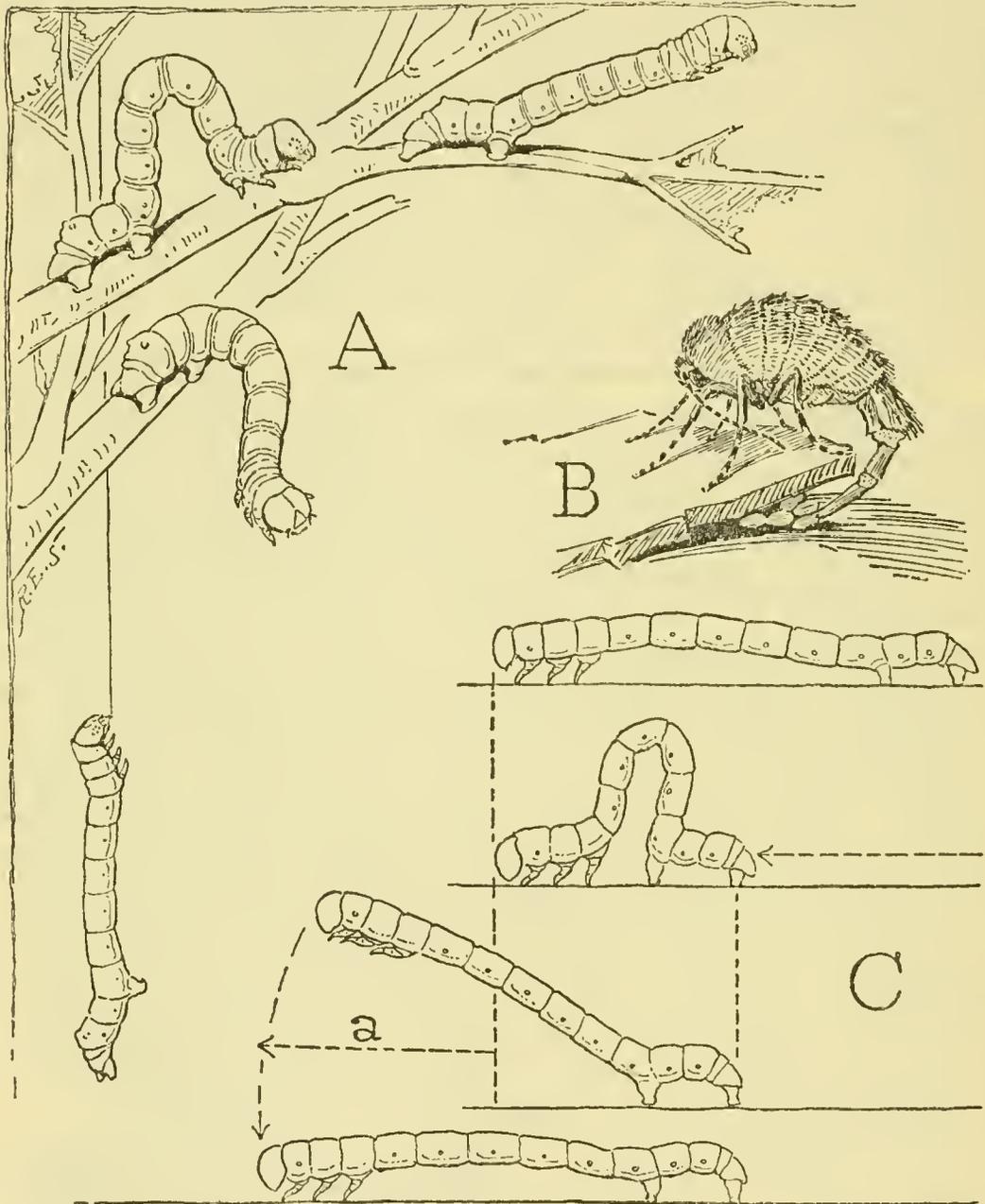


FIG. 12.—Geometridae.

A, Caterpillars of the spring cankerworms *Paleacrita vernata*. B, Female moth of spring cankerworm laying eggs. C, Successive locomotor phases of a geometrid caterpillar; *a*, distance advanced with each extension after looping.

stage would seem to attest the efficiency of the caterpillar as a provider for the whole life span of the individual. The only organs not particularly involved in the adaptive specialization of the caterpillar are the heart, the tracheal system, and the nervous system in its gross structure.

The larval tracheal system is highly elaborate (fig. 13), but in no way specialized. The nervous system of a noctuid caterpillar is described by DuPorte (1914) and that of a hepialid by Swaine (1920-21). In the hepialid *Sthenopsis thule* and an eriocraniid, according to Swaine, there are eight abdominal ganglia, but the connectives in both the thorax and the abdomen are fused into single interganglionic strands. The same is true of a species of *Hepialus* examined by the writer. The union of the nerve connections is thus a specialized feature in this otherwise relatively primitive group. On the other hand, in caterpillars of the higher Lepidoptera the last two ganglia are united in the seventh abdominal segment.

The theory that would explain the different forms of holometabolous larvae on the assumption that they have hatched at different stages of embryonic development assigns the caterpillar to the polypod stage of embryogeny. The polypod stage is that in which rudiments of the gnathal and thoracic appendages are well formed, and vestiges of limbs are present on the abdomen. This stage of the embryo presumably represents a disappearing "centipede" stage in the evolution of the insects.

The polypod theory as applied to the caterpillar encounters two principal objections. First, it assumes that the abdominal prolegs of the larva are serially homologous with the thoracic legs, an assumption that is highly improbable. Second, if we look at an embryo in the polypod stage of development, such as that shown by Eastham (1930) for *Pieris rapae* (fig. 14), it is seen that the head is still in a very primitive state. The gnathal segments are not yet added to the embryonic head (*emH*), and the prospective mouth parts (*Md*, *1Mx*, *2Mx*) are mere undifferentiated lobes. Yet, when the larva leaves the egg it is already a perfectly formed young caterpillar. The head is a syncephalon, the mouth parts are fully developed for feeding and silk spinning. All this is quite at variance with the idea that the caterpillar is an arrested polypod stage of the embryo.

While in most ways the caterpillar is structurally and functionally subservient to the adult, in one respect it has been self-centered. This is in its production and spinning of silk, which seems to have no primary relation to the welfare of the moth or butterfly. The silk is formed in the labial glands, which ordinarily in other insects secrete saliva. Since caterpillars use their silk in various ways, it is not clear what use it may have been to them in the first place.

