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BY

JOHN B. SCHMITT

Assistant Entomologist, New Jersey Agricultural
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INTRODUCTION

The mechanism of the feeding apparatus of moths and butterflies has been studied by a number of anatomists since Reamur and Latreille, but the exact means by which the proboscis is extended has not been determined, and it is this problem with which this paper is chiefly concerned. The morphology of the sucking pump has also engaged the writer's attention, as have various other parts of the lepidopterous head.

The literature is not extensive and (as the general information on the head is contained in most textbooks) there is little need except for historical purposes to review the contributions previous to the work of Burgess (1880) who was the first worker to describe correctly the muscles within the proboscis. Kirbach (1883) wrote on the sucking pump of *Vanessa io* and also on the muscles within the proboscis. In 1890 Burgess published further information on the structure of the head of the milkweed butterfly, followed by Kellogg (1893) on the same subject. In 1895 Kellogg showed that the pilifers are labral lobes

and not mandibles. Berlese's "Gli Insetti" (1910) contains some information on the maxillary musculature. Tillyard (1923) demonstrated that the maxillary lobes forming the proboscis are probably the galeae. Weber (1924) has contributed to our knowledge of the occipital area and the cervix of certain species. Snodgrass (1935) described the sucking pump of a sphingid.

This study was made possible only through the invaluable instruction and encouragement of R. E. Snodgrass, of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture, and I am therefore especially indebted to him. I am also indebted to Dr. T. J. Headlee, of Rutgers University, and to Dr. E. N. Cory, of the University of Maryland, for their cooperation while at their respective institutions. I also appreciate the aid of Dr. A. B. Klots, of the City College of New York, in determining microlepidoptera. This study formed the larger part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Rutgers University.

I. GENERAL STRUCTURE OF THE HEAD AND MOUTHPARTS

The cranium of the lepidopterous head is a relatively simple structure showing very few sutures. The clypeus forms an elongate anterior area and is not marked off from the frons. A suture extends on each side from the invagination of the anterior arm of the tentorium to the antenna fossa in the butterflies and most of the higher moths, but is usually absent in the more generalized groups. Whether this suture is a true frontal suture is questionable, for, as will be seen later, its internal ridge seems to have been developed secondarily for the purpose of bracing the cranium against the pull of the antenna muscles, which originate on the anterior arms of the tentorium. The internal ridge of this suture will be called the antennal ridge (fig. 1, A, *AR*). The parietals are large, and in the higher Lepidoptera their size is further increased by the great development of the compound eyes. The ventral and anterior ends of each parietal are recurved mesally, thereby providing between them a recess for the maxillae and the labium (fig. 12, B). Posteriorly and dorsally, the parietals merge with the occiput, there being no limiting suture. The postoccipital suture has a well-developed internal ridge and is itself usually evident externally. It limits the dorsal part of the posterior edge of the occiput, the ventral part being limited by the much lengthened hypostomal sutures. The invaginations of the posterior arms of the tentorium are located in the ends of the postoccipital suture, and since most of each hypostomal suture lies in the same dorsoventral line as the lateral part

of the postoccipital suture, the posterior tentorial pits appear to be "higher" in the lepidopterous head than they are in most other insects. Internally, this part of the hypostomal suture is marked by a well-developed ridge, on which are inserted the ventral intersegmental muscles from the thorax. The postocciput and the posterior part of the hypostoma are either poorly developed or entirely membranous.

The ventral areas of the parietals are not marked off from the subgenal areas by sutures, so it may be said that the pleurostomal and anterior part of the hypostomal sutures are nonexistent. Since the invaginations of the anterior tentorial arms of pterygote insects are always found in either the pleurostomal or the epistomal sutures, it might be supposed that the furrow extending ventrally from each anterior tentorial pit is the pleurostomal suture. Such, however, is not the case. This deep infolding is the line along which the clypeus and the parietal have been brought into juxtaposition, so that the true pleurostomal suture would necessarily be within the infolded area. In some groups, as in the Tineidae and the Pyralidae, this infolding is not pronounced, but in the butterflies it is extremely well developed. From a practical viewpoint, these infolded ridges are continuous with the ridges that brace the floor of a sucking pump, and will be described later.

The cephalic endoskeleton, or tentorium, of moths and butterflies presents practically the same structure throughout the order (fig. 1 A). The anterior arms of the tentorium are well developed and are the most important part. They are without dorsal arms, and the antennal muscles arise directly on them. The anterior arms are attached to the posterior bridge, close to the invaginations of the posterior arms. In many cases the actual posterior tentorial pits are really large open depressions, so that when seen from the inside of the head the anterior arms and the tentorial bridge appear to have separate invaginations. The posterior bridge is always small and poorly developed, and no muscles actually arise on its span.

The only muscles arising on the anterior arms of the tentorium are the antennal muscles and two pairs of muscles affecting the extension of the proboscis, which will be described later. In the butterflies and in moths having functional mouth parts the tentorial arms are often provided with large flanges and ridges, to allow greater attachment surface. In moths having degenerate or obsolete mouthparts the tentorial arms are often bulging and thin-walled, especially in the anterior halves.

The foramen magnum is sharply constricted near the invaginations of the posterior tentorial arms, although the degree of constriction

varies considerably throughout the order. However, the posterior bridge of the tentorium is always short.

The mouth parts of adult Lepidoptera consist of the maxillae, the labium, the labrum, and the hypopharynx. The maxillae, as is well known, are the most important, their galeae forming the long succtorial proboscis in those which have functional feeding mechanisms. Various degrees of degeneracy may be found, until the point is reached, as in the males of *Thyridopteryx*, where the maxillae are no longer recognizable as distinct appendages. The hypopharynx of moths and butterflies is incorporated in the floor of the sucking pump

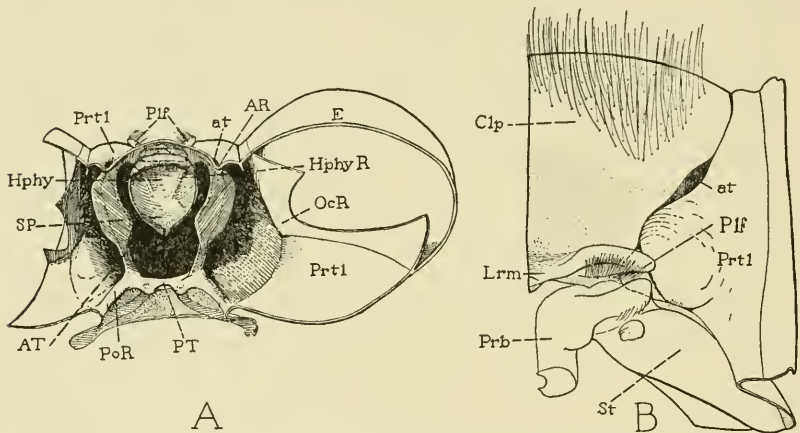


FIG. 1.—Structural details of the head and feeding mechanism of *Argynnis* and *Danaus*.

A, right half of head, mesal view, of *Argynnis cybelle*, showing endoskeleton and floor of sucking pump (SP) formed by hypopharynx (Hphy). B, left half of clypeus and base of left maxilla attached to parietal part of head of *Danaus menippe*, anterior view.

and will be described under that heading. The labrum, like the hypopharynx, is really a part of the cranium, but since it plays a part in the mechanics of feeding it may be described as a mouthpart. The lateral lobes of the labrum, called the *pilifers*, bear against the proboscis base, and in some butterflies the labrum is sufficiently flexible to move as a unit with the proboscis base. In such cases (fig. 1 B) the proboscis base is provided with a knob that fits against the pilifer under its fringe of setae. In many moths, however, the labrum does not have this function. The labium is evident only as a small triangular area bearing the three-segmented labial palpi. These palpi are usually so placed that the coiled proboscis can be clasped between them and be almost completely hidden from view. The labial palpi

are capable of some motion, each palpus having usually one or two muscles at its base, which enable the palpi to clasp the coiled proboscis or to release it.

The mouth cavity, or preoral cavity, is defined by Snodgrass (1935) as "an external space bounded anteriorly by the epipharyngeal wall of the labrum and clypeus, posteriorly by the labium, and laterally by the mandibles and the maxillae." The hypopharynx is described as lying in this cavity as a tonguelike lobe. The cibarium is that part of the preoral cavity which is anterior to the hypopharynx; that is, the anterior surface of the hypopharynx forms its "floor." The salivary meatus is the portion of the preoral cavity which is posterior to the hypopharynx, i. e., enclosed between the hypopharynx and the anterior surface of the prementum. The median salivary duct pours its secretions into this cavity from a small pocket called the salivarium, between the labium and the hypopharynx.

