THE BIOLOGY OF THE MECOPTERA

BY FRANK M. CARPENTER*

Among the curious phenomena of nature none is more unfortunate than the close correlation which exists between the number of species in an insect order and the number of entomologists concerned with it. The entomological world is filled with students investigating the classification, economies, society, pathology, eugenics, intelligence and morals of the Hymenoptera. Our National Parks and Forests are menaced annually by coleopterists, destroying the natural geology and tearing the barks from the trees in their search for new species. The Lepidoptera, especially the more attractive groups, are gradually becoming extinct, because of the enthusiastic quest for aberrations and queer varieties. But the smaller orders of insects are rarely the object of biological or taxonomic investigation. A list of the neuropterists in all the world would not equal a list of the coleopterists in some of our larger cities.

This evening I propose to discuss the habits and life-history of one of the smallest and therefore most neglected orders of insects—the Mecoptera, or scorpion-flies. Many of you have probably never seen one of these insects outside a museum, for they are very seclusive. They fly seldom and for short distances only, and usually keep close to the ground. When disturbed they either dart to the ground and hide among the dead leaves, or they fly to the under surfaces of the leaves and branches of shrubs, where they can be seen only with difficulty. So far as humans are concerned they are entirely inoffensive: they do not feed upon valuable crops, they have no selfish desire for human

*Address of the retiring president of the Cambridge Entomological Club, January 13, 1931. Contribution from the Entomological Laboratory of Harvard University.

blood, and they do not transmit disease, although I have several specimens of *Panorpa lugubris* from Nichols, South Carolina, which were held responsible by the inhabitants of the town during the fall of 1928 for an epidemic of fits among the dogs.

Because of their seclusive habits the scorpion-flies apparently escaped the attention of the ancient and early medieval naturalists more persistently than most other types of insects. According to Figuier,[1] Aristotle thought that the males of the Panorpidæ were flying scorpions because they possessed a swollen bulb at the end of the abdomen resembling the poison sac of the true scorpions. But I consider that this statement is incorrect, for Aristotle was one of the few ancient naturalists who believed that scorpions could not fly.[2]

Pliny the Elder, however, quoting Appoloderus of Athens (144 B. C.) states in his "Natural History" that some scorpions have wings, and it is possible that these flying scorpions were in reality males of Panorpidæ. Definite references to the scorpion-flies seem to be absent from all the so-called encyclopedias and natural histories of the Middle Ages until 1605, when Ulissi Aldrovandi published the insect volume of his "De Animalibus." In this work there are the first recognizable descriptions of Mecoptera, which he placed with the flies, and there are several good figures of Panorpas, showing the elongate beak and other characteristic features (fig. 1A). In 1634 there appeared the "Insectorum sive Minimorum Animalium Theatrum," which is usually attributed to Thomas Moufet. This interesting compilation was originally begun by Edward Wotton, a prominent English physician of about 1550, and was continued by Conrad Genner, Thomas Penny, and Moufet. On page 62 there are three figures of Panorpas, depicting clearly the genital forceps of the males (fig. 1B). The illustrations used in both these works were later republished by Johannes Johnston in his "Historia Animalium," which appeared in 1653. All these figures are really remarkably accurate, and

[1] Les Insectes, 1st ed., 1867, p. 512.
[2] De Partibus Animalium, Bk. 4, Ch. 3, p. 123.

seem especially realistic when they are compared with the serious reproductions of dragons and hydras which are included in the serpent section of Johnston's volume. Linnæus, whose tenth edition of the Systema appeared a little more than a century after Johnston's publication, described only three species of scorpion-flies, placing them in the genus Panorpa of the Neuroptera. About a quarter of a century later (1801) Latreille decided that they required a separate family, which he called Panorpatæ.