True silk is formed only by arthropods, particularly the insects and spiders, but the silk-producing organs may be glands in quite different parts of the body having no homology with one another. Silk produc-

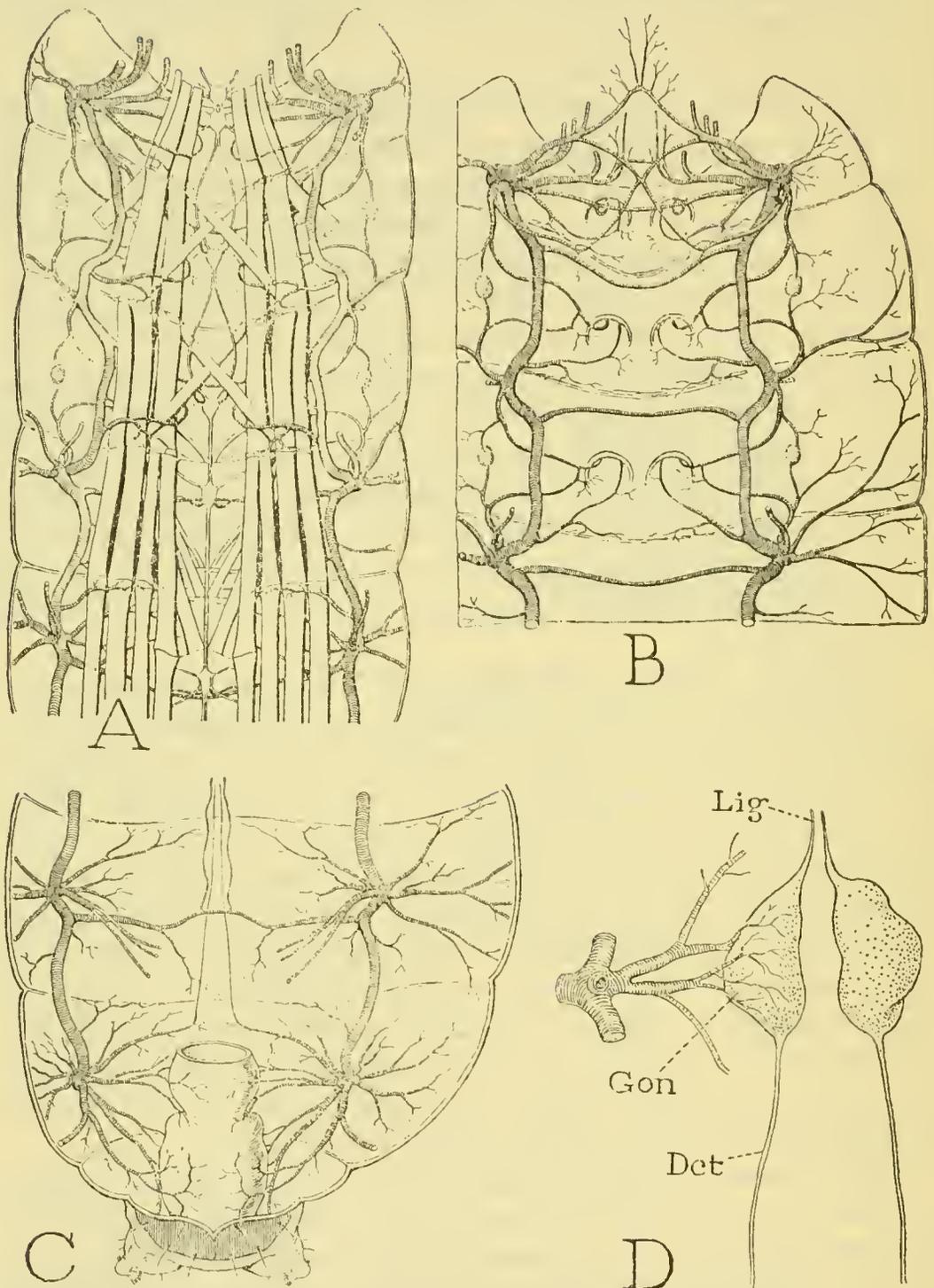


FIG. 13.—Examples of the tracheal system of a caterpillar.

A, Cutworm (noctuid), ventral half of thorax and first two abdominal segments. B, Same, thoracic segments with muscles removed. C, Same, ventral tracheation of end of abdomen. D, Corn ear worm, *Heliothis zea*, gonads and their tracheation in fifth abdominal segment; *Dct*, duct; *Gon*, gonad; *Lig*, suspensory ligament.

tion by the labial glands is common to the larvae of Trichoptera, Lepidoptera, and Hymenoptera, and it may be supposed that the functional change in the glands took place in the common ancestors of these three groups. Among the Neuroptera some species secrete silk in the Malpighian tubules and spin it from the anus. The female of the water beetle *Hydrophilus pisticus*, described by Lesperon (1937), deposits her eggs on the lower surface of the leaves or stems of water plants enclosed in a cocoon of silk spun from glands opening into the oviducts at the bases of the ovaries. A luminous, silk-spinning

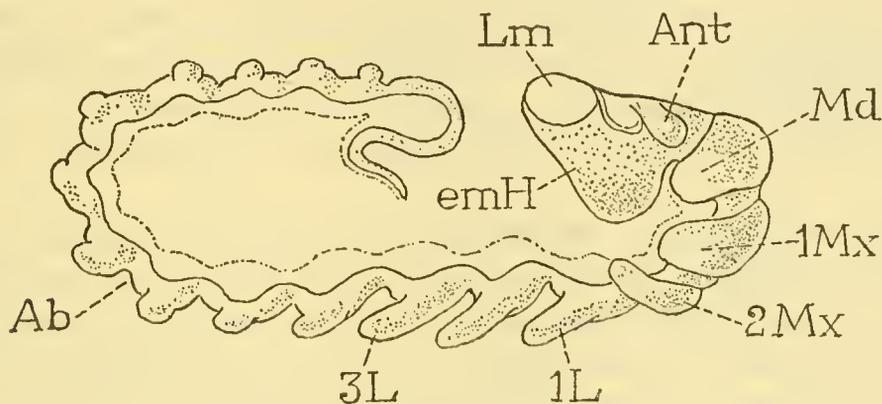


FIG. 14.—The polyopod stage of the embryo of *Pieris rapae* (from Eastham, 1930).

*Ab*, abdomen; *Ant*, antenna; *emH*, embryonic head; *L*, thoracic leg; *Md*, mandible; *1Mx*, first maxilla; *2Mx*, second maxilla.

mycetophilid fly larva, *Bolitophila luminosa*, as described by Ganguly (1960), produces silk in the labial glands and spins it as a snare for capturing insects attracted by light generated in its Malpighian tubules. The so-called balloon fly, *Hilara* of the Empididae, has been shown by Eltringham (1928) to spin its silk from glands in the enlarged basal tarsomeres of the fore legs. The Embioptera are well known to spin silk from glands in the fore tarsi. The art of silk spinning has been most highly cultivated by the spiders, whose silk glands are in the abdomen.

Lesperon (1937) has described the histology and physiology of the silk glands and the secretion of silk in the several groups of silk-spinning insects. Bradfield (1951) discusses the relation of phosphatases and nucleic acids in the silk glands of spiders and caterpillars, showing their function in the secretion and discharge of silk from the glands.

Of the various ways that caterpillars use their silk, we may note the following. Some species that live in trees but pupate on the ground let themselves down by dropping at the end of a thread drawn

out from the spinneret. Others spin a web on the smooth surface of a leaf on which they are feeding to obtain a better foothold. Still others construct a shelter or retreat by drawing leaves together and securing them by strands of silk. Then there are the casemakers and bagworms that enclose themselves in a close-fitting jacket or a bag by weaving together bits of leaf. The webworms and tent caterpillars make those large silken domiciles in trees, in which a whole family hatched from one batch of eggs lives a communal life. As the tent caterpillars go out on the limbs to forage, they leave a trail of silk to guide them back to the nest where they spend the night. When ready to pupate, tent caterpillars simply jump off the tree. Caterpillars of butterflies spin a small web mat against a support from which they can hang awaiting pupation. Some secure themselves with a silken girdle around the thorax which remains as a suspensorium for the pupa.