In the Lepidoptera most of the cibarium is incorporated with a part of the pharynx in the sucking pump, as will be demonstrated later. There is a small portion of the epipharyngeal surface which is not a part of the sucking pump, and this part is usually applied against the proboscis base. The salivary meatus is practically nonexistent, as the hypopharynx has completely lost its lobular character, and there is no protrusion of a prementum beyond the salivarium. The hypopharynx, in fact, forms most of the "floor" of the sucking pump (fig. 1 A) as a single well-sclerotized piece.

II. THE PROBOSCIS

Savigny long ago discovered that the proboscis of Lepidoptera is derived from the maxillae or rather from one pair of the lobes of the maxillae. The cardo and the stipes are usually quite distinct, and form no part of the proboscis as such; hence the term *proboscis* should be reserved for the conveying structure itself. Tillyard (1923) has produced evidence that the proboscis is derived from the galeae.

Structure and musculature.—Each half or unit of the proboscis is therefore a tube, the lumen of which is continuous with the body cavity through the stipes. Each proboscis unit is rendered flexible by a series of fine rings separated by membrane, as described by Burgess. These rings are absent in nonfunctional proboscides. In the butterflies and higher moths the rings are made up of many small flat circles of hard cuticula, like small beads set in rows. The food channel is also lined with rings, similar but having only about one-third the width of the outer rings. Muscles passing obliquely between the rings were

described by Burgess as effecting the coiling of the proboscis, a finding verified by Berlese and later writers.

The cardo in functional maxillae is usually a small flat sclerite just anterior to the labial palpi. The stipes varies in shape throughout the

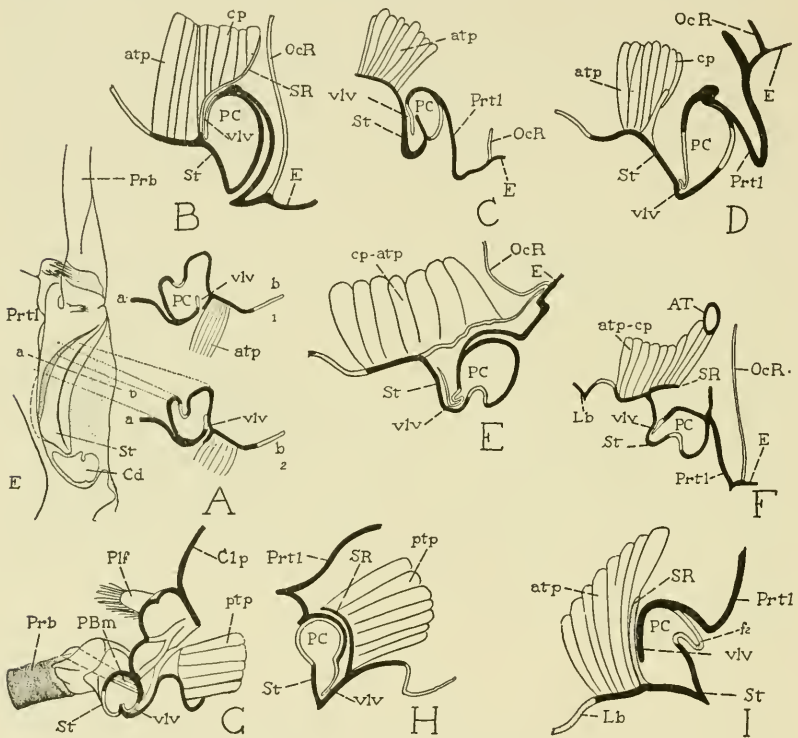


FIG. 2.—Pressure-producing mechanisms of the maxillae.

A, base of right maxilla of a swallowtail butterfly, ventral view (morphologically posterior), showing at *A*, a cross-section through the line *ab*, giving appearance of stipes when proboscis is coiled. B, cross-section of stipes of *Catocala* sp., showing appearance of pressure chamber (PC) formed by stipes. C, same of *Arcyonis alope*. D, same of *Hemaris thysbe*. E, same of *Danaus menippe*. F, same of *Pieris rapae*. G, base of proboscis of *Danaus menippe*, lateral view, showing insertion of posterior tentorial proboscis extensor (*ptp*). H, cross-section of stipes of *Hemaris thysbe* near insertion of posterior tentorial proboscis extensor (*ptp*). I, cross-section of stipes of *Atrytone zabulon*, showing appearance of pressure chamber.

families above the Tineidae, but when functional always presents fundamentally the same structures. The proximal portion in cross-section always has a median flat sclerite continuous with a tubular lateral part (fig. 2). This tubular part fits into the recurved ventral and anterior ends of the parietal, the lateral edge of the stipes being

continuous with the parietal. In some cases the curved lateral part of the proximal portion of the stipes is membranous, as in *Cercyonia alope* (fig. 2 C). In others the lateral part is heavily sclerotized and the tubular half is modified so that in effect there are two tubes set side by side with membrane between. This arrangement is found in the Pieridae (fig. 2 F). The distal portion of the stipes is also recessed under the parietal. The mesal surfaces of the maxillae bear against each other or against a small projection of the labium.

In addition to the muscles within the proboscis mentioned above there are three pairs of maxillary muscles inserting on each stipes and originating within the cranium. Two of these muscles originate

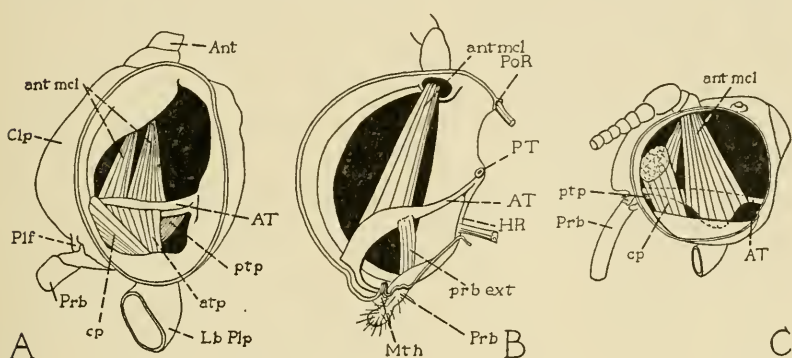


FIG. 3.—Proboscis extensor musculature.

A, left half of head of *Danaus menippe*, showing interior by removal of eye. B, right half of head, mesal view, of *Thyridopteryx ephemeraeformis* (male), as exposed by median sagittal cut. C, left half of head of *Desmia funeralis*, showing interior by removal of eye.

on the anterior arm of the tentorium, and the third originates on the anterior part of the gena. Of the tentorial muscles, one arises on the lateral surface of the anterior arm and inserts on the distal part of the stipes, on the median flat sclerite. It is therefore called the *anterior tentorial proboscis extensor* (fig. 3 A, *atp*). The second muscle originates on the mesal surface of the anterior arm of the tentorium and inserts near the distal point of the stipes. Its origin on the tentorium is always posterior to that of the anterior tentorial proboscis extensor, so that the paths of these muscles cross within the head. This second muscle is called the *posterior tentorial proboscis extensor* (fig. 3 A, *ptp*). The genal muscle originates on the anterior part of the gena and inserts on the flat mesal sclerite of the stipes. It is called the *cranial proboscis extensor* (fig. 3 A, *cp*).

Mechanism of coiling and extension.—It should now be possible to understand the functions of these muscles. A study of figure 2 shows that by their contraction, the anterior tentorial proboscis extensors draw the tubular part of the stipes up against the recurved end of the gena. (This action is shown diagrammatically in fig. 2 A.) It will be noticed that there is a valve arrangement between the tubular part of the stipes and the flat sclerite on which the muscles are inserted. As the muscles draw the stipes upward, the valve (*vv*) closes, with the result that the tubular part becomes a closed cylinder. Thus pressure is exerted against the blood within the stipes cylinder as it is forced against the recurved flange of the gena. The stipes cylinder forms a closed point at its proximal end, and therefore the blood displaced as the pressure continues must move outward through the stipes, toward the proboscis. The stipital ridge is enlarged at the proximal end of the stipes and thus practically covers the lumen of the proboscis unit. The posterior tentorial proboscis extensor is inserted on this ridge, and contraction of this muscle not only creates pressure on the blood enclosed within the stipes, but also moves the base of the proboscis unit upward, which effects a tight seal with the functional mouth (fig. 2 G, H; 9 D).