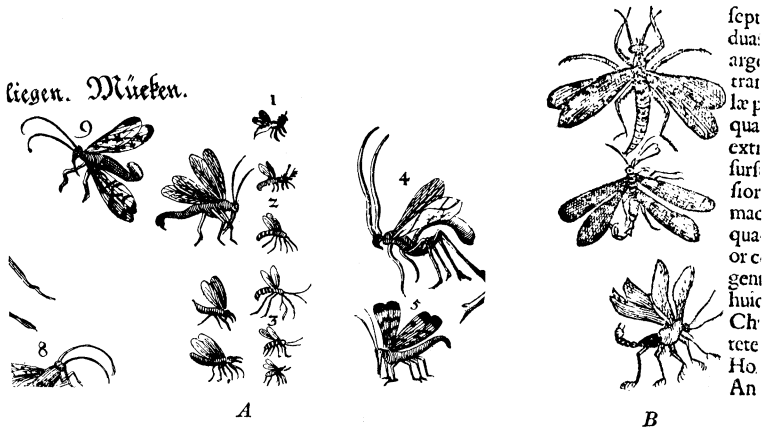

Fig. 1. Early illustrations of scorpion-flies:
A (5, 9), from Aldrovandi's *De Animalibus,* 1605;
B, from Moufet's *Insectorum sive Minimorum Animalium Theatrum,* 1643

In 1886 Packard erected the order Mecaptera for them, in reference to the long wings; and in 1895 Comstock changed the name to Mecoptera, the form in which it has subsequently been used. At the present time five families of the order are usually recognized: Notiothaumidæ, including a single species, which is restricted to Chile; Meropidæ, also including a single species, found along our Atlantic coast from Maine to Georgia; Panorpidæ, consisting of about 250 species and being generally

distributed over the holarctic regions, with a few representatives in the Australian, Oriental, and Neotropical zones; Bittacidæ, containing about 60 species, which occur in all parts of the world; and Boreidæ, with about a dozen species confined to parts of the Nearctic region and the western edge of the Palearctic.

In a group of insects as primitive as the Mecoptera we should expect to find simple and uninteresting habits. But during the two hundred million years since the first appearance of the order in the lower Permian rocks, there has been ample time for the development of peculiar traits in habits, even though the insects have undergone few structural changes. Unfortunately, nothing is known of the habits of Notiothauma and Merope, except that the latter is positively phototropic. Curiously enough, those habits of the other Mecoptera concerned with courtship and mating show the highest development and diversity; the courtship of the Panorpidæ involves peculiarities which have been found in few other groups of insects. The male Panorpa, on approaching the female, vibrates his wings rapidly and the female usually responds in like manner. Then the male stretches out his abdomen, seizes that of the female with his strong genital forceps, and then moves the forceps along until the female genitalia are reached. During copulation the bodies of the two insects diverge in the form of a "V." Usually the insects remain *in coitu* for a quarter of an hour or even an hour. Campion (1915)[3] observed a pair of *P. germanica* which started to mate at 11:30 A. M. and continued all day; at night when several aphids were introduced into the box, the pair fed together, while still in copulation. Miyaké (1913) has made some interesting observations on the mating habits of *P. klugi:* "One male is usually surrounded by two or three females which seem to the observer to be coquetting with the male. I saw on June 5th a pair in copulation beside two females. At last one of the two (I think the stronger one) began

[3] References not given here will be found in the bibliography of my revision of the Nearctic Mecoptera, now in press (Bull. Mus. Comp. Zool.).

to disturb the pair in copulation, using its long beak as a weapon, and succeeded in separating them. The successful rival then effected a pairing on the spot."

The most interesting feature of the mating habits of Panorpa concern the salivary glands of the male. Brant (1839) and Dufour (1841) observed in their anatomical studies of certain neuropterous insects that the salivary glands of the male Panorpas were much larger than those of the females. Mercier (1915) studied this peculiarity more carefully in *Panorpa germanica, alpina,* and *cognata,* with surprising results. He found that the salivary apparatus in the male consisted of two glands, each of which was composed of three long, filiform branches, and which opened into a common reservoir. The two reservoirs in turn opened into a common excretory duct. This complex structure was not developed until the male was four or five days old, at which time sexual maturity was reached. During the first few days after emergence of the male from the pupa the glandular tubes were only two or three millimeters long, but in eight days they had reached the length of 12 millimeters. Mercier observed that when a male, with its wings vibrating, approached a female, it suddenly ejected from its mouth a small drop of liquid, which coagulated almost the instant it was expelled, forming a small opaline pellet about the size of a pinhead. The male then moved several centimeters away from the pellet and again vibrated its wings. The female advanced and fed on this ball of saliva, whereupon the male rapidly approached, grasped her abdomen with his forceps, and entered into copulation. During the whole process the female continued to feed on the excretion, which (according to Mercier) it dissolved with a brown liquid. As soon as the first pellet of saliva was consumed, the male ejected another one, which was likewise devoured or dissolved in a similar manner. This process continued as long as the two were paired. Mercier believes that this excretion helps the male to secure a mate. Shiperovitsh (1925) has repeated Mercier's observations on *P. communis,* although there seem to be some points of difference, for the males of that species