The most important use of silk would seem to be that of many moth caterpillars of enclosing themselves in a closely woven cocoon, within which they shed the last larval cuticle and change to the pupa. Cocoon spinning evidently began among the Micropterygidae, since Tillyard (1922) describes the larva of *Sabatinca* as spinning a cocoon of rather coarse silk having a leathery appearance. However, he says that "no definite spinneret apparatus could be discovered," and he makes no mention of the silk-producing glands. On the other hand, in *Micropteryx calthella* Hannemann (1956) describes and figures a pair of oval glands in the thorax having a common duct that opens into a salivarial chamber between the hypopharynx and the labium, but these glands he says secrete saliva that is discharged on the food. The leaf-mining larva of the eriocraniid *Mnemonica auricyania* is described by Busck and Böving (1914) as having a spinneret from which it spins a cocoon in the ground. Of all the insects the caterpillar is the best-known silk-spinner, and the silkworm probably outranked the honey bee as an insect of commercial importance until the production of competing artificial fabrics. Artificial honey has not yet been invented.

Though the faculty of producing and spinning silk was evidently not acquired by the ancestral caterpillars for any specific purpose, yet the evolution of their modern spinning apparatus involved a very considerable reconstruction of their mouth parts, and the conversion of the salivary glands into silk-producing organs.

The ordinary salivary glands of insects lie in the thorax; their ducts unite in a common outlet duct that opens into the space between the hypopharynx and the labium, known as the salivarium. On the walls of the salivarium near the mouth of the duct are attached opposing

muscles from the hypopharynx and the labium, which probably regulate the flow of the saliva.

The silk glands of the caterpillar are a pair of long tubes (figs. 7, 8 C, *skGld*) extending from the head far back into the abdomen. Each gland is thrown into loops and coils, and the slender ducts open

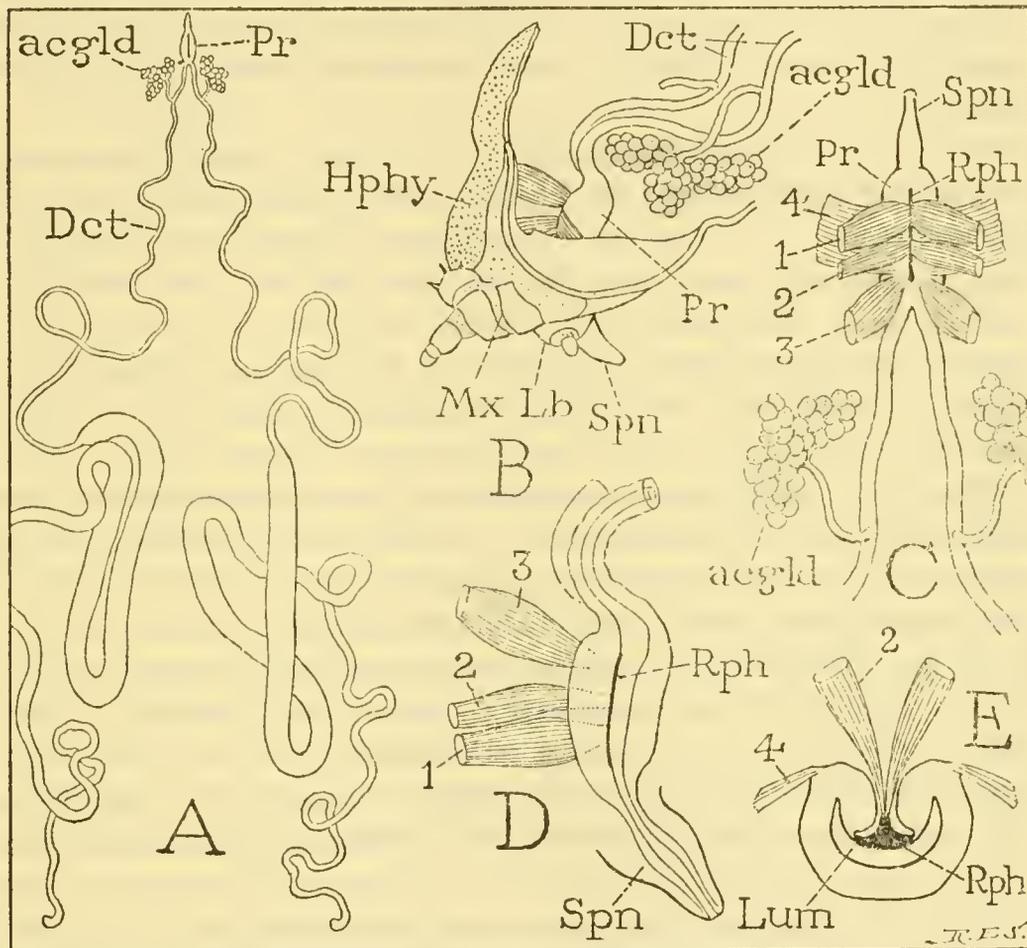


FIG. 15.—Silk glands and spinning apparatus of the tent caterpillar, *Malacosoma americanum*.

A, The silk glands. B, Section of head lobe formed of the labium, maxillae, and hypopharynx containing the silk press and bearing the spinneret. C, Silk press and ends of ducts, dorsal. D, Longitudinal section of silk press. E, Transverse section of silk press.

*acgld*, accessory gland; *Dct*, silk gland duct; *Hphy*, hypopharynx; *Lb*, labium; *Lum*, lumen of silk press; *Mx*, maxilla; *Pr*, silk press; *Rph*, raphe; *Spn*, spinneret. 1, 2, 3, dorsal muscles of silk press; 4, ventral muscle of press.

into a small chamber called the *silk press* (fig. 15 A, *Pr*), which opens through the spinneret at the end of the labium. A small accessory racemose gland (*acgld*) opens into each duct near its termination.

The silk press of the caterpillar is clearly the salivarium of other insects, which has been converted into a closed chamber by the union of the hypopharynx with the basal part of the labium (fig. 5 E, *Pr*). The salivary muscles are strongly developed (fig. 15 C), three pairs

(1, 2, 3) from the hypopharynx being inserted on a sclerotic bar, or *rhaphe* (*Rph*), in the dorsal wall of the press, and a single pair from the labium (4) attached laterally. The lumen of the press is continued into a narrow exit tube (D) that opens on the end of the spinneret (*Spn*). The hypopharyngeal wall of the press is deeply inflected (E) into the lumen (*Lum*), but evidently can be lifted by the muscles, and then by an elastic springback drive the liquid silk from the spinneret. The silk press is probably also a silk ejection pump.

As already noted, the maxillae are closely associated with the labium, forming a prominent lobe on the underside of the head bearing the spinneret (fig. 5 B,C), but the hypopharynx (*Hphy*) also is involved in this structure, since it is united with the inner wall of the labium (*Lb*). While these parts are movable by their own muscles, the characteristic figure-eight movements of the spinning caterpillar are made by the head and the freely swinging fore part of the body, activated by the elaborate head and body musculature (fig. 11 A,B).

When the caterpillar in its evolution had once become fully adapted structurally for the performance of its functions in relation to its future pupal and adult state, its successors were then free to vary in superficial ways, and to adopt habits suitable to their own interests. So, as the adults in their evolution were diversified into many species, their caterpillars likewise underwent evolutionary changes as they adopted different ways of living and feeding, until they became as distinctive of their species as the adults. Though most caterpillars have remained vegetarians, feeding in the open on the leaves of herbs or trees, some have penetrated the fruit, others have taken to mining the leaves, boring into stems or wood, or burrowing into the ground, while a few have become aquatic and have developed gills in the form of slender tracheated filaments growing from the back. All these are plant feeders.