The blood displaced from the stipes is thus forced out into the lumen of each tightly coiled proboscis unit, thereby causing the proboscis to unroll. The diagonal muscles within each proboscis unit, described by Burgess, cause the proboscis to coil. That blood pressure might be the agency for uncoiling the proboscis was first suggested to the writer by R. E. Snodgrass, who, in his "Principles of Insect Morphology" points out the mechanical analogy of such a mechanism with the toy paper snake which a child uncoils by blowing into it. The uncoiling action of one proboscis unit is shown diagrammatically in figure 4.

The mechanism described above is the simplest which the writer has seen. In many moths and butterflies the stipital cylinder is further modified, but the principle is invariably the same, as may be seen in figure 2. The musculature concerned in the extension of the proboscis seems to be fundamentally the three pairs of muscles described, but in a large number of insects one or two pairs may be absent. However, functional maxillae always have at least two pairs.

Comparative structure in lepidopterous families.—The maxillae of a number of species representing the more important families were examined, primarily to determine the fundamental musculature of the lepidopterous maxilla. Moths having degenerate or obsolete mouthparts were also studied and, indeed, proved to be one of the most interesting phases of this investigation. To expose the proboscis extensor musculature, a simple procedure is first to make a complete

median sagittal cut, and then, using either half of the head, to remove the compound eye, the brain, subesophageal ganglion, and the sucking pump.

Tineidae: In the females of the common Yucca moth, *Pronuba yuccasella*, all three pairs of proboscis extensors are present, very much as described above. There is a single muscle at the base of each maxillary palpus and each maxillary tentacle. The common clothes moth, *Tineola*, lacks the cranial proboscis extensors, but otherwise its musculature is complete. In certain other *Tineidae*, determined

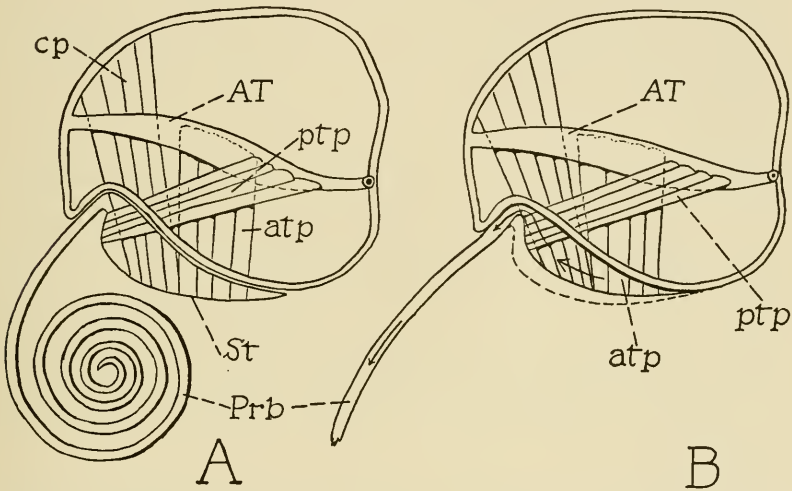


FIG. 4.—Diagram of the action of the proboscis extensor muscles of the right half of the head, mesal view.

A, proboscis coiled. B, proboscis extended by blood forced into it by compression of stipes (see fig. 2).

to family only, there are no tentorial muscles but only the cranial proboscis extensors, a very unusual condition.

Coleophoridae: A number of coleophorids, determined to family only, were found to possess both pairs of tentorial proboscis extensors, but to lack the cranial proboscis extensors.

Limacodidae: A single representative, *Euclea cloris indetermina*, was studied. This moth has practically no proboscis, but only two very small lobes, each a remnant of a proboscis unit. A single pair of tentorial proboscis extensors is all that is left of the maxillary musculature.

Oecophoridae: A species of the genus *Agonopterix*, with a well-developed proboscis, was also examined. All three pairs of extensors

are well developed, and strands of the anterior proboscis extensor have migrated onto the clypeus, so that there appears to be a fourth pair of muscles.

Pyralidae: In the pyralids examined, the cranial proboscis extensor is often absent. In the common wax moth, *Galleria mellonella*, both tentorial muscles are clearly evident and apparently able to act. The proboscis does not appear to be functional, and it is probable that the proboscis extensors serve only to move the maxillary palpi. The lesser wax moth, *Achroia grisella* Fab., has only remnants of the tentorial extensors, the proboscis being evident only as two short lobes, apparently nonfunctional. Two other pyralids, *Nomophila noctuella* and *Ephestia kuehniella*, have the proboscis well developed. The musculature is complete and the cranial muscle is especially well developed.

In figure 3 C the head of a pyralid, *Desmia funeralis*, is represented with the left eye removed. In this case all three proboscis extensor muscles are present, although the anterior tentorial proboscis extensor is very small. The cranial proboscis extensor is remarkably large, but since it originates on the ocular ridge, a relatively thin structure, it may be doubted whether it exerts much force. It may also be seen that a large lobe has been formed on each anterior tentorial arm in order to accommodate a very large antennal muscle, thereby depriving the proboscis extensor muscles of their usual position. Such a sacrifice of feeding structures for nonfeeding structures may be found in many moths.

Tortricidae: The tortricids usually possess all three pairs of proboscis extensors. Figure 10 B represents the head of the common codling moth, *Carpocapsa pomonella*, as seen when opened by a median sagittal cut. The sucking pump is shown in place, but the tentorial extensors may be seen just below the pump.

Psychidae: The male of the common bag-worm moth, *Thyridopteryx ephemeraeformis*, was studied in this group. These moths were found to have an extremely degenerate proboscis (fig. 3 B) represented only by two large lobes. Each lobe has a single proboscis extensor muscle, arising on the anterior arm. The antennal muscles, however, are by far the largest muscles in the head.

Sphingidae: The feeding mechanisms found in this family are generally very well developed. The musculature of the head of one species of sphingid, *Sphinx convolvuli*, has already been described to some extent by Berlese (1910). The proboscis musculature which he found homologizes thus: his no. 190 is the cranial proboscis extensor, his no. 171 is the anterior tentorial proboscis extensor, and his no. 172 is the

posterior tentorial proboscis extensor. However, Berlese apparently did not examine the insertions of these muscles and makes no reference to their functions. In discussing the possible mode of extension of the proboscis Berlese followed the suggestion of Burgess, that it is unrolled by its own elasticity.

The proboscis musculature of one species of sphinx moth, *Hemaris thysbe*, may be taken as generally typical of the family. In this moth (fig. 10 D) the tentorial muscles are equally well developed and are well spaced on the anterior arms of the tentorium. The cranial proboscis extensor is moderately developed and in general the whole arrangement is well balanced.

Yet, in some sphingids, there are decidedly inferior proboscis extension mechanisms. For example, the sucking pump in *Smerinthus geminatus* is so large that there is very little space left for the proboscis musculature, and the brain also is reduced in size and displaced posteriorly (fig. 10 C). In this moth there is no cranial proboscis extensor, and only one tentorial muscle, which appears to be the posterior tentorial proboscis extensor judging by its insertion. Another sphingid, *Darapsa pholus* (fig. 6 B), has an extremely large cranial proboscis extensor.

Geometridae: The feeding mechanisms of members of this family are weak or degenerate. The proboscis musculature of *Haematopsis grataria* is shown in fig. 9 C. All three stipital muscles are present, but very weak, especially the tentorial muscles. The cranial proboscis extensor is also very short. In the little green geometrids (subfamily Hemitheinae) the proboscis musculature resembles that of *Haematopsis*.

The geometrid *Ennomos subsignarius* is typical of further degeneracy in this family. Only the tentorial muscles are present and they are very weak (fig. 5 B). Each anterior arm is very thin-walled and is considerably enlarged. This enlargement, of course, "lightens" the head by replacing blood volume with air and is of interest in view of the remarkable flights of this insect. *Caberodes confusaria* resembles *Ennomos* in this respect but has a functional cranial proboscis extensor.

The adults of the spring cankerworm, *Paleacrita vernata*, differ, as is well known, in that the males are winged and the females wingless. However, there is practically no difference between the sexes in the proboscis and its musculature. The proboscis itself, in both cases, is represented by two small lobes. Only a pair of tentorial proboscis extensors can be found, and they are very weak.

Noctuidae: In this family the proboscis and its musculature are very well developed. The cranial proboscis extensor here reaches a remarkable size and importance, in comparison with the tentorial proboscis muscles. This is of interest in view of the fact that the cranial proboscis extensor is the muscle most frequently absent in cases where there is not a full complement of proboscis muscles. The proboscis musculature of a large moth, *Catocala nubilis*, is shown in figure 6 A and is in general typical of the family.