ejected several cylindrical pellets, instead of drops of saliva. It is probable, however, that Shiperovitsh did not examine the drops until they had hardened. This particular type of bribery on the part of the male is, I believe, unique among all the insects, inasmuch as it involves a product of the digestive system. But the dipterous family Empidæ is famous for the peculiar tactics employed by the males, who offer the females particles of food as a preliminary to mating, although some degenerate and more modernistic species have reduced their gifts to inedible debris, such as small pebbles and bits of wood. In a very different group of insects, the cockroaches, we find another instance, more unlike that of the Panorpas. The males of Œcanthus, as shown by Hancock, possess a gland in the center of the metanotum, which secretes a fluid apparently much desired by the female. Just before actually mating the female climbs on the male's back and inserts her mouth at this gland, devouring the secretion ravenously. Unlike the condition in Panorpa, the feeding must end before copulation begins.

The mating habits of the other genera of Panorpidæ besides Panorpa are not known sufficiently to enable us to determine whether on not the males employ similar devices during courtship. Tillyard has made a few observations on the Australian genus Chorista, but has mentioned no such tactics. "If a male and a female be put alive into a glass tube, the male at once seizes the female fiercely with his anal forceps, taking hold of her in any position haphazard. He then quickly moves his appendages to the posterior end of the body of the female, opening his forceps to a great width, and then closing them quickly upon the tip of the abdomen. The result is a lock-grip, the two insects facing opposite directions. When once the male has got his correct hold, no amount of annoyance will persuade him to let go."

The Bittacidæ have apparently not developed any specialized habits in connection with mating; at least, no one has recorded such behavior. Mercier, however, mentions incidentally that the males of Bittacus present the females

with particles of food, as a part of courtship, as in the Empidæ, but he does not imply that he has actually seen this done, and he gives no reference to a published account. Miyaké has noted that the males retain the body of a victim for some time after they have finished with it, possibly as a lure to the females, who "come and try to take away the bait," whereupon the males attempt to mate with them. Such behavior, unless carefully observed, might easily be misinterpreted and be the basis of Mercier's remark. During copulation the specimens of Bittacus hang suspended from the branches or leaves, facing each other ventrally.

The snow scorpion-flies of the family Boreidæ have no mating habits like those of Panorpa, although the act of mating itself is a very curious process, and demonstrates the function of the bristle-like wings of the males, as shown by Withycombe. When a male becomes enamoured of an attractive member of the opposite sex, he runs along at her side for a short distance; then, by a series of sudden movements he grasps her near the base of her abdomen with his hooked wings and pulls her upon his back. Next he pushes her around into a more comfortable position, until he is able to seize her abdomen with his forceps and bring about copulation. Then he releases the hold with his wings and "wanders about on the surface of the ground with the female seated on his back and apparently helpless." This manœuver has been observed by Cockle (1908) in *Boreus californicus,* and by Withycombe (1926) in *B. hyemalis.*

The feeding habits of the adult scorpion-flies have been the cause of considerable discussion and the object of several investigations. The earlier writers thought that the Panorpidæ were exclusively predacious, and this view has persisted until within very recent years. Lyonnet started the notion in 1742, in Lesser's "Théology des Insectes ou Demonstration des Perfections de Dieu," where he states that he saw a fly of the size and appearance of a scorpion-fly attack a damsel-fly ten times its own size, and bring it