There are species of caterpillars, however, that have renounced vegetarianism for other kinds of food. A good review of these aberrant feeders has been given by Brues (1936), and Clark (1926) has described the carnivorous caterpillars. The wax moth invades beehives and its larvae burrow destructively through the honeycomb, feeding on the wax and the bees' store of pollen. Larvae of the clothes moth eat fur, wool, and feathers. A number of species have become carnivorous, feeding as predators on live aphids, larval coccids, other young homopterons, pupae of moths, spider eggs, and eggs of the bagworm. A lycaenid caterpillar has imitated the aphids by excreting from glands on the end of its abdomen a liquid agreeable to ants.

For protection the ants take this caterpillar into their nest, and here the treacherous creature eats the ants' larvae.

Finally, there are species that have descended to parasitism. Members of the Epipyropidae live as external parasites on the back of fulgorids or other homopterons, and several pyralid species are ectoparasites on live sloths. Two species are known to be internal parasites of the coccid *Kermes*. Rau (1941) records the rearing of six species of moths from nests of the wasp *Polistes*. The larvae of these species are parasitic on the wasp larvae, and spin their cocoons in the host cell, where they pass the winter. Egg laying by the moths has not been observed, but the females are suspected of entering the wasps' nest at night when the inmates are asleep.

All this diversity of habits on the part of the caterpillars shows that the caterpillar structure, though highly specialized and standardized, is still adaptable to various ways of living. It is a presumed tenet of evolution that all perpetuated adaptations are beneficial to the species. However, since it would seem that there is enough vegetation in the world to support all the caterpillars there are, why have some species departed from the ways of their ancestors? Brues (1936) points out that the preference of insects for certain kinds of food is an instinct, not a matter of conscious taste, and that aberrant food habits are therefore due to basic hereditary changes in instinct. We are then left with the question of why do instincts change.

The caterpillar goes through several stages of increasing growth between moults, but it preserves its larval form and structure up to the end. Then at one final moult, after shedding its caterpillar skin, it appears to have suddenly changed into a pupa. That the change of form is not so sudden as it appears to be will be shown later.

The larval status and the pupal-adult development are regulated by two opposing hormones. A juvenile hormone, formed in the corpora allata of the head, maintains the larval form; a hormone discharged from glands in the prothorax, under stimulus by a hormonal secretion from the brain, controls moulting and permits further development. The prothoracic gland hormone is known as the moulting hormone because, as said by Van der Kloot (1961), it "acts on the tissues to promote all the changes characteristic of a molt," but it has no influence on the development that follows the moult. This hormone then might be likened to a green traffic light that allows traffic to cross the intersection, but has nothing to do with where it goes after crossing. The developmental course of the insect after the moult depends on its hereditary factors, it may become another larva, a pupa, or an adult. The prothoracic gland hormone has been named "ecdysone," unfor-

tunately since it has no relation to ecdysis. The corpus allatum hormone has been supposed to operate entirely by inhibiting adult development, but more recent investigations indicate that it actively affects the larva. The immature insect grows between moults and may undergo slight or considerable changes at the moults. Hence, Wigglesworth (1959) has pointed out that "the hypothesis that this hormone merely inhibits differentiation toward the adult becomes untenable." Further, he says, "the corpus allatum hormone is clearly doing something active and positive in causing differential growth of larval type." A review of the structure and function of the endocrine glands of Lepidoptera has been given by Hinton (1951).

While most of the adult development either is somehow inhibited in the larva, or the thoracic-gland hormone is not always secreted in sufficient amount, some adult structures do develop from an early stage in the larva. A striking example is that described by Eassa (1953) of the growth of the adult antennae and mouth parts in the larval stages of *Pieris brassicae*. The adult antenna begins its development in the first larval instar as a thickening of the epidermis beneath the larval organ. As the antennal rudiment enlarges, the epidermis folds inward as a containing peripodal pocket. During the following instars the base of the antenna moves upward beneath the larval cuticle until it reaches the position of the adult organ on the face. The peripodal pocket likewise elongates, but as an open slit, and finally it opens out so as to free the antenna, still beneath the larval cuticle. The everted wall of the pocket becomes the imaginal epidermis of the head between the adult and the larval antennae.

Likewise, as shown by Eassa, the rudiments of the adult maxillae appear in the first larval instar as thickening of the epidermis beneath the larval maxillae. Through the following instars they develop within pockets of the epidermis. The galeae grow to such an extent that they become wrinkled, and when everted in the early pupal stage they are long and folded upon themselves. The larval mandibles shrink to the vestigial organs of the adult. The imaginal labium develops mostly during the fifth larval instar.

It is well known that the invaginated leg and wing buds of most holometabolous insects develop during the larval stage. In some of the nematoceros Diptera they are evaginated beneath the larval cuticle in the last larval instar, as the writer (1959) has noted in the mosquito.

The postembryonic development of the internal reproductive organs of the psychid lepidopteron *Solenobia triquetrella* is described by Ammann (1954) and by Brunold (1957). Rudiments of the testes

and ovaries are present at hatching, and are in the process of dividing into compartments. No considerable change occurs during the first four larval instars, but further development proceeds during the rest of the larval life, including formation of the outlet ducts.

From these examples of imaginal development during the larval stage it is evident that an inhibitory influence does not equally affect all adult structures. Bodenstern (1957) has given some attention to this phase of the subject. He notes that in the larva of *Drosophila* the imaginal discs (i.e., rudiments of imaginal organs) grow at a rather constant rate, as shown by Eassa in *Pieris*. The growth of these rudiments during the intermolt periods indicates that the concentration of the thoracic-gland hormone is sufficient for the growth of these parts, but is not enough to induce moulting. "From all this," Bodenstern says, "one must conclude that the ability of different tissues to respond with growth to a given titer of prothoracic-gland hormone varies. Some tissues are able to grow in a low, others only in a higher titer."

The thoracic-gland hormone brings about moulting, but the development of the next larval instar and whatever differentiation it may make is controlled by the corpus-allatum hormone. It would seem, therefore, that the whole developmental process that takes place in the larva depends on the relative concentration of the two hormones in the blood. The way it works out seems to be that development is permitted in adult tissues and organs whose growth does not interfere with the functions of the larva, while the purely larval structures are maintained and larval growth is allowed to proceed.

The body wall, the alimentary canal, the muscular system, the nervous and circulatory systems, the tracheae are all preserved intact to the end of the active state of the caterpillar. With species that spin a cocoon and remain quiescent within it a varying length of time before pupation, metamorphic changes may begin during or shortly after spinning. In the silkworm, *Bombyx mori*, Verson (1905) says that degeneration of the mesenteron epithelium begins after the emptying of the alimentary canal at the time of spinning. As the larval cells are thrown off they are replaced by regenerative cells, so that the mesenteron wall remains continuous. It is observed likewise by Deegener (1908) that metamorphic changes in the alimentary canal of *Malacosoma castrensis* begin in the spinning larva. In *Vanessa*, according to Henson (1929), degenerative changes in the mesenteron take place in the fifth larval stage. In *Heterogenea limacodes* it is said by Samson (1908) that the larval epithelium of the mesenteron degenerates and is replaced by the imaginal epithelium even during the spinning by the

caterpillar, which takes place in October, though pupation does not occur until the following May. Also histological changes in the Malpighian tubules begin just after the larva has spun its cocoon; reconstruction of the tubules is completed in the pupa. After a short rest the silk glands degenerate, and in the course of the winter a part of the larval musculature is lost.