Arctiidae: All examined members of this family have degenerate feeding mechanisms. Figure 6 C shows a section through the head of a typical species, *Apantesis virgo*. Both *A. virgo* and *A. vittata* have

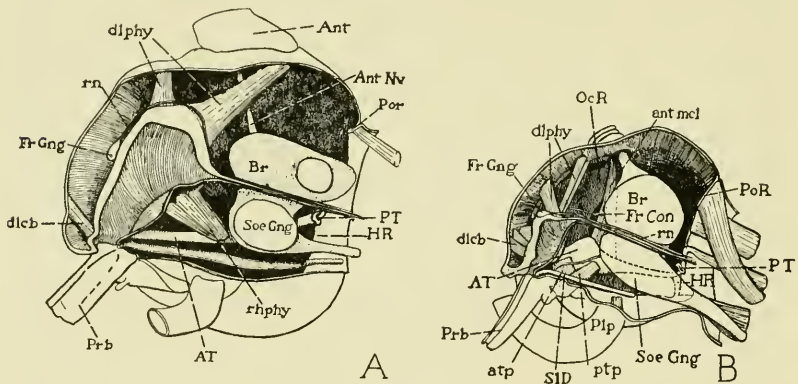


FIG. 5.—Proboscis extensor musculature and the sucking pump.

A, right half of head, mesal view, of *Haematopsis grataria*, as exposed by median sagittal cut. B, same of *Ennomos subsignarius*.

all three pairs of proboscis extensors. The posterior tentorial proboscis extensor originates well back on the anterior arm of the tentorium. *Estigmene acraea* and *Utetheisa bella* show about the same conditions.

The members of the genus *Haploa* exhibit the strongest proboscis musculature seen in this family, and there can be but little doubt that the proboscis is functional. The members of the genus *Diacrisia*, on the other hand, have the most degenerate feeding mechanisms seen in this family. In *D. virginica* the anterior tentorial proboscis extensor has been lost and the posterior muscle is very weak. The cranial proboscis extensor is still evident.

In *Isia isabella* all three pairs of proboscis muscles are present and apparently functional. The anterior tentorial proboscis extensor, however, has migrated to the antennal ridge, above the anterior arm.

Saturnoidea: The degeneracy of the feeding mechanism in the giant silk moths is so complete that there are few traces left of the

proboscis musculature. In the large moth *Samia cecropia*, for example, the proboscis is represented by two small shapeless lobes (fig. 11 B, *Prb*), associated with which there is a single pair of tentorial muscles. The position of these muscles suggests that they may be the posterior tentorial proboscis extensors.

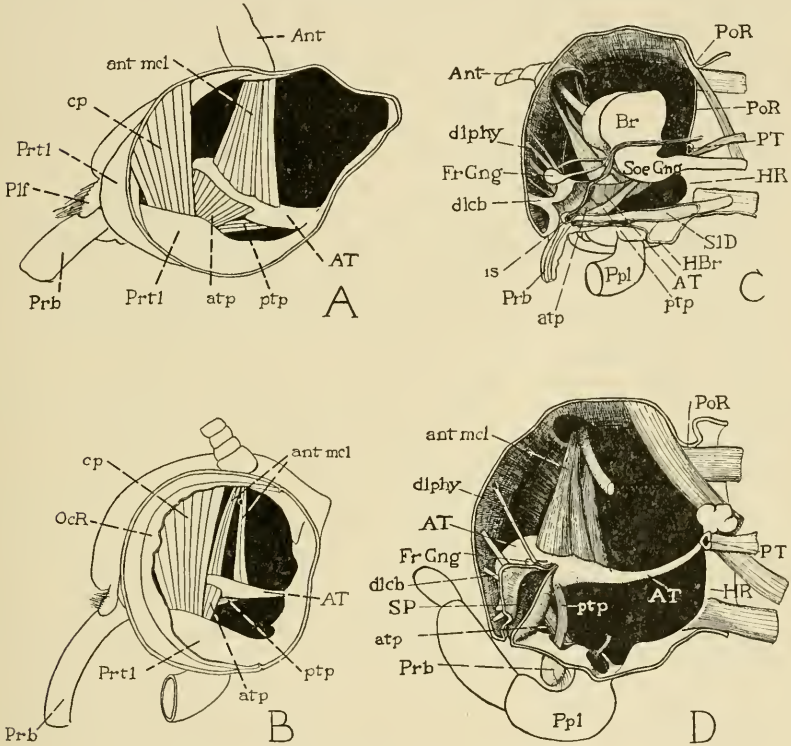


FIG. 6.—Proboscis extensor musculature.

A, left half of head of *Catocala nubilis*, showing interior by removal of eye. B, same of *Darapsa pholus*. C, right half of head, mesal view, *Apantesis virga*, as exposed by median sagittal cut. D, same of *Malacosoma americana*.

The tentorium of this moth has developed a peculiar secondary function. In addition to having the anterior part of the anterior arms thin-walled and bulging, displacing blood with air, the posterior part of the anterior arms is tubular and curved to provide a sort of cradle for the brain and suboesophageal ganglion. This is done by having each arm pass between the brain and the optic lobe on its side. If it were not for this the brain would be supported only by the optic lobes.

In other saturniids remnants of one or both pairs of the tentorial proboscis muscles can be found, but the cranial proboscis extensor is

invariably absent. In *Basilona imperialis* (Ceratocampidae) the proboscis still has a tubular shape and shows a food channel. Both tentorial muscles are present, but no cranial muscle.

In all saturniids examined, the position of the tentorium in the head—that is, the length of the hypostomal area below the posterior tentorial pits—suggests that the ancestors of these moths had powerful feeding mechanisms with the tentorial muscles well developed. The antennal muscles in these moths are always large and powerful, and it may be that the great enlargement of the anterior part of the anterior arms results from the need for a large base for these muscles rather than from an effort to lighten the head. However, the latter purpose is unmistakably served.

Lasiocampidae: The adult of the eastern tent caterpillar, *Malacosoma americana*, was studied as an example of a lasiocampid, but its resemblance to a saturniid was so complete that no new information was obtained. The antennal, proboscis, and sucking pump musculature is illustrated in figure 6 D.

Bombycidae: Similar conditions were found in the common silk moth, *Bombyx mori* (fig. 7 A). The proboscis is represented by two shapeless lobes. Both pairs of tentorial muscles are present.

Papilionoidea: Representatives of five families of butterflies were studied, and some interesting differences were found. In the Nymphalidae and Danaidae the three pairs of proboscis extensors are most perfectly preserved. Figure 11 shows the proboscis extensor of *Danaus menippe*, known as the "Monarch butterfly." All three pairs of muscles are well developed. The musculature of *Vanessa atalanta*, the red admiral butterfly, closely resembles it, as does also the mourning cloak butterfly, *Aglais antiopia*, and the great spangled fritillary, *Argynnis cybela*. In certain other Nymphalidae, however, the cranial proboscis extensor has been lost. Such butterflies include the viceroy, *Basilarchia archippus*, and the common grayling, *Cercyonis alope*. A few species of Lycaenidae were also examined. In *Lycaenopsis argiolus*, the common blue, and *Everes comyntas*, the tailed blue, the musculature consists of the familiar three pairs. In *Chrysophanus hypophleas* the cranial muscle has been lost, but both tentorial muscles are well developed.

Thus, in these two families nothing unusual was found. In the Papilionidae and the Pieridae, however, no trace was found of the cranial proboscis extensor, but instead there was a remarkable migration of part of the anterior tentorial proboscis extensor. Inserting on each stipes with the anterior tentorial proboscis extensor but arising on the *clypeus*, between the anterior tentorial arms, there is a single

large muscle. This is illustrated in figure 7 B, showing the musculature of *Pieris rapae*. The migrant is marked atp_2 , and it really passes laterad of the posterior tentorial proboscis extensor, its strands inserting with those of the anterior tentorial proboscis extensor which originate on the anterior arm. *Papilio polyxenes*, *P. troilus*, and *P. marcellus* show similar conditions. Sometimes there is a continuous band of muscle from the clypeus to the anterior arm of the tentorium.