to the ground. The Odonatan was unable to repel its aggressor, and would have perished from the repeated thrusts of the scorpion-fly's beak, had not Lyonnet interfered. Kirby and Spence (1828) describe this encounter in the fifth edition of their "Introduction," and state without reserve that the offending insect was *Panorpa communis*, although there was certainly no evidence for this conclusion; and in view of the more recent observations it seems clear enough that this "tyrant of insect creation" was not a Mecopteron. Brauer (1863) fed adult Panorpas on bits of meat and on insects which had just been killed. In the "Feuille des jeunes naturalistes" for 1880 there is an anonymous note describing several specimens of *Panorpa communis* which were eating portions of fish that had been placed upon a bank near a stream. Felt (1896) fed adults of one of our American species, probably *P. canadensis,* on injured lepidopterous larvæ, and he was also able to keep one female alive for eighteen days on a diet of fresh meat. He believed, however, that only the juices were consumed. Poulton (1906) saw several European species of Panorpa feeding on other Arthropods, but the latter were dead when he first examined them. He suggests that the scorpion-flies feed only on dead prey. Lucas (1910) mentions one Panorpa which was feeding on a "whitish grub." Campion (1915) concluded from several experiments on *P. communis* and *P. germanica* that they feed on dead or nearly dead animal matter. Miyaké (1912) was convinced from his extensive studies on the Japanese *P. klugi* that the food of Panorpas usually consists of dead or injured insects, although he saw one female attack a living and healthy larva of its own species. Shiperovitsh (1925) states that all the investigations on the subject prove that the adults of Panorpa are exclusively saprophagous. However, the term "saprophagous," if so used, must be understood in a very broad sense, for the injured insects and fresh meat used by the authors mentioned above could hardly have started to decay by the time they were devoured by the Panorpas. Also, it must be remembered that some adults have been seen feeding on the nectar of flowers and on

fruits, and Miyaké notes that several of his specimens fed on the petals of Sweet William (*Silene armeria* Linné); in every case the entire petal was affected and later wilted. The sum of all these observations seems to me to suggest that the various species or species groups of the genus have widely different sources of food.

The Bittacidæ are essentially predacious and their legs are modified for grasping and holding prey: the femora and tibiæ are covered with strong spines, the tarsal joints are very flexible, and the single tarsal claw can be bent back against the rest of the tarsus. Bittacus is a slow-flying creature and it rarely if ever catches prey in flight. It usually remains motionless under a leaf or twig for many minutes or even hours, until another insect alights within reach of its legs. Then it suddenly reaches out and grasps the victim with its tarsus. When the captured insect has been turned into a satisfactory position, it is carried within reach of the beak, which usually penetrates between the abdominal segments or at the junction of the head and thorax. Probably only the juices are consumed. Soft-bodied insects, like the Diptera, seem to be preferred as food, but Hymenoptera, Hemiptera, Lepidoptera, and even Coleoptera are frequently taken as well. Miyaké has found that the Japanese Bittacus will feed on dead insects, decayed leaves, and even soil. The process by which a slow moving Bittacus attacks and devours active or even stinging insects is a most fascinating one. A splendid description of such an encounter between an Australian Bittacus and a bee has been given by Jarvis (1908) and is worth quoting in full: "Whilst standing by a large bush of *Daviesia corymbosa,* watching the number of specimens of bees that were attracted by the blossoms, I heard a sudden loud buzzing, louder than that caused by the continuous murmur of the bees, and saw that a specimen of *Bittacus australis* had just seized a large honey-bee which was making frantic but ineffectual struggles to escape from its clutches. It had grasped its victim with both hind legs and was holding it as far as possible from its body, with the flexible tarsi wrapped around the unfortunate bee and

working continually, just like the fingers of a hand, to prevent it from turning towards its enemy. In such a position, with its back to the fly, the poor insect was unable to make any use of its sting, and all efforts to twist around were anticipated and prevented by the movements of the numerous sharp spines of the encircling tarsi. Some muscular effort is doubtless required to enable the fly to keep its hind legs in an extended and rigid position in spite of the struggles of the large, winged insect, which may account for their being larger and stouter than the others, with the femora being somewhat incressated and the tarsi being larger and more powerful. So intent was it upon securing its prey that I was allowed to examine its every movement minutely, and whilst wondering what would happen next, it suddenly put out its two mid-legs and caught the tips of each primary wing of the bee between the last two joints of the tarsus, in much the same manner as we should take hold of anything between our finger and thumb, and pulled them out to their fullest expanse, thus effectually preventing the last remote chance of escape by these organs of flight. The scorpion-fly was now hanging from the bush by its two arms, and holding its prey with extended wings and body still grasped by the hind tarsi. And now came the closing scene of this insect tragedy; the hind legs slowly contracted to bring the body of the victim nearer, and the cruel, beak-like mouth approached, and, after hovering close to it for a few seconds, was inserted between the head and prothorax of the bee, which was unable to make the slightest resistance while its captor was piercing and biting through the slender, fleshy neck."