Considering the growth of adult organs that may proceed in the active larva, and the metamorphic changes that take place in the quiescent larva after spinning its cocoon, it seems that there must be some mechanism that regulates the hormone secretions. Actually, the two hormone sources are in communication with the brain. The thoracic glands receive their stimulus for activity from the hormonal secretion of the brain by way of a pair of bodies in the back of the head of nerve-tissue origin, known as the corpora cardiaca. These bodies are directly connected by nerves with the secreting centers of the brain, and a nerve from each corpus cardiacum goes to the corpus allatum of the same side. It is possible, therefore, that the brain is the regulatory center of the entire endocrine system. In fact, it has been shown by Scharrer (1952) in the cockroach *Leucophaea* that the corpora allata are affected histologically and functionally by the amount of brain secretion in the corpora cardiaca. When the brain nerve to one corpus cardiacum is cut, preventing the brain secretion from entering the latter, the connected corpus allatum increases in size, its cells appear to contain more cytoplasm, the nuclei become more vesicular, and the nucleoli more distinct. Corpora allata in this condition, Scharrer says, are "functionally equal to, or perhaps even more competent than, normally innervated glands." This would seem to indicate that the more brain secretion there is in the corpora cardiaca the less active are the corpora allata, and vice versa. The brain, of course, does not act autocratically; it is itself activated by external or internal stimuli transmitted through the sensory nerves. When the brain activities cease, all growth and developmental processes stop, and the insect goes into diapause. This is shown by Van der Kloot (1955) to be true of the diapausing pupa of the *Cecropia* moth. After prolonged exposure to low temperatures, endocrine activity of the brain is restored, "diapause ends and the development of the adult moth begins."

Inasmuch as most animals grow from youth to maturity without the aid of a juvenile hormone, it is not clear why or how the early insects acquired glands for producing this hormone. However, it is reported by Schneiderman and Gilbert (1959) that substances having at least the effect of the corpus-allatum hormone when injected into

insects have been extracted from Crustacea and other invertebrates, and even from the adrenal cortex of cattle. These writers suggest, therefore, that something of the nature of the insect juvenile hormone may be widely present in all animals, and that evolution has produced specific sensitivity to it in certain tissues, as in the insects. In any case, it seems certain that if the early insects did not have a juvenile hormone, they could never have developed their special kind of metamorphosis.

The corpora allata arise at an early age of the embryo from the ventral ectoderm of the head between the mandibular and maxillary segments, and migrate to their dorsal position in most insects behind the brain. Though the Thysanura do not have typical corpora allata, they do have a pair of apparently glandular bodies attached to the outer surfaces of certain muscles of the maxillae. These bodies are termed the *corps jugaux* by Chaudonneret (1949), who reasonably contended that they are the corpora allata in a primitive position between their ventral points of origin and their usual dorsal position in other insects. The function of these bodies in the Thysanura, however, is not determined, and, so far as known to the writer, thoracic endocrine glands have not been observed in these insects. Yet the thysanurans molt throughout their entire life. Perhaps the *corps jugaux* are really moulting glands that have remained in the head, where they take their origin.

#### METAMORPHOSIS

When at last the juvenile hormone that has maintained the caterpillar in its larval form gives way entirely to the thoracic-gland hormone, the caterpillar comes to the end of its life, provided it has not already been eaten by a bird or other predator, killed by some parasite, or poisoned by an insecticidal spray. If the caterpillar were a sentient being, knowing the ordeal it must now go through, it should be filled with apprehensions. However, the caterpillar is a creature of instincts, with no consciousness of self to be carried over into the butterfly. The butterfly is a new thing entirely, having its own instincts and outlook on life, and very probably no memory of ever having been a caterpillar. The transformation processes are purely biochemical, under the guidance of hormones and the factors of inheritance.

Yet the caterpillar seems to feel the approach of its time for pupation; it becomes restless and food no longer has any appeal. Tent caterpillars suddenly rush out from their tents to the ends of twigs

on the tree and recklessly jump off to the ground, where they may travel long distances to find a suitable place for pupation. Others wander about in search of a secluded place, and some species pupate in the ground. The caterpillars of most moths enclose themselves in silken cocoons. The spinning of a cocoon is a complex piece of architectural work, but the caterpillar is endowed with a sensory-neuromuscular spinning mechanism that works automatically as a series of coordinated acts. If its cocoon is destroyed when partly spun, most caterpillars cannot begin over again, but must go on from where they left off. The stimulus for spinning has been shown by Van der Kloot and Williams (1953) to be of internal origin, in part hormonal, but largely the condition of the silk glands. The activating nerve center, however, according to these investigators (1954), is in the brain.

The caterpillars of butterflies do not enclose themselves in cocoons. In preparation for pupation they spin a mat or cone of silk on the underside of a twig or leaf or against some upright object, and then hang themselves from it head down by means of the claws of the anal prolegs and spines on the suranal plate. Some give themselves extra security by spinning a loop of silk from the support that forms a girdle around the thorax. When the pupa is formed it splits the larval skin over the back and down the face. Then by convulsive movements it pushes the larval skin up to its rear end and hangs freely from the attached skin. It is commonly said that the pupa holds on by pinching a fold of the skin between the movable segments of its abdomen. According to Riley (1879), however, there are small ridges and knobs on the end of the pupal abdomen that serve partly to grasp the suspended larval skin, but the principal suspensorium is the "rectal ligament," which evidently is the extracted cuticular lining of the intestine held by the anal sphincter of the pupa. This "ligament," Riley says, will support a weight 10 to 12 times that of the pupa. The tenth abdominal segment of the pupa is prolonged into a process known as the *cremaster* (or hanger) armed at the end with spines and hooks. The pupa now extracts itself from the larval skin by swinging the cremaster to one side and anchoring it into the silken support. Here the pupa hangs independently by the cremaster until the butterfly emerges. The shriveled larval skin may remain on the support until it drops off or is blown away by the wind.