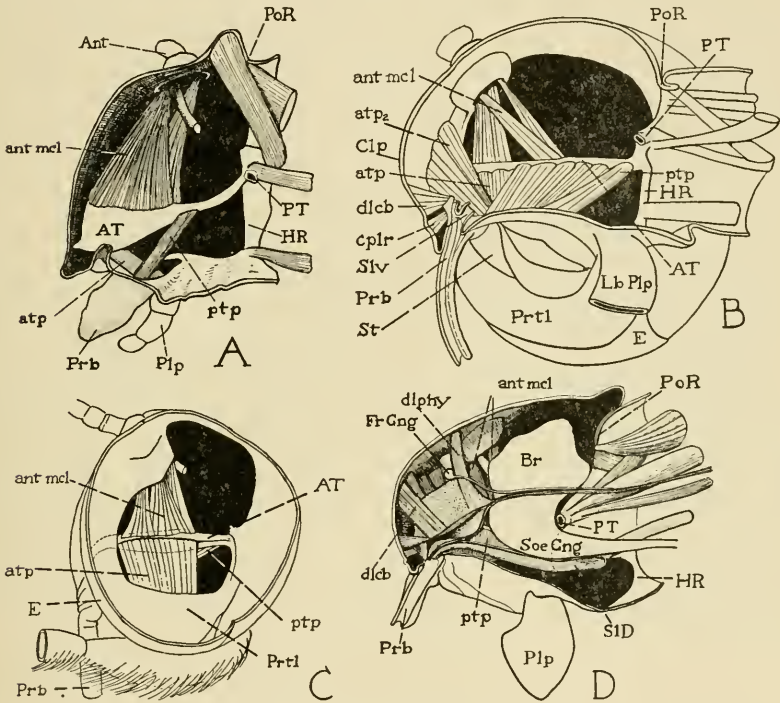


FIG. 7.—Proboscis extensor musculature.

A, right half of head, mesal view, of *Bombyx mori*, as exposed by median sagittal cut. B, same of *Pieris rapae*. C, left half of head of *Pieris rapae*, showing interior by removal of eye. D, right half of head, mesal view, of *Epargyreus tityrus*, as exposed by median sagittal cut.

In the Pieridae this modification is more complete, with the "migrant" atp_2 originating higher on the clypeus than in the Papilionidae. In *Pieris protodice*, the checkered white, this muscle originates just anterior of the antennal socket. The musculature of *Pieris rapae* is illustrated in figure 7 B. Other pierids examined included *Colias eurytheme* and *Anthocharis genutia*.

By eliminating the cranial proboscis extensor, the Papilionidae and Pieridae seem to have considerably narrowed the parietal area, or per-

haps it should be said, increased the extent of the compound eye, yet without sacrificing muscular power. In effect, this muscle is here located between the anterior arm of the tentorium and the anterolateral surface of the sucking pump, thus utilizing what might be characterized as "waste space." At the same time, the development of this muscle is necessarily limited by the sucking pump and its muscles.

A fourth pair of muscles should now be described. This pair consists of one muscle located in each proboscis unit, arising on the stipital ridge and inserting in the proboscis base, and called the *proboscis base muscle* (*PBm*). In direction it is a continuation of the posterior tentorial proboscis extensor. Its position in the head of *Papilio* is indicated in figure 9 B, *PBm*, also in figure 2 G.

Hesperiidae: Only two species of skippers have been examined: *Epargyreus tityrus* and *Atrytone zabulon*. In this family the proboscis extensors are short but very well developed. The anterior arms are greatly broadened to provide greater attachment surface, while the cranial proboscis extensors in *Epargyreus* have invaded the antennal ridge to secure greater attachment surface.

The remarkable simplicity of the stipital tube in *Atrytone* is well worthy of note. In figure 2 I it is represented in cross-section under compression. In this type, closure of the pressure chamber is effected directly by the cranial proboscis extensor, as it presses the membranous stipital ridge against the recurved flange of the parietal. The membranous fold labeled *F2* becomes much larger as it approaches the base of the proboscis unit, at which point its outer portion is firmly sclerotized, while its inner lateral section (that is, its morphologically lateral section) remains membranous.

III. THE SUCKING PUMP

Among the orders of insects equipped with sucking pumps, the Hemiptera and the Diptera have received considerable study. Snodgrass (1935) has shown that the pump of the cicada is prepharyngeal in origin and evolved almost entirely from the preoral cibarium. Similarly, Jobling (1929) and Snodgrass (1935) have demonstrated that the sucking pump in Diptera is derived from the cibarium. In respect to the sucking pump of the Hymenoptera, Snodgrass (1935) states that "while the morphology of the organ is not entirely clear, . . . judging from the musculature, it includes without doubt the pharynx and the buccal cavity and perhaps the cibarium." It is, therefore, of interest to determine to what extent the sucking pump of Lepidoptera is preoral in derivation.

Generalized structure.—In the more generalized insects there is usually a large preoral cavity bounded anteriorly by the epipharyngeal wall of the labrum and clypeus, laterally by the mandibles and the maxillae, and posteriorly by the labium. The hypopharynx is suspended between these organs (fig. 8 A, *Prc*) and thus divides the preoral cavity into an anterior *food meatus* (*fm*), having the anterior wall of the hypopharynx for its floor, and a posterior *salivary meatus* (*sm*) enclosed between the posterior wall of the hypopharynx and the anterior surface of the prementum.

The food meatus, of course, is not part of the stomodaeum, but simply space enclosed by certain mouthparts. It leads to the true mouth which marks the beginning of the alimentary canal. A portion

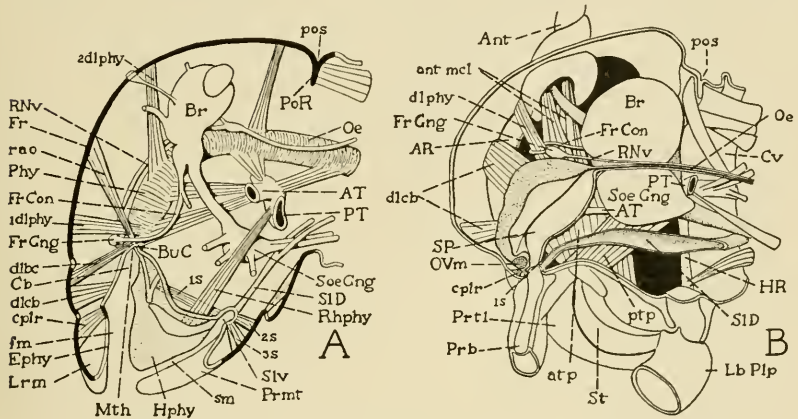


FIG. 8.—Comparison of the orthopteroid head with the lepidopterous head.

A, diagram of orthopteroid head (from Snodgrass). B, right half of head, mesal view, of *Danaus menippe*, as exposed by median sagittal cut.

of the food meatus just before the mouth is used to hold food before swallowing and is therefore known as the *cibarium* (fig. 8 A, *Cb*). The dilators of the cibarium always arise on the clypeus.

The part of the stomodaeum just inside the mouth is termed the *buccal cavity* (*BuC*). Beyond the buccal cavity, extending to the cerebral nerve connectives, we may distinguish the *pharynx* (*Phy*). The dilators of the buccal cavity (*dlbc*) arise on the clypeus, but the dilators of the pharynx (*dlphy*) arise on the frons. The frontal ganglion (*Fr Gng*) lies on the anterior wall of the stomodaeum between the buccal cavity and the pharynx. The connectives of the frontal ganglion (*Fr Con*) always pass laterad of the dilators of the pharynx. From figure 8 A it may be seen that the pharyngeal dilators are thus encircled by two nerve rings, outside of which they cannot migrate.

Pump of Lepidoptera.—Snodgrass (1935) has shown that the sucking pump of moths and butterflies includes at least the buccopharyngeal region of the stomodaeum. This is evidenced by the fact that the dilator muscles of the pump are inserted both before and behind the connectives of the frontal ganglion, which lies on the dorsal wall of the pump. The sucking pump of a butterfly, *Danaus menippe*, is illustrated in figure 8 B showing the dilators of the true pharynx inserted on the posterior portion of the pump. Whether the cibarium or any portion of the food meatus is also incorporated in the lepidopterous sucking pump has therefore been an open question.

The labrum (*Lr*) of moths and butterflies is usually described as a narrow transverse band at the lower edge of the clypeal region, bearing the pilifers (*Plf*) on its lateral extremities (fig. 1 B). In orthopteroid insects there is a pair of muscles, the compressors of the labrum (*cplr*), originating on the anterior wall of the labrum and inserting on the epipharyngeal wall. If the small lobe between the pilifers is the labrum, as it appears to be, this pair of muscles exists in the Lepidoptera (fig. 8 B and 9 B), and the cibarium then necessarily forms part of the anterior section of the pump.