Of all the Bittacidæ, certainly the most curious is the Californian *Apterobittacus apterus*, which is completely devoid of wings and resembles a phylangid with a pair of legs missing. But this creature is nevertheless as successful at catching prey as its winged relatives. It replaces its want of wings by great dexterity in climbing, swinging itself monkey-like from twig to twig, often supported by one tarsus. Osten-Sacken (1882) once observed a speci-

men devouring a tipulid with vestigial wings,[4] and he suggests a possible mimicry of this species on the part of the Bittacid.

The feeding habits of the Boreidæ have been more or less obscure until recently. Brauer observed that the adults fed on moss, as well as on Produra and other small animals living among the moss roots. Whitycombe concluded from investigations which he made in 1921 that they fed on damaged or dead insects, although he found some specimens feeding on the bases of moss plants. Subsequently, however, he made further inquiries into the feeding habits and decided that the food is normally moss, although in captivity, when proper food is not available, other substances may be consumed. He also found that the amount of food needed was very slight, but a great deal of moisture was required.

In the preceding pages we have reviewed what is known of the habits of the adult Mecoptera, and we shall next consider the main features of their metamorphosis. Here again, we have no knowledge of the life-history of the Meropidæ and Notiothaumidæ, and our acquaintance with the development in the other families is almost entirely confined to old-world species of Panorpa, Bittacus, and Boreus. Curiously enough, Swammerdamm, who investigated the metamorphosis of many groups in 1669, including some Neuroptera and Trichoptera, apparently made no observations on the Mecoptera. The earliest research of this kind was done in 1831 by Maquart, who briefly described the pupa and showed that it was the *libera* type. The pupa was also described and figured by Stein in 1838, and the complete life-history of three European species (*P. variabilis, montana,* and *communis*) was worked out by Brauer in 1863. Some of the larvæ and pupæ which he bred sixty-seven years ago are now in the Hagen collection of the Museum of Comparative Zoology. In 1894 Felt succeeded in rearing the larvæ of a Panorpa (probably *P. canadensis*) at Ithaca, New York, but he was not able to obtain a pupa.

[4] Dr. C. P. Alexander tells me that this species is almost certainly *Tipula vestigipennis* Doane.

This is the only account published on the life-history of a New World Panorpa. Miayké has carried out some splendid studies on the Japanese *klugi,* securing all stages; and Shiperovitsh has more recently reared two European species, *communis* and *cognata.* The following discussion of the metamorphosis of Panorpa is based largely on these investigations, supplemented by a few observations of my own on *P. maculosa* Hagen.

The eggs are spherical or oval, and usually white; they vary somewhat in size, depending on the dimensions of the species, but are usually less than a millimeter long. Normally they are laid in the soil in clusters of various sizes, including as many as 97 eggs. The eggs have an extremely thin shell and require a great deal of moisture for development. I have had eggs of *maculosa* dry up and shrivel within a couple of hours from the time they were deposited, when they were exposed to the normal atmosphere, even though placed on a non-absorbent surface. In about 6 or 8 days the larva within the egg pushes up the shell at one pole with the frontal part of its head and, after the shell has broken away, it unrolls itself and crawls out. In comparison with the size of the egg the larva is quite large, about 5 millimeters long. On emergence it has a pure white body, a yellow head, and pink eyes; but in a few hours these colors darken. The antennæ are small, consisting of 4 short segments, but the eyes are large and composed of about 25 ocelli. There are 3 pairs of thoracic legs, each consisting of 4 segments, and there are also 4 pairs of abdominal prolegs. The first 9 abdominal segments bear a pair of stout annulated spines, those of the eighth and ninth segments being much enlarged. The tenth segment possesses a single, very long spine, projecting posteriorly. The larvæ probably pass through seven instars in about two weeks' time, although Shiperovitsh claims that there are only four instars in *P. communis.* During these stages the larva undergoes very few changes: the abdominal legs become relatively shorter, the head smaller, and the spines on the abdominal segments are greatly reduced. The larvæ feed readily on fresh meat, fish, or injured insects; and