When the caterpillar (fig. 16 A) sheds its last cuticular skin and reveals the pupa (D) that has taken its place, the change is indeed striking. The fully formed pupa, however, is the finished product of a transformation process. The caterpillar itself in its final stage (B)

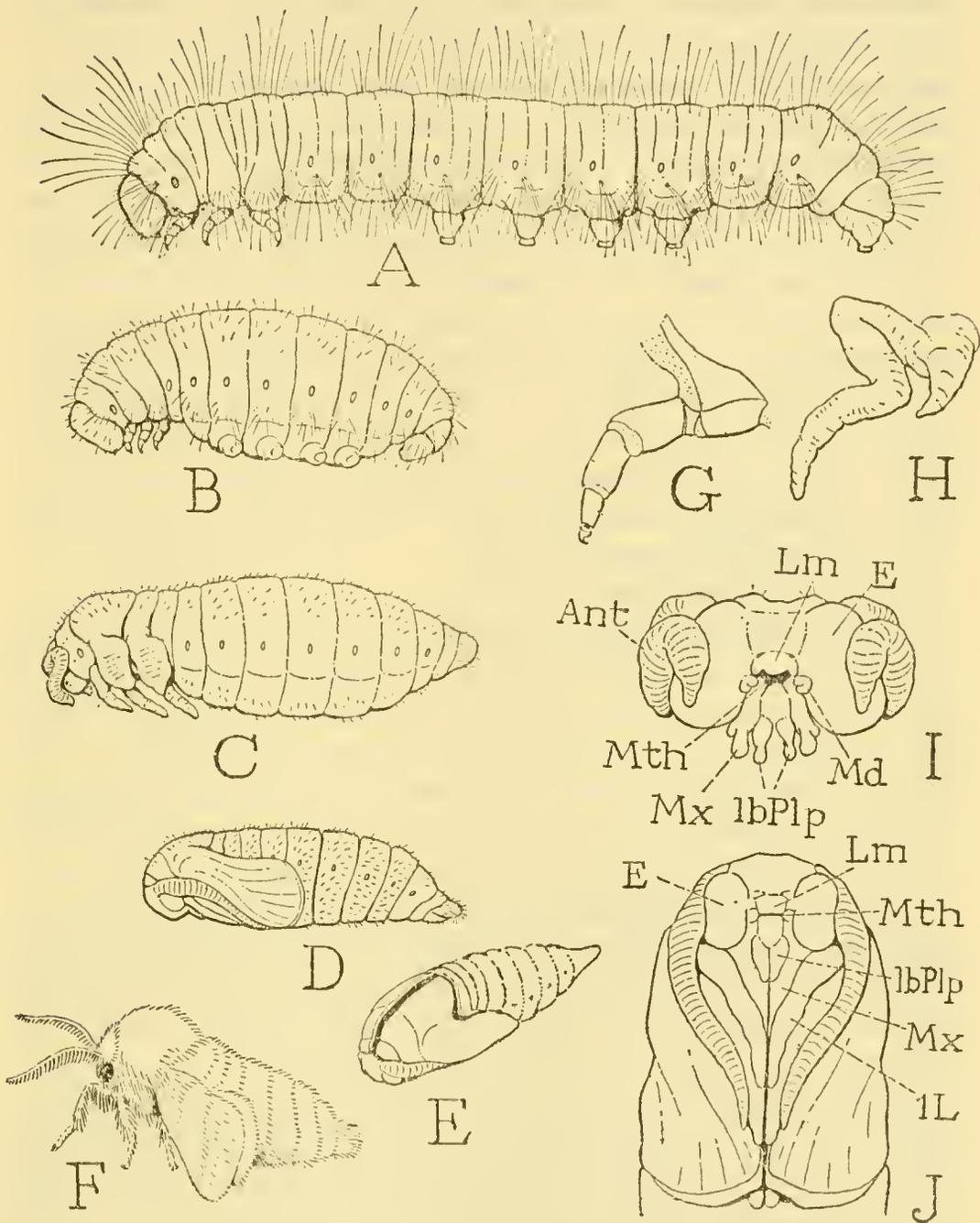


FIG. 16.—External changes during metamorphosis of the tent caterpillar, *Malacosoma americanum*.

A, The mature active caterpillar (length  $3\frac{1}{4}$  inches). B, Final contracted stage of caterpillar in cocoon. C, The pharate pupa in last larval cuticle. D, The mature pupa. E, The split pupal shell after emergence of the moth (F). G, A larval leg. H, Leg of pharate pupa. I, Head of pharate pupa, anterior. J, Head and thorax of mature pupa, ventral.

*Ant*, antenna; *E*, compound eye; *1L*, first leg; *lbPlp*, labial palpus; *Lm*, labrum; *Md*, mandible; *Mth*, mouth; *Mx*, maxilla.

becomes immobile and greatly contracted. When it moults, the remodeled body still within the unshed larval cuticle appears as a preliminary stage of the pupa (C). An entirely new and different cuticle has been secreted by the epidermis, and the larval prolegs have been discarded with the larval skin. The wings are now everted, and the legs have taken on more of the adult structure (H). On the head (I) the large adult antennae (*Ant*) are conspicuous, and the mouth parts are undergoing development, except the mandibles (*Md*) which are reduced to small knobs. This concealed early period of the pupa has been called the "prepupa" or "propupa," but it is not a stage of the pupa equivalent to a larval instar, since it is not separated by a moult from the mature pupa (D). It is therefore better named by Hinton (1958) the cloaked, or *pharate*, pupa. By further development within the larval cuticle the pharate pupa becomes the mature pupa (D) in which the wings are enlarged, the legs and antennae are lengthened, and the mouth parts somewhat larger.

With the final shedding of the larval cuticle (the pupal ecdysis) the fully formed pupa (fig. 16 D) is liberated. The pupal mouth parts, antennae, wings, and legs lie flat against the body. In most Lepidoptera they become cemented to the body by an exuding, gluelike substance that soon hardens to a shell-like glaze over the entire surface. The pupa is then called a *chrysalis*. From now on the pupa does not change externally, but within it the special tissues of the larva go into dissolution, and adult development proceeds to the completion of the imago.

With most Lepidoptera the mouth parts continue their development within the pupal cuticle until they attain the typical adult structure (fig. 17 A). In the pupa of the tent caterpillar here described, however, the mouth parts actually regress from their state of development seen externally on the pupal cuticle (fig. 16 J) because the moth is one that does not feed. In the adult moth (fig. 17 B) the maxillae (*Mx*) have been reduced to small, entirely separate lobes at the sides of the mouth. The labium (*Lb*) also is much reduced, but its palpi have increased to long, three-segmented appendages. There is no trace of mandibles.

The degree of change that takes place within the pupa from larva to adult differs in different insects. In some, many of the larval tissues simply begin a new growth that forms directly the corresponding adult tissues. In others the special larval tissues break down, and their disintegration may be so nearly complete that little is left of the original larva. In extreme cases, therefore, the so-called metamorphosis of the insect is not literally a transmutation of the larva into the imago. The caterpillar, for example, does not actually become a

moth or butterfly. The newly developing adult takes whatever parts of the larva can be utilized with adaptive modifications, such as the heart, the tracheae, and the nervous system. Otherwise it is a new creature built up from imaginal cells that have remained undifferentiated during the life of the larva, while the unused parts of the larva are cast off or go into dissolution within the pupa. As already noted, some adult organs may begin their development in an early instar of the larva.