However, there is certain other evidence that the cibarium is included in the pump, based on the structure of the floor of the pump. At the base of the salivary meatus in many generalized insects there is a small cuplike depression or pocket into which the median salivary duct pours its secretions. This pocket is known as the *salivarium* (fig. 8 A, *Slv*). It is supplied with three pairs of muscles, a dorsal pair (*ts*) arising on the suspensorial sclerites of the hypopharynx, and two ventral pairs, arising on the prementum. In the Lepidoptera, only the dorsal pair of muscles, arising on the hypopharynx, may be found. Their point of origin is on the floor of the sucking pump (fig. 9 A, B) showing that the anterior part of the floor is derived from the hypopharynx and therefore that this portion of the sucking pump belongs to the cibarium.

In orthopteroid insects the hypopharynx has a pair of retractors (fig. 8 A, *rhphy*) originating on the tentorium. In a geometrid moth, *Haematopis grataria* (fig. 5 A), a pair of muscles was found inserting on the floor of the pump and originating on the anterior arms of the tentorium. Since the ventral dilators of the true pharynx in orthopteroid insects pass *between* the circumoesophageal connectives, they could not possibly migrate from the tentorial bridge to the anterior arms. Hence, this pair of muscles in *Haematopis* must represent the retractors of the hypopharynx, and although they may have migrated beyond the limits of hypopharynx, their presence, neverthe-

less, is evidence that the hypopharynx is incorporated in the sucking pump. In an oecophorid, *Agonopterix* sp., a similar pair of retractors occurs.

The highest development of the sucking pump is to be found in the Sphingidae, the Noctuidae, and especially in the butterflies. Dilation of the pump is produced by the muscles originating on the wall of the head; contraction in the lower moths is produced by the intrinsic elasticity of the pump itself, but in the above-named groups, bands of

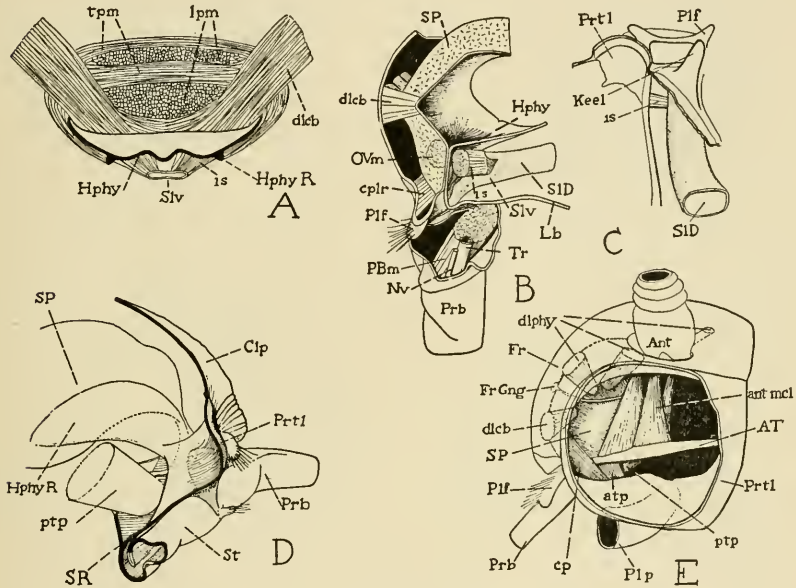


FIG. 9.—Various structural details of the head.

A, cross-section of sucking pump of *Danus menippe*. B, mesal view of right half of head and base of right proboscis unit of *Papilio* sp. C, ventral view of salivarium of *Lycaenopsis argiolus*. D, base of proboscis and sucking pump of *Papilio* sp. as seen from right side. E, left half of head of *Haematopsis grataria*, showing interior by removal of eye.

muscles passing around the pump are mainly responsible. The "floor" of the pump is heavily sclerotized and well braced to withstand the pull of the dilating muscles. Figure 1 shows the pump in a specimen cleared in KOH, with a portion of the dorsal wall of the pump removed. The infolded ridge on each side between the parietal and the clypeus can be seen passing under the floor of the pump (*HphyR*), thus providing support. Morphologically, these ridges are more difficult to trace. Figure 9 D shows the bracing arrangement of the pump of a butterfly, *Papilio* sp. The infolded ridge between the clypeus

and the parietal can be seen to merge with the hypopharyngeal ridge, which is apparently formed jointly by the epipharynx and the hypopharynx. In effect, the hypopharynx has contributed the median surfaces of each ridge and the area in the floor of the pump between the ridges. The dorsal dilators (*Is*) of the salivarium usually arise on these ridges, indicating that at least that much is hypopharynx.

The dorsal wall of the pump varies greatly throughout the order in the particular arrangement of its dilating muscles, but shows interesting consistency in the relative development of the true dilators of the pharynx and the dilators of the cibarium. Moths beginning with the Tineidae were examined, but no means was found whereby muscles which might be dilators of the buccal cavity could be differentiated from dilators of the cibarium. Therefore, any dilator muscles not included in the frontal complex (i. e., encircled by the connectives of the frontal ganglion, hence true pharyngeal dilators) are labeled as dilators of the cibarium. With very few exceptions, the true pharyngeal dilators are restricted to the posterior part of the sucking pump. It does not follow, of course, that the portion of the pump derived from the pharynx is necessarily limited to this area; it merely shows the extent to which the dilators of each part have contributed to the musculature of the pump.

Mechanism.—In figure 12 A the complete musculature of the pump of *Danaus menippe* is indicated. The muscles compressing the pump are shown in cross-section in figure 9 A also. These muscles are arranged in two groups, transverse pump muscles (*tpm*) and longitudinal pump muscles (*lpm*), with two layers in each group. Figure 9 A was drawn from a hand-cut section of the pump imbedded in paraffin. Focusing through the section showed that fibers of the transverse pump muscles passed directly into the dilating muscles, indicating a possible origin of the compressor muscles from the dilators.

At the anterior end of the pump, a group of transverse pump muscles are often arranged in a distinct group, forming what Burgess (1880) called the "oral valve" (fig. 8 B, *OVm*). Its purpose is believed to be to prevent the imbibed juices from escaping when the pump is emptied. This arrangement was found to be especially well developed in the butterflies and in the Sphingidae.

Comparative structure in lepidopterous families.—A number of undetermined tineids were examined, including the common clothes moth, *Tineola biselliella*. In this family the axis of the sucking pump, that is, a straight line from the anterior to the posterior end of the pump, is practically perpendicular to the longitudinal body axis. Such a pump is illustrated in figure 10 A. A single pair of pharyngeal

dilators is encircled by the frontal connectives. The remainder of the pump dilators form four or more pairs of well-developed short muscles. The pump musculature of the *Yucca* moth is poorly developed although the pump floor is fairly well sclerotized.

In a coleophorid (fig. 10 A) practically the same type of pump was observed, except that the dilators of the cibarium were grouped an-

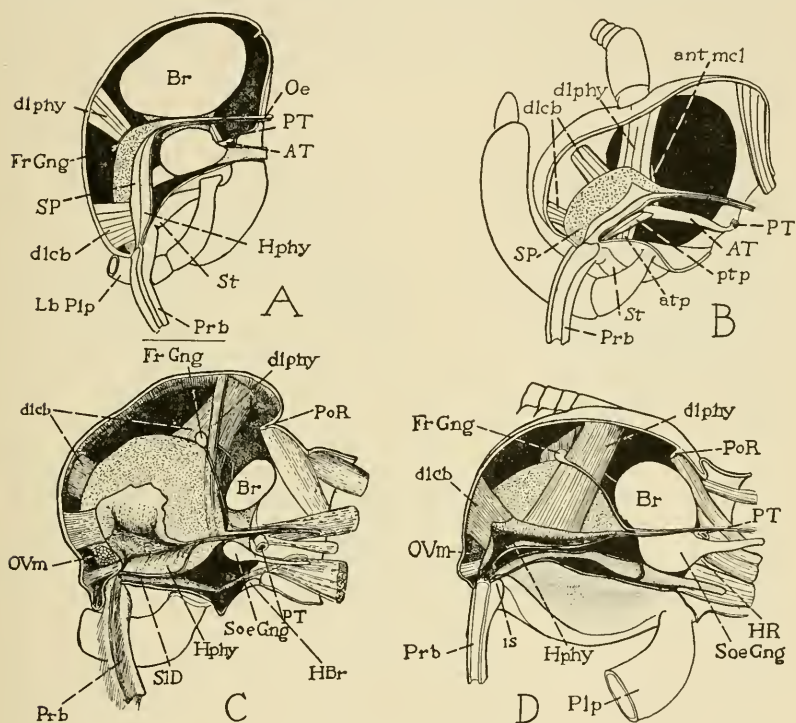


FIG. 10.—The sucking pump.