according to Felt, some of the larvæ are predacious, the larger ones sometimes attacking and devouring the smaller. Usually the larva forms a short burrow in the soil, but it may leave the burrow entirely and feed above the ground. The last instar of the larva is much longer than the others, usually lasting about a month, and this appears to be the hibernating stage. The pupa is formed in a cell constructed in the soil by the last instar larva. It is characteristic of the *libera* type, as found by Maquart, the appendages being free, though immobile. The antennæ and legs are like those of the adult, but the mouth is not prolonged into the beak and there is no genital bulb in the male. In about a week or ten days the pupal case ruptures in the usual fashion and the adult makes its appearance. No observations seem to have been made on the condition of the adult as it emerges, or on the amount of time which elapses before it is able to fly. The adult Panorpas usually prefer dark and rather moist woods, or sometimes more open areas which are low and near water. In New England I have found them most abundant in woodlands containing *Myrica asplenifolia* and associated plants. In the more central and southern states they frequently inhabit open fields; and in the Smoky Mountains of Tennessee I have found a new species to be most abundant on the very edges of a rapid stream, and even resting on the bare rocks in the middle of a large creek.

Much less is known of the life-history of Bittacus than of Panorpa. No one has secured the larva or pupa of an American species, and Brauer alone has succeeded in rearing a species through all stages of development. He found that the eggs are laid in small clusters within the soil during the fall and remain over the winter in that conditon; but both Felt and Miyaké observed the females drop their eggs singly at random while flying over the soil. According to Brauer, if the soil in the egg chamber dries up in the late fall, the eggs hatch the following April; but if the soil stays moist, the eggs remain over until the spring of the second year following. The larvæ live above ground, among leaves and grass, not in the soil like those of Panorpa. Brauer fed

his larvæ on raw meat, but he did not determine the natural feeding habits. The larvæ are much more spiny than those of Panorpa and are considerably stouter. They are also more active than the Panorpas; when frightened or disturbed they roll themselves up in the manner of many lepidopterous larvæ, or they throw the anterior part of the body in an erect position, much like the sphingid larvæ. About ten days before pupation the larvæ bury themselves in the soil and form a chamber. The pupæ are similar to those of Panorpa in general appearance, although of course they are very slender and have the habitus of a Bittacus. The adult emerges in about two weeks. Brauer states that the adult of *B. italicus* forms a chamber of leaves or twigs and lives within, feeding on the insects which are unfortunate enough to enter. No such chamber has been observed in the case of the American species, and I am certain that none is used by *B. strigosus*. One species of the genus, *chilensis,* is decidedly cavernicolous. The Bittacidæ are usually very local in their distrbution; in New England *strigosus* can frequently be taken in woodlots less than an acre in extent, but will not occur elsewhere for miles around. Martin (1892) has shown that *B. tipularius* occurs very irregularly in France; in some years, as 1888, it may be very abundant, literally covering the "wheat, clover, broom, heath and thicket," although in a few years' time it may be almost entirely absent. He attributes this decrease in the number of specimens to the corresponding increase of a parasite, although none has ever been found in Bittacus or Panorpa. Certain species of Bittacus, at least our *occidentis* and *strigosus,* are positively phototropic and are frequently caught in light traps.

The life-history of Boreus was also worked out by Brauer (1862), but he did not succeed in carrying any one species through all its stages of development. Additional observations have been made by Williams (1916) and Withycombe (1924, 1926), who has given a splendid account of the biology of the European *B. hyemalis*. The eggs are laid one or two at a time among moss roots. The larvæ hatch in about ten days, usually during December; they possess

abdominal prolegs during the first instar (according to Brauer), but lose them later. There are at least four instars, during which time the larvæ feed on moss roots and liverworts. The full grown larva, usually about 6 or 7 millimeters long, is shorter and stouter than that of Bittacus. The larval stage is the longest, lasting from December to August, when the larva prepares for pupation by forming a vertical tube in the soil, nearly extending to the surface. The pupa is more active than the larva, rapidly wriggling up and down the tube when it is disturbed. After from 4 to 8 weeks the imagines appear. The adults may be found in the spring and early summer among moss roots and under stones, but they are only active in the winter, when on sunny days they can be seen hopping about on the surface of the snow, covering as much as 6 inches in a single leap.

From this survey of the biology of the Mecoptera I hope it is clear that our knowledge of the life-history of the American species of scorpion-flies is very meagre and that we have great want of further observations on their habits. This is particularly true of the remarkable *Merope tuber,* which inhabits only our Atlantic states. Perhaps one of you, while searching in the soil for a beetle or a member of some other large order, will be fortunate enough to stumble upon the larva or pupa of Merope, and thus fill in one of the most disconcerting gaps in our knowledge of complete metamorphosis.