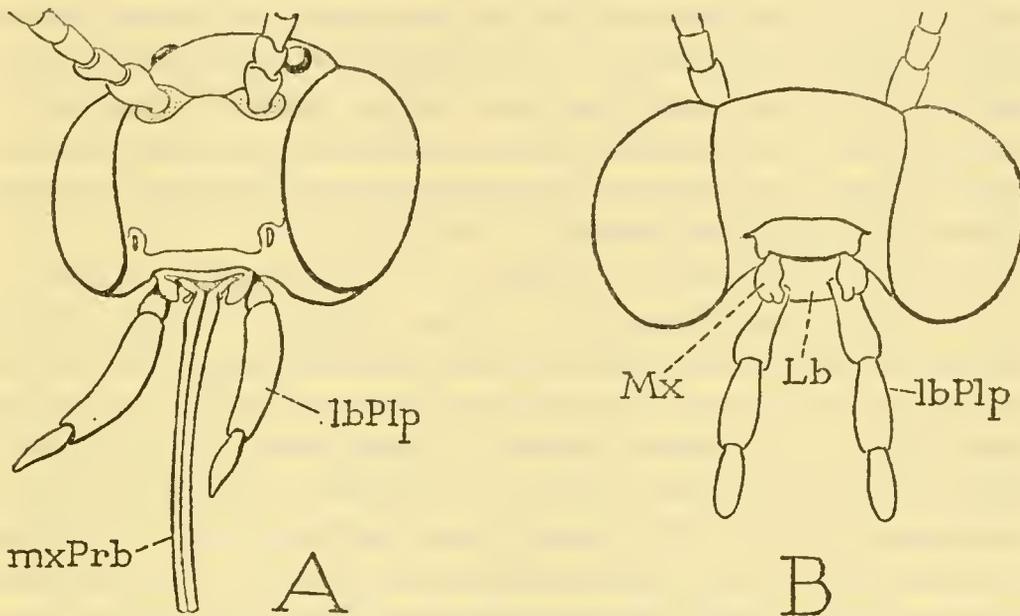


FIG. 17.—Examples of moths with and without a proboscis.

A, Head of peach borer moth, *Sanninoides exitiosa*, with fully developed maxillary proboscis. B, Tent caterpillar moth, *Malacosoma americanum*, with greatly reduced maxillae, no organs of feeding.

*Lb*, labium; *lbPlp*, labial palpus; *Mx*, maxilla; *mxPrb*, maxillary proboscis.

The interior of a lepidopterous pupa is filled with what appears to be a thick creamy substance. Under the microscope it is seen to consist of a clear, pale, amber-yellowish liquid containing a mass of minute bodies, some of which are blood cells and phagocytes, but most of them are disintegrating fat cells and liberated granules and fat droplets. The principal structural changes that take place within the pupa of a moth or butterfly affect the musculature, the fat tissue, and the alimentary canal.

The transformation of the muscular system differs in degree in different insects according to the difference in the musculature of the larva and the adult. Some larval muscles go over unchanged into the adult, others undergo a certain amount of reconstruction without losing their identity, and still others that are specifically larval muscles

go into complete dissolution. Important muscles of the imago having no representatives in the larva are newly formed in the pupa.

In the Lepidoptera the dorsal and ventral bands of longitudinal larval muscles are preserved at least into the pupa. In the pharate pupa of *Malacosoma americanum* these muscles remain clean and intact with distinct striations, and are active through the pupal stage, enabling the pupa to move its abdomen. According to Finlayson (1956) the longitudinal muscles degenerate during the first two days of adult life. On the contrary, the fibers of the outer system of body wall muscles in the larva of *Malacosoma* are already in the pharate pupa distinctly in a state of disintegration. They have lost their healthy appearance, looking soft and flabby, and their striations are faint or gone. Associated with these muscles are always large numbers of phagocytic cells, and in the mature pupa this system of larval muscles completely disappears.

The adult musculature of the thorax of *Telea polyphemus* has been fully described and illustrated by Nüesch (1953). Both the thorax and its musculature are entirely reconstructed in the pupa. Blaustein (1953) gives a detailed account of the histogenesis of a longitudinal wing muscle in *Ephestia kühniella*. Small undifferentiated cells destined to become muscle cells, or myocytes, assemble where the new muscle is to be. By division these myoblasts form a syncytium of muscle cells during the first days after pupation. The cells then unite into long strands that become muscle fibers. The nuclei move to the periphery, a sarcolemma is formed, and fine thickenings in the myoplasm become fibrillae. Development of the muscle is completed by the twelfth day of the pupa, on the thirteenth the striations appear. Finally the completed muscle is attached to the body wall.

The vision of a muscle being independently formed in the midst of chaos within the pupa is a most mysterious thing in insect metamorphosis. In the first place, what directs the wandering myoblasts to assemble at the place where a specific muscle must be? Second, what compels the assembled myoblasts to go through the changes and complex associations that result in the formation of a contractile muscle?

The formation of most imaginal muscles, at least in some lepidopterous pupae, depends on their connection with nerves. Williams and Schneiderman (1952) and Williams (1958) describe experiments on diapausing pupae of *Cecropia* and *Polyphemus* from which the entire nervous system had been removed. When induced to develop, these pupae transformed into externally perfect moths, but on dissection they were found to be completely without muscles, except for the muscles of the alimentary canal and the heart. Others likewise have

observed that the imaginal muscle rudiments must first be innervated to begin development. It seems, then, that myoblasts can assemble at the mechanically correct place for a specific new muscle, but here they must wait for a nerve connection before they can form the muscle. Finlayson (1956), in a further discussion of the relation of innervation to muscle development, says that sheets of fine muscle fibers lying under the epidermis of adult moths develop in the absence of innervation. (Possibly he refers to the heart muscles.)

The fat tissue, or so-called fat body, of older caterpillars still in an active condition consists of flat branched and lobulated cell masses having sharply distinct outlines. In the early pupa the fat masses break up into large granular cells, which later become ragged and frayed, and finally go into a state of disintegration, liberating their granular inclusions and droplets of oily fat. This material becomes food for the developing imaginal tissues, and in the lepidopteron much of it must be carried over to the adult to supplement the meager diet of the moth or butterfly.

The alimentary canal of the larva (fig. 7), as already shown, is entirely remodeled in the pupa in adaptation to the liquid diet of the adult (fig. 4). Verson (1905) gives a detailed description of the larval alimentary canal of the silkworm *Bombyx mori* and the metamorphic processes beginning at the time of cocoon spinning. The stomodaeum and proctodaeum are enlarged from circular growth centers, the so-called imaginal rings, at their inner ends. The degenerating larval epithelium of the mesenteron is thrown off into the lumen, and is replaced by an imaginal epithelium formed from groups of persisting regenerative cells. Essentially the same process of mesenteron reconstruction is described by Henson (1929) for *Vanessa*, and by Blaustein (1935) for *Ephestia kühniella*. The moth of *Ephestia* takes no food, and the stomodaeum is said by Blaustein to be reduced to a narrow tube closed from the mesenteron by a solid mass of cells. Some other moths that do not eat, such as the tent caterpillar moth, still retain an intact alimentary canal, suggestive that fasting in the adult stage is a recently acquired habit with them.

The fact that the organs of the pupa, external or internal, are those of the adult in a formative stage, and that the larval organs are cast off with the moult to the pupa, or go into dissolution within the pupa, supports the view that the pupa is a preliminary stage of the adult. For the attachment of the muscles on the adult cuticle, therefore, a secondary moult is necessary. This is the theory of Poyarkoff (1914), which is upheld by Hinton (1948), by Rockstein (1956), and by DuPorte (1958). An opposing theory, that of Jeschikov (1929),

elaborated by Heslop-Harrison (1958), contends that the larva is a free-living stage of the embryo, and that the pupa represents the condensed nymphal instars of insects without metamorphosis. The idea of embryos climbing trees, eating leaves with fully developed mouth parts, and spinning cocoons, however, sounds like something from science fiction, and the condensation of several active instars into a single immobile stage having no resemblance to a nymph is biologically hard to visualize. Particularly it would seem strange that a flightless "nymphal" stage of a lepidopteron should have adult mouth parts, and the same might be said of other insects having specialized feeding organs in the adult stage, which appear first in the pupa.