A, right half of head, mesal view, of *Coleophora coruscipennella*, as exposed by median sagittal cut. B, same of *Carpocapsa pomonella*. C, same of *Smerinthus geminatus*. D, same of *Hemaris thysbe*.

teriorly into a large median band of muscles, with a large band placed laterally on the pump. An oecophorid, *Agonopterix* sp., has a similar and well-developed pump. Males of the common bagworm moth, *Thyridopteryx ephemeraeformis*, possess a very degenerate pump, with the muscles evident but very weak.

In the Tortricidae the axis of the sucking pump is inclined to a more horizontal position. In the codling moth, *Carpocapsa pomonella* (fig. 10 B), there is a single large pair of pharyngeal dilators, and the dorsal

pump wall itself is well supplied with muscles. *Archips* offers nothing unusual in either pump or proboscis.

Excellent development of the sucking pump may be found in such pyralids as *Desmia funeralis* and *Nomophila noctuella*. The cibarial dilators are strong and well spaced, although the pharyngeal dilators are limited to a single pair. In other pyralids, such as the common wax moth, *Galleria mellonella*, and the lesser wax moth, *Achroia grisella*, the pump is relatively weak, especially in the last-named species. Other species of pyralids were studied, but nothing unusual was found.

Sphingidae: Snodgrass (1935) has described the sucking pump of a *Sphinx* moth. In *Hemaris thysbe* the structure of the pump is typical of this family (fig. 10 D). The pair of pharyngeal dilators is large and set close together, and with the cibarial dilators, provide the pump with powerful suction. In one species, *Smerinthus geminatus* (fig. 10 C), this development of the sucking pump has reached such a point that little space is left for the brain and the suboesophageal ganglion. The proboscis extensor musculature is also reduced to a single pair of extensors. In fact, the anterior arms of the tentorium are curved laterally in order to accommodate the expanded pump. In *Darapsa pholus* the pump is of more moderate proportions, although quite well developed. In this species there are two pairs of pharyngeal dilators. A mouth valve or oral valve is common in this family. The dorsal salivarium muscles are also easily found in the sphingidae.

Geometridae: In this family the sucking pump is generally weak. Figure 5 B shows the head of a typical geometrid, *Ennomos subsignarius*. There are three pairs of pharyngeal dilators and three pairs of cibarial dilators, but all are relatively thin muscles. The dorsal salivarium muscles are also evident, although very small. *Caberodes confusaris* shows about the same pump as *Ennomos*. The sucking pump of both the males and the females of the spring cankerworm moth, *Paleacrita vernata*, is very weak, although provided with four pairs of dilators.

The sucking pump of *Haematopsis grataria*, in addition to possessing a pair of hypopharyngeal retractors (fig. 5 A; *rhphy*), is of interest because of its unusual formation. There are three pairs of pharyngeal dilators, the posterior pair originating posterior to the antennae and passing between the antennal nerves (fig. 9 E). There are also two pairs of cibarial dilators.

Noctuidae: Members of this family possess well-developed sucking pumps, of which that of *Heliothis obsoleta* (fig. 11 A) is typical. Laterally, the pump is provided with a sheet of fibers on each side, the

posterior bundle of which is shown by the position of the frontal connective to be derived from the pharyngeal dilators. In addition to these sheets of muscle, there are two pairs of dilators on the anterior part of the pump. The dorsal salivarium muscles are well developed. The sucking pump of *Autographa falcifera* resembles that of *Heliothis*.

Arctiidae: Moths of this family are provided with poorly-developed feeding mechanisms. Figure 6 C illustrates the head of an arctiid, *Apantesis virgo*. The pump muscles are mere strands, and the floor of the pump is but weakly sclerotized. In *Isia isabella* the pump and

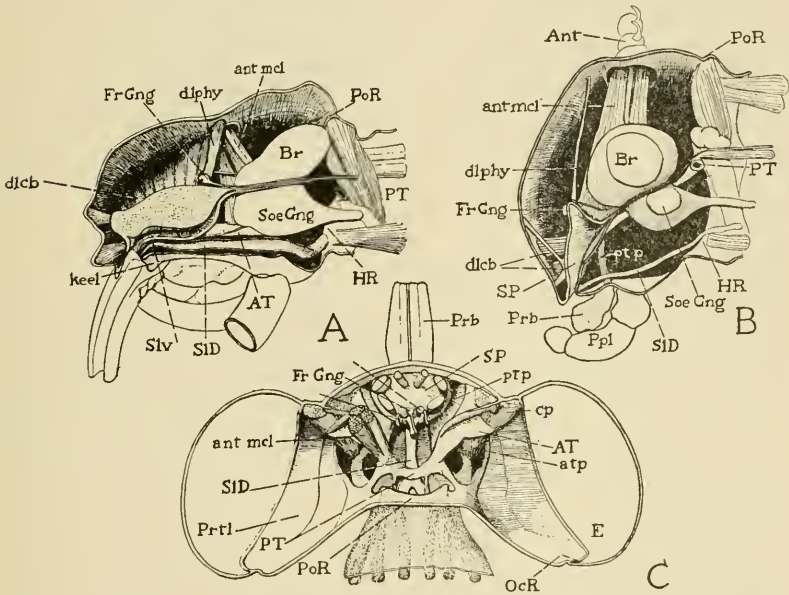


FIG. 11.—The sucking pump.

A, right half of head, mesal view, of *Heliothis obsoleta*, as exposed by median sagittal cut. B, same of *Samia cecropia*. C, head of *Epargyreus tityrus*, as seen with dorsal wall removed.

proboscis are weak but apparently functional. In the genus *Haploa* the pump is relatively strong. *Diacrisia virginica* shows the most degenerate condition observed in this family, the pump dilators being mere strands. Yet, in many arctiids the dorsal salivarium muscles are present and probably functional.

Saturniidae: In this family the sucking pump is extremely weak. Figure 11 B illustrates the sucking pump of *Samia cecropia*. There is a single pair of pharyngeal dilators, still recognizable by means of the frontal ganglion. Laterally, there are two pairs of muscles which might be functional. No salivarium muscles could be found. The

sucking pumps of other saturniids have about the same development as in *Samia*.

Bombycidae: The well-known silk-moth, *Bombyx mori*, also has a very feeble sucking pump (fig. 7 A). The remnants of only two pairs of muscles are present, one pair being pharyngeal dilators.

Ceratocampidae: The sucking pump of *Basilona imperialis* is very weak and in general much as in the saturniids. There are two pairs of pharyngeal dilators.

Lasiocampidae: The adult of the eastern tent caterpillar, *Malacosoma americana*, was studied as an example of this family (fig. 6 D). The pump has a single pair of pharyngeal dilators and three pairs of cibarial dilators, but all are mere threads.

Hesperiidae: The skippers have well-developed sucking pumps, not unlike those of the butterflies. The head of *Epargyreus tityrus* is illustrated in figures 11 C and 7 D. There is only a single pair of pharyngeal dilators, most of the contraction being provided by the anterior muscles.

Papilionoidea: The swallowtail butterflies have a large sheet of muscle on each side of the pump, as well as a pair of median muscles and a pair of pharyngeal dilators. In the family *Pieridae* the pump very much resembles that in *Papilionidae*, except that two pairs of pharyngeal dilators are usually present. The *Nymphalidae* and *Danaidae* show one or two pairs of pharyngeal dilators; in *Argynnis cybele* the dilators of the pharynx originate as two pairs but insert practically as one. The sucking pump of *Danaus menippe* is illustrated in figures 8 B and 12 A.

However, throughout the families of the *Lepidoptera* it is probable that these pairs of pharyngeal dilators do not represent original pairs of muscles immediately homologous with the dilators of the pharynx of such insects as *Dissosteira*. For example, in *Dissosteira* there is a pair of *retractors of the mouth angles* encircled by the frontal connectives, but it is improbable that any of the muscles encircled by the frontal connectives in *Haematopsis* are exactly homologous with the retractors of the mouth angles (see fig. 8 A, *rao*).

IV. THE LABIUM

The structure and limits of the labium in adult *Lepidoptera* have been previously described by other writers, most recently by Snodgrass (1935). In figure 12 B the labium of *Hemaris thysbe* is illustrated. In this case the labium is limited to a median strip passing to the base of the proboscis, and a small area around each labial palpus. Posteriorly, the labium is supported by a hypostomal bridge (*HBr.*).

In the yucca moth, *Pronuba yuccasella*, there is a small paired fleshy lobe at the distal end of the labium. The Oriental fruit moth, *Grapholitha molesta*, also has a pair of minute lobes at the tip of the labium, but it is improbable that these lobes have any significance.

The labium of many moths and butterflies possesses a strong ventral ridge at the distal end (figs. 11 A and 9 C, *Keel*). A possible function of this ridge is to serve as a bearing surface for the proboscis base.

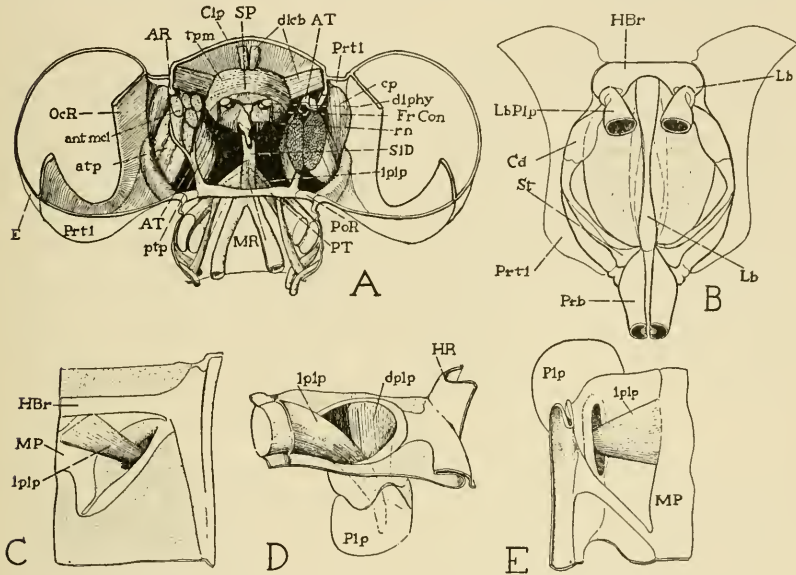


FIG. 12.—Various structural details of the head.

A, head of *Danaus menippe*, as seen with dorsal wall removed. B, labium and basal part of maxillae, ventral view, of *Hemaris thysbe*. C, labial palpus musculature of *Papilio glaucus*. D, same of *Danaus menippe*. E, same of *Pieris rapae*.

The musculature of the labium is limited to the palpi muscles. Berlese and Burgess have figured palpus muscles arising on the tentorium, but apparently did so by mistaking proboscis extensors for palpi muscles. In every moth and butterfly examined by the writer there were never more than two pairs of palpus muscles, and these arise either on the labium itself or on the hypostomal bridge. The articulation of the labial palpus with the head is so formed that little or no blood passes out into the palpus. If the palpus of a live butterfly is snipped off, it will be found that the walls of both the first and the second joints are barely moist inside. This, of course, greatly lightens the palpi.

The palpus musculature of *Danaus menippe* is illustrated in figure 12 D. Each palpus is supplied with two muscles, a levator (*lplp*) and a depressor (*dplp*). Nymphalidae usually have a pair of muscles for each palpus, although the depressor is often very weak. In the Papilionidae and the Pieridae there is no depressor muscle, but the levator is always well developed (fig. 12 C, E). In this case the levator arises either on the sclerotized *median plate* (MP) of the labium, or on the hypostomal bridge.

The presence or absence of labial palpus muscles is extremely variable in the other families. *Pronuba yuccasella* has no palpus muscles, nor does an *Agonopterix* sp. Each palpus of *Galleria mellonella* has a single large muscle. Geometridae show only a single palpus muscle or none at all. In the Arctiidae there is only a single muscle, usually arising on the hypostomal bridge. Sphingidae have either one or two pairs of palpus muscles, commonly only one. Saturniids and other extremely degenerate groups usually lack any palpus musculature, and the trembling motion of the palpi sometimes seen in this family is usually caused by the remnants of the proboscis extensors. However, *Basilona imperialis* has a single muscle in each palpus, as does also *Malacosoma americana*.

V. SUMMARY

1. The coiled proboscis of Lepidoptera is extended by means of blood pressure created in the stipes of each maxilla. This pressure is caused by three pairs of muscles, which by their contraction press the stipes against the head wall. Two pairs of these muscles arise on the anterior arms of the tentorium and the third pair arises on the gena.

2. The sucking pump is a compound organ, derived from the pharynx, the buccal cavity, and the cibarium. This is evidenced by these facts: (1) true pharyngeal dilators are inserted only in the posterior part of the pump; (2) muscles homologous with the compressors of the labrum are present in some Lepidoptera; and (3) the dorsal salivarium muscles arise on the pump floor, showing that the hypopharynx forms at least the anterior part of the floor.

3. There is no labial musculature except that of the palpi. There are generally two pairs of palpus muscles, but in many families only one pair, or none at all, may be found.

4. The area posterior to the labial palpi is bounded by the hypostoma, the hypostomal ridge offering an insertion for the ventral intersegmental muscles. A hypostomal bridge is sometimes present.

5. The anterior arms of the tentorium are well developed but lack dorsal arms. The posterior tentorial bridge is short and weak. The

great length of the hypostoma in Lepidoptera elevates the tentorium to a higher position in the head, with respect to other cephalic structures, than is common.

6. The antennal muscles arise on the anterior arms of the tentorium and vary in number from one to five pairs. They are always well developed, sometimes at the expense of other head structures and, in moths with obsolete feeding structures, are often the only functional muscles within the head.

ABBREVIATIONS USED ON THE FIGURES

<i>Ant</i> , antenna.	<i>Nv</i> , nerve.
<i>ant mcl</i> , antennal muscle.	<i>Oc</i> , occiput.
<i>Ant Nv</i> , antennal nerve.	<i>OcR</i> , occipital ridge.
<i>AR</i> , antennal ridge.	<i>ocs</i> , occipital suture.
<i>AT</i> , anterior tentorial arms.	<i>Oe</i> , oesophagus.
<i>at</i> , invagination of anterior arm.	<i>OVm</i> , oral valve muscle.
<i>atp</i> , anterior tentorial proboscis extensor.	<i>PBm</i> , proboscis base muscles.
<i>BuC</i> , buccal cavity.	<i>PC</i> , pressure chamber.
<i>Br</i> , brain.	<i>Phy</i> , pharynx.
<i>Cd</i> , cardo.	<i>Plf</i> , pilifer.
<i>Clp</i> , clypeus.	<i>Plp</i> , palpus.
<i>cp</i> , cranial proboscis extensor.	<i>Poc</i> , postocciput.
<i>Cv</i> , cervix.	<i>PoR</i> , postoccipital ridge.
<i>dlbc</i> , dilator of buccal cavity.	<i>pos</i> , postoccipital suture.
<i>dlcb</i> , dilator of cibarium.	<i>Prb</i> , proboscis.
<i>dplp</i> , depressor of palpus.	<i>Prb Ext</i> , proboscis extensor.
<i>dlphy</i> , dilator of pharynx.	<i>Prtl</i> , parietal.
<i>E</i> , eye.	<i>PT</i> , posterior tentorial arms.
<i>fm</i> , food meatus.	<i>pt</i> , invaginations of posterior arms.
<i>Fr</i> , frons.	<i>ptp</i> , posterior tentorial proboscis extensor.
<i>Fr Con</i> , frontal connective.	<i>rao</i> , retractor of mouth angles.
<i>Fr Gng</i> , frontal ganglion.	<i>rhphy</i> , retractor of hypopharynx.
<i>HBr</i> , hypostomal bridge.	<i>rn(RNv)</i> , recurrent nerve.
<i>Hphy</i> , hypopharynx.	<i>rs</i> , anterior salivarium muscle.
<i>HphyR</i> , hypopharyngeal ridge.	<i>zs, zs</i> , posterior salivarium muscle.
<i>HR</i> , hypostomal ridge.	<i>SLD</i> , salivary duct.
<i>hs</i> , hypostomal suture.	<i>Slv</i> , salivarium.
<i>Hst</i> , hypostoma.	<i>sm</i> , salivary meatus.
<i>Lb</i> , labium.	<i>Soe Gng</i> , suboesophageal ganglion.
<i>Lb Plp</i> , labial palpus.	<i>SP</i> , sucking pump.
<i>lplp</i> , levator of palpus.	<i>SR</i> , stipital ridge.
<i>lpm</i> , lateral pump muscle.	<i>St</i> , stipes.
<i>Lrm</i> , labrum.	<i>tpm</i> , transverse pump muscle.
<i>MP</i> , median plate.	<i>Tr</i> , trachea.
<i>Mth</i> , mouth.	<i>vlv</i> , valve.