There is nothing inherently improbable about the occurrence of an adult moult between the pupa and the imago; adult moulting occurs in other arthropods, in the apterygote insects, and the mayflies. Experimentally, moulting can be induced in the adult insect as well as in the nymph and larva (see Wigglesworth, 1954, p. 48). The corpus allatum hormone governs both nymphs and larvae alike, and at the end of the juvenile period it gives way to the prothoracic-gland hormone, which produces a moult followed by either an imago or a pupa according to whether the insect is hemimetabolous or holometabolous. These glands in insects without a pupal stage degenerate at the moult to the adult, but in holometabolous insects they persist into the pupal stage. Bodenstein (1953) has shown that even in the cockroach the prothoracic glands do not degenerate at the moult to the adult if the corpora allata are removed without injury to the corpora cardiaca. The young adult cockroach then moults again. In the holometabolous pupa, therefore, when the corpora allata have ceased to be functional, the moult to the imago can be an adult moult effected by the thoracic-gland secretion.

#### LIFE OF THE ADULT

The moth or butterfly is fully formed within the pupal shell and then emerges as a mature insect, except that the internal organs of reproduction may not yet be fully functional. The adult escapes through a slit along the back of the pupa (fig. 16 E). The butterflies have an easy time of getting out, since they are immediately free on emergence. Among the moths, however, many species on emergence from the pupa find themselves still enclosed in a cocoon. Some are fortunate in that the pupa itself has protruded its front end from the cocoon and thus allows the moth to escape. The pupae of Eriocraniidae have large active mandibles by which they tear open the cocoon and come to the surface of the ground where the adult can

emerge into the air. In some cases the caterpillar is activated by an instinctive foresight and either leaves the head end of the cocoon very weakly woven, or makes a hinged door that the moth can open.

Those moths that on escape from the pupa find themselves still imprisoned in a closed cocoon are confronted with the problem of how to get out. Help comes from an unexpected source. In these species the shrunken silk glands of the larva now secrete a clear liquid, which issues from the mouth of the moth and softens the adhesive coating of the cocoon threads, thus enabling the moth to push its head through the end of the cocoon and escape. Trouvelot (1867) described the pre-emergence activities of *Telea polyphemus* as seen through a mica window inserted into the side of the cocoon. When the moth is fully formed within the pupa it becomes highly active and soon splits the pupal skin over the thorax. The head and legs are at once disengaged and the solvent liquid flows from the mouth. The insect now waits for the liquid to take effect on the cocoon. Then it makes strong contractions and extensions of the body, which force its head through the moistened silk. The strands separate, spread apart, and the moth issues without breaking a fiber.

Some of the moths and many of the butterflies are the most beautifully colored of living things, their only rivals being among the birds and the flowers. With the birds it is principally the males that are endowed with beauty, and for the utilitarian purpose of attracting the females. Of the flowers, it has been said that many are born to blush unseen and waste their sweetness on the desert air, but the poet did not know that the flowers too have a practical reason for both their perfume and their color, which is to attract the pollinating insects. The Lepidoptera, on the contrary, seem to make no use of their ornamentation. Though in many species the males are more brightly colored than the females, it is the males that are attracted to the females, and not by the charm of color in this case, but by odor. Kellogg (1907) has shown that the male of the silkworm moth finds a female entirely by her scent. The scent glands are eversible from the last abdominal segment of the female. When the glands are cut off, the male reacts as strongly to the glands themselves as to an intact female, and entirely ignores a female deprived of her glands. The silkworm moths cannot fly, but the males of some other moths are well known to be attracted to the females from long distances. The males themselves of many butterflies produce scents, some of which are attractive, others repellent.

If color plays no important part in the lives of moths and butterflies, except in the case of protective imitation and mimicry, it is difficult

to understand why so many of them are endowed with such brilliant coloration and color patterns—surely not to appeal only to *our* esthetic sense and make attractive displays in the specimen cases of entomologists. It would seem, then, that we need a theory to explain their colors on a scientific basis of usefulness to the insects themselves. The same might apply to the colors and designs of seashells (or perhaps also to the beauty of a landscape).

Most butterflies live lives of unfettered freedom. They toil not, neither do they spin, nor make provision for the future, and yet no other insect is arrayed like some of them. Flitting from flower to flower, sipping nectar, courtship and marriage—this is the life of a butterfly. Only when the time comes for egg laying does the female moth or butterfly meet her one responsibility. Since many caterpillars are very particular about what plants or other material they feed on, the adult female must deposit her eggs where the young caterpillars on hatching will find their proper food. It seems as if the female retains a memory of her own caterpillar days, and the same maternal instinct is shared by various other insects. This "instinct," however, has been shown by Thorpe and Jones (1937) and by Thorpe (1938, 1939) to be due, in some insects at least, to the olfactory conditioning of the larva to its food, which is carried over to the adult female and induces her return to a source of the same odor. This is not exactly memory in the human sense, and it is probably more reliable, but it does not explain the possession by the female of a return instinct. A remarkable example of this instinct is shown by the monarch butterfly, the larvae of which feed on the milkweed. In the fall many adults in northern regions migrate in flocks to the south, where they spend the winter; in the spring the females return north and find milkweeds on which to deposit their eggs.

The conditioning factor of the return instinct is not always food; the female dragonfly or the female mosquito must deposit her eggs in an aquatic environment suitable to the larvae. The same is true of the moth *Nymphula*, the larvae of which are aquatic. The females of *N. maculalis* described by Welch (1916) lay their eggs on the undersides of leaves of the yellow waterlily, using wherever available oviposition holes cut in the leaves by the beetle *Donacia*. The moth inserts her abdomen through one of these holes and attaches her eggs to the underside of the leaf in concentric circles around the beetle eggs. The moths are said to remain in the neighborhood of the water, but certainly no larval conditioning could account for their special ovipositing instinct. The larvae live submerged on the undersides of

the leaves, where they enclose themselves in cases formed of cut-out pieces of leaves, but they do not swim.

Butterflies have many natural enemies, including entomologists with collecting nets, but those of northern and temperate regions that survive the summer may be still plentiful at the end of the season. In the fall or early winter when cold weather comes on most of them simply die a peaceful death. Hardy individuals of some species, such as the mourning-cloak butterfly *Nymphalis antiopa*, however, live through the winter under logs or stumps lying on the ground, and the monarch butterfly imitates the birds in flocking south for the winter.

For the others, both moths and butterflies, nature has made some provision for carrying their species through the winter in an immature stage. Perhaps most commonly it is the pupa that hibernates, but with some species the caterpillar lives through the winter, or the winter is passed in the egg stage. The overwintering caterpillar is usually within the protection of a cocoon, but the brown woolly bear hibernates in a covering of its own wool, and young tent caterpillars remain in the egg shells. The female moth of this species, *Malacosoma americanum*, lays her eggs in late spring attached to a twig of a favorite tree of the caterpillar, and covers them with an impervious coating of material from the accessory glands of her reproductive system. Within three weeks or a little longer the young caterpillars are fully formed in the eggs. Here they remain protected under the egg covering through the summer, fall, and winter to emerge early the following spring.

It is interesting to note how the lives of insects in northern regions have become adapted to the alternation of winter with summer. By contrast, tropical species can go on indefinitely as a succession of broods without interruption. The northern insects, therefore, have undergone a special evolution to meet the condition of survival imposed upon them. Even within a single order such as the Lepidoptera different species have solved the problem of survival in different ways.